

CARBON BRIDGE TO THE ARCTIC

EDITED BY: Marit Reigstad, Maria Vernet, Jacob Carstensen and
Camilla Svensen

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CARBON BRIDGE TO THE ARCTIC

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Table of Contents

06 Editorial: Carbon Bridge to the Arctic

Maria Vernet, Jacob Carstensen, Marit Reigstad and Camilla Svensen

PHYSICS

10 Seasonality of the Physical and Biogeochemical Hydrography in the Inflow to the Arctic Ocean Through Fram Strait

Achim Randelhoff, Marit Reigstad, Melissa Chierici, Arild Sundfjord, Vladimir Ivanov, Mattias Cape, Maria Vernet, Jean-Éric Tremblay, Gunnar Bratbak and Svein Kristiansen

26 Properties of Sediment Trap Catchment Areas in Fram Strait: Results From Lagrangian Modeling and Remote Sensing

Claudia Wekerle, Thomas Krumpen, Tilman Dinter, Wilken-Jon von Appen, Morten Hvitfeldt Iversen and Ian Salter

CHEMISTRY

42 Net Community Production and Carbon Exchange From Winter to Summer in the Atlantic Water Inflow to the Arctic Ocean

Melissa Chierici, Maria Vernet, Agneta Fransson and Knut Yngve Børsheim

66 Inter-Annual Variability of Organic Carbon Concentration in the Eastern Fram Strait During Summer (2009–2017)

Anja Engel, Astrid Bracher, Tilman Dinter, Sonja Endres, Julia Grosse, Katja Metfies, Ilka Peeken, Judith Piontek, Ian Salter and Eva-Maria Nöthig

83 Asynchronous Accumulation of Organic Carbon and Nitrogen in the Atlantic Gateway to the Arctic Ocean

Maria L. Paulsen, Lena Seuthe, Marit Reigstad, Aud Larsen, Mattias R. Cape and Maria Vernet

100 Influence of Glacial Meltwater on Summer Biogeochemical Cycles in Scoresby Sund, East Greenland

Miriam Seifert, Mario Hoppema, Claudia Burau, Cassandra Elmer, Anna Friedrichs, Jana K. Geuer, Uwe John, Torsten Kanzow, Boris P. Koch, Christian Konrad, Helga van der Jagt, Oliver Zielinski and Morten H. Iversen

PRODUCTIVITY

124 Episodic Arctic CO₂ Limitation in the West Svalbard Shelf

Marina Sanz-Martín, Melissa Chierici, Elena Mesa, Paloma Carrillo-de-Albornoz, Antonio Delgado-Huertas, Susana Agustí, Marit Reigstad, Svein Kristiansen, Paul F. J. Wassmann and Carlos M. Duarte

135 Relationship Between Carbon- and Oxygen-Based Primary Productivity in the Arctic Ocean, Svalbard Archipelago

Marina Sanz-Martín, María Vernet, Mattias R. Cape, Elena Mesa, Antonio Delgado-Huertas, Marit Reigstad, Paul Wassmann and Carlos M. Duarte

150 *Influence of Phytoplankton Advection on the Productivity Along the Atlantic Water Inflow to the Arctic Ocean*

Maria Vernet, Ingrid H. Ellingsen, Lena Seuthe, Dag Slagstad, Mattias R. Cape and Patricia A. Matrai

BIOLOGY-BACTERIA

168 *Microbial Communities in the East and West Fram Strait During Sea Ice Melting Season*

Eduard Fadeev, Ian Salter, Vibe Schourup-Kristensen, Eva-Maria Nöthig, Katja Metfies, Anja Engel, Judith Piontek, Antje Boetius and Christina Bienhold

BIOLOGY-PHYTOPLANKTON

189 *Pelagic Ecosystem Characteristics Across the Atlantic Water Boundary Current From Rijpfjorden, Svalbard, to the Arctic Ocean During Summer (2010–2014)*

Haakon Hop, Philipp Assmy, Anette Wold, Arild Sundfjord, Malin Daase, Pedro Duarte, Slawomir Kwasniewski, Marta Gluchowska, Józef M. Wiktor, Agnieszka Tatarek, Józef Wiktor Jr., Svein Kristiansen, Agneta Fransson, Melissa Chierici and Mikko Vihtakari

BIOLOGY-MICROZOOPLANKTON

210 *Microzooplankton Distribution and Dynamics in the Eastern Fram Strait and the Arctic Ocean in May and August 2014*

Peter J. Lavrentyev, Gayantonia Franzè and Francisco B. Moore

BIOLOGY-MESZOOPLANKTON

226 *Seasonal Variation in Transport of Zooplankton Into the Arctic Basin Through the Atlantic Gateway, Fram Strait*

Sünnje L. Basedow, Arild Sundfjord, Wilken-Jon von Appen, Elisabeth Halvorsen, Slawomir Kwasniewski and Marit Reigstad

248 *Summer Mesozooplankton Biomass Distribution in the West Spitsbergen Current (2001–2014)*

Jacob Carstensen, Anna Olszewska and Slawomir Kwasniewski

262 *Zooplankton Communities Associated With New and Regenerated Primary Production in the Atlantic Inflow North of Svalbard*

Camilla Svensen, Elisabeth Halvorsen, Maria Vernet, Gayantonia Franzè, Katarzyna Dmoch, Peter J. Lavrentyev and Slawomir Kwasniewski

275 *Advection of Mesozooplankton Into the Northern Svalbard Shelf Region*

Paul Wassmann, Dag Slagstad and Ingrid Ellingsen

BIOLOGY-MACROZOOPLANKTON

285 *Pelagic Amphipods in the Eastern Fram Strait With Continuing Presence of *Themisto compressa* Based on Sediment Trap Time Series*

Franz Schröter, Charlotte Havermans, Angelina Kraft, Nadine Knüppel, Agnieszka Beszczynska-Möller, Eduard Bauerfeind and Eva-Maria Nöthig

FOOD WEBS

296 *Food Web Functions and Interactions During Spring and Summer in the Arctic Water Inflow Region: Investigated Through Inverse Modeling*

Kalle Olli, Elisabeth Halvorsen, Maria Vernet, Peter J. Lavrentyev, Gayantonia Franzè, Marina Sanz-Martin, Maria Lund Paulsen and Marit Reigstad

BLUE CARBON

312 *Valuing Blue Carbon Changes in the Arctic Ocean*

Claire W. Armstrong, Naomi S. Foley, Dag Slagstad, Melissa Chierici, Ingrid Ellingsen and Marit Reigstad



Editorial: Carbon Bridge to the Arctic

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Editorial on the Research Topic

Carbon Bridge to the Arctic

Seasonality influences temporal and spatial variability in the Arctic Seas, controlled by daylength and modulated by sea ice extent. Under climate warming, incident light remains mostly unchanged, but changes in sea ice cover and melting as well as oceanic currents (Onarheim et al., 2014) regulate the ecosystem, its structure, and function. Results from the Research Topic “Carbon Bridge to the Arctic” indicate that a shorter ice-covered season to the west and north of the Svalbard Archipelago extends the growth season and sustains higher annual productivity, allows for Arctic species to have food for an extended period and for temperate species reaching the Arctic to survive and even reproduce further north. The inflow of Atlantic Water from the West Spitsbergen Current greatly modulates this region (WSC in **Figure 1**). The current has intensified over the last several decades (Schauer et al., 2004), causing the ocean heat transport and the water temperature to increase in Fram Strait and northern Barents Sea (Lind and Ingvaldsen, 2012; Polyakov et al., 2017; Lind et al., 2018). As the advective inflow contributes both nutrients and living biomass in the form of plankton (Hegseth and Sundfjord, 2008; Kosobokova and Hirche, 2009), the interaction of the West Spitsbergen Current with the sea ice edge additionally modifies the ecosystem at this Arctic gateway. This region is thus affected by polar climate, as reflected in changing sea ice conditions and also by southern climate through the Atlantic Water Inflow.

The Carbon Bridge project aimed at understanding the processes that impact productivity and carbon cycling along the gateway to the Arctic Ocean, characterizing ecosystem properties affected by sea ice in conjunction with organisms advected by the Atlantic Water Inflow. Field studies were carried out in eastern Fram Strait as well as north of the Svalbard Archipelago and the adjacent Arctic Ocean (**Figure 1**). This is the Arctic Ocean region experiencing the most prevailing sea ice decline (Onarheim et al., 2014). The Carbon Bridge comprised field measurements to test model predictions of substantial changes in productivity due to sea ice retreat in this region (Slagstad et al., 2015). In addition to the publications compiled in the Research Topic, the project provided policy makers, managers, stakeholders, and the general public with an understanding of the ecosystem and regime shifts that may develop in response to climate change (Wassmann, 2018).

The main findings, based on results from the Carbon Bridge project with the added contributions from the Hausgarten project (Nöthig et al., 2015), are summarized below highlighting the role of daylength as well as ice cover, advection, and meltwater input in shaping the structure and function of the pelagic ecosystem. This critical European Arctic region absorbs, transforms, and loses carbon by chemical and biological processes affecting biomass and composition of planktonic communities:

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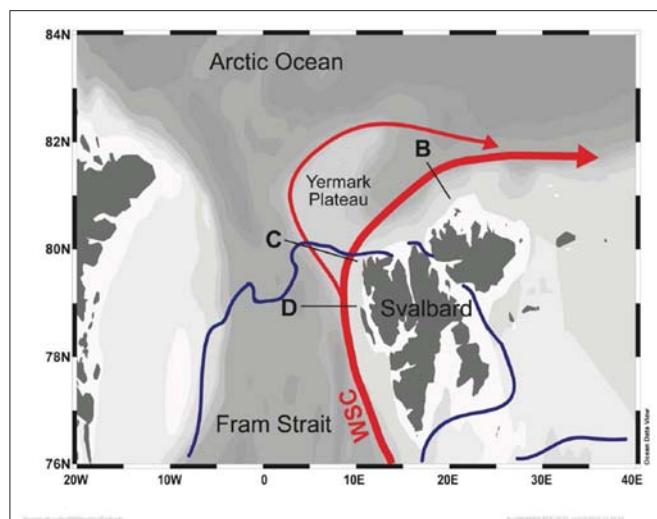


FIGURE 1 | The inflow of warm Atlantic Water into the Arctic Ocean where the West Spitsbergen Current (WSC) is a continuation of the North Atlantic Current through the Fram Strait. The WSC divides north of Svalbard, with the main branch following the Svalbard shelf break and another smaller branch flowing north of the Yermak Plateau. The Polar Front marks the boundary between Polar Water and Atlantic Water (blue line), with subduction of Atlantic Water Inflow that is found as a subsurface current throughout the Arctic Ocean (Rudels et al., 1996). Cruise transects for main cruises carried out in May and August 2014 are shown in black (identified as **B**, **C**, and **D**). Due to heavy sea ice conditions sampling north of Svalbard Archipelago was restricted.

1. Seasonality of the primary producers and consumers

Carbon pools characterizing the plankton abundance vary between 1 and 3 orders of magnitude between the spring bloom at the ice edge in comparison to the ice-free summer communities (Sanz-Martín, Vernet et al.). Thermal convection of warmer Atlantic Water north of Svalbard likely enhances vertical nutrient fluxes to the surface (Randelhoff et al.). Stratified water column conditions are provided by sea ice melt which leads to the development of the spring bloom (Chierici et al.; Randelhoff et al.). If the seasonality of phytoplankton primary production is divided into early-, peak-, decline-, and post-bloom stages, modeling suggests that both micro- and mesozooplankton shift from nearly pure herbivory (92–97% of total food intake) during the early-bloom stage to an herbivorous, detritivorous, and carnivorous, or mixed, diet as the bloom progresses (Olli et al.). Overall, microzooplankton was the most important grazer, followed by copepods and nanoflagellates. Three *Calanus* species and the chaetognath *Eukrohnia hamata* constituted the bulk (or 90%) of the mesozooplankton biomass in the West Spitsbergen Current with almost similar dominance by *E. hamata*, *C. finmarchicus*, and *C. hyperboreus* in the western Atlantic Water Inflow branch whereas *C. finmarchicus* dominated in the eastern and coastal branches, constituting there about half of the biomass (Carstensen et al.). Modeled losses of carbon sedimentation out of the euphotic zone increased gradually from 19% (early phase) to 20% (peak phase) to 38% (late bloom phase) of the Gross Primary Production, with post-bloom phase presenting considerable variability (17–70%) (Olli et al.). These modeled

sedimentation rates are challenging to test: sediment traps provide information on the origin and sequestration of carbon with depth; however, when Particulate Organic Carbon (POC) vertical export is measured in the field, collected material in sediment traps varies with depth and particle sinking rates (Wekerle et al.). For phytoplankton, physiological differences in algal communities could affect productivity estimates. While productivity measured by oxygen production was higher than carbon uptake in the spring communities dominated by the colonial *Phaeocystis pouchetti* and diatoms, the summer communities of dinoflagellates and cryptophytes had higher carbon uptake than oxygen production, suggesting a variable Carbon:Oxygen ratio in Arctic photosynthesis (Sanz-Martín, Vernet et al.). In addition to nitrate, dissolved organic nitrogen (DON) was also an essential nitrogen source during the spring bloom at the sea-ice edge, decreasing in concentration from winter to spring faster than inorganic nitrogen sources (Paulsen et al.). In contrast, dissolved organic carbon (DOC) increased from spring toward the late bloom phase. This organic nutrient imbalance resulted in an asynchronous availability of carbon and nitrogen sources increasing the C:N ratio of the dissolved organic pool while maintaining Redfield ratios in the particulate organic pool.

2. Seasonality of carbon balance

The Atlantic Water Inflow entering the Arctic Ocean is enriched in carbon dioxide compared to the original North Atlantic waters, as the waters of the West Spitsbergen Current absorb through primary production more carbon dioxide (CO_2) than they release through respiration (Chierici et al.). Dissolution of calcium carbonate particles, either from advected shells or derived from sea ice, sustain $p\text{CO}_2$ undersaturation in surface water. However, low carbon dioxide partial pressure conditions due to enhanced primary production produce episodic events of carbon limitation; gross primary production (GPP) increases from 32 to 72% with CO_2 additions in spring, not in summer (Sanz-Martín, Chierici et al.). Loss rates through predation or geographic retention [locally or with Atlantic water recirculation toward the west, (Marnela et al., 2013; Hattermann et al., 2016)] exceeds the local production of mesozooplankton resulting in reduced *Calanus finmarchicus* biomass advected northward. Furthermore, food limitation could become more prevalent toward the north: carbon consumption north of Svalbard is higher than annual productivity converting this system into one of net heterotrophy (Carstensen et al.; Wassmann et al.). However, the pelagic food web retains energy resources—high community respiration always exceeds sedimentation losses—which results in high efficiency of carbon transfer to higher trophic levels (Olli et al.).

3. Observed seasonal changes help predict ecosystem changes in the future Arctic

As the northern Svalbard Archipelago becomes ice-free, as predicted for the second half of the twenty-first century, present-day summer conditions are expected to become more widespread, affecting microbial dynamics and the biogeochemical cycling that they maintain. Autotrophic processes dominate in sea-ice associated communities in pre- and early-bloom conditions, while communities in ice-free

conditions are considered post-bloom, with a prevalence of heterotrophy and recycled nitrogen sources (Olli et al.; Paulsen et al.; Sanz-Martin, Vernet et al.; Svensen et al.). As of today, eastern and western microbial communities in the Fram Strait demonstrate that changes in sea ice will affect ecosystem structure, as the diversity of bacteria and eukaryotes found associated with sea ice differs substantially from planktonic communities in ice-free waters (Fadeev et al.). Grazing of phytoplankton by microzooplankton will be enhanced in ice-free waters of the Svalbard region when summer-like planktonic communities prevail, consuming up to 79% of primary production (Lavrentyev et al.). Under ice-free conditions, *Calanus finmarchicus* and the small copepod *Oithona similis* may become more dominant, as they are able to feed and reproduce during extended periods of summer regenerated production, even when these conditions sustain low phytoplankton biomass (Svensen et al.).

4. Advection modulates seasonality of planktonic processes at this Arctic gateway

The transport of phytoplankton by the Atlantic Water Inflow increases *in-situ* primary production up to 50 times and enhances growth rates in the West Spitsbergen Current, compared to waters at the same latitude in the Greenland Sea (Vernet et al.). The advection affects phytoplankton production phenology, increasing early-spring carbon uptake in the West Spitsbergen Current and extending summer production north of Svalbard. The transports of water and zooplankton are decoupled, with minimum water transport in August and minimum zooplankton biomass transport in spring (Basedow et al.). Year round, a total of $18.8 \text{ g C m}^{-2} \text{ year}^{-1}$ of mesozooplankton are advected, becoming available to predators. This advection increases 12 times the *in-situ* average secondary production north of Svalbard (Wassmann et al.).

If not the quantity, the nature of the advected carbon to the Arctic Ocean will change under climate warming. There was no multi-year trend in the variability in advected zooplankton biomass in the period 2001 to 2014. However, individual species show trends, with increases in biomass for *Calanus finmarchicus* and *C. glacialis* while *Pseudocalanus* sp. decreases (Carstensen et al.). While dissolved organic carbon (DOC) and chlorophyll a concentration have remained constant since 2009 in the West Spitsbergen Current, there has been a decrease in summer particulate organic carbon (POC), total organic carbon (TOC), and POC:TOC ratio suggesting a higher partitioning of carbon to the dissolved phase (Engel et al.). Increased abundance of amphipods, that was first discovered in this region during a warm anomaly in 2004–2007, persists to the present, with *Thermisto compressa* accounting for the most recent increase in total amphipod biomass (Schröter et al.). These results underlie the importance of investigations on the species level to detect responses to a changing climate.

5. Increased meltwater at the ice-ocean boundary can change the spatial variability of productivity in nearshore waters

Svalbard and Greenland are bordered by fjord systems with high freshwater input to the marine environment. These glacially-influenced fjords are considered hot-spots for carbon export to depth as silt in the meltwater acts as ballast for sinking particles (Seifert et al.). While fjord productivity is limited by seasonal light and nutrient supply, productivity increases toward the fjord mouth due to higher water transparency and increased nutrient supply from offshore waters (Hop et al.). The continued warming of the Atlantic Water Inflow is expected to increase the contribution of planktonic boreal species available at the fjord mouth, in concert with the increased pelagic production in the Arctic Ocean (Kahru et al., 2016). As distinct phytoplankton communities characterize the offshore Atlantic warm water and polar fjord waters (Hop et al.), increased glacier meltwater as a result of atmospheric and ocean warming will increment polar communities within nearshore waters, establishing a sharper gradient in species composition from the fjord's head toward offshore waters.

6. The Arctic Ocean will continue to store excess anthropogenic carbon dioxide

In concert with other regions of the Arctic Ocean, the waters of the West Spitsbergen Current act as a net sink of atmospheric CO_2 , absorbing more carbon than they release by $2.3 \text{ mmol C m}^{-2} \text{ year}^{-1}$ (Chierici et al.). For the Arctic Ocean, modeling efforts predict an increase of 1.0% to 2.3% in carbon storage in different climate scenarios (Slagstad et al., 2015; Armstrong et al.). Using integrated data to evaluate the ecosystem services in terms of economic value and change in carbon storage in the Arctic Ocean, it is possible to quantify a value of this region for the anthroposphere, highly relevant for future management and risk assessment. The estimates combine model runs with climate scenarios RCP 4.5 and RCP 8.5 from the Max Planck Institute (IPCC, 2014). This carbon storage is associated with an increased value of Arctic blue carbon from €27.6 billion to €1 trillion, when using social cost of carbon (SSC) and carbon market values from 2019 to 2099, respectively (Armstrong et al.).

In brief, the Carbon Bridge project demonstrated how the interaction among seasonal patterns in ecosystem processes, species-specific responses to climate warming, changes in sea ice distribution and advection of phyto- and zooplankton all result in enhanced food availability to higher trophic levels at the gateway to the Arctic Ocean.

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Seasonality of the Physical and Biogeochemical Hydrography in the Inflow to the Arctic Ocean Through Fram Strait

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Eastern Fram Strait and the shelf slope region north of Svalbard is dominated by the advection of warm, salty and nutrient-rich Atlantic Water (AW). This oceanic heat contributes to keeping the area relatively free of ice. The last years have seen a dramatic decrease in regional sea ice extent, which is expected to drive large increases in pelagic primary production and thereby changes in marine ecology and nutrient cycling. In a concerted effort, we conducted five cruises to the area in winter, spring, summer and fall of 2014, in order to understand the physical and biogeochemical controls of carbon cycling, for the first time from a year-round point of view. We document (1) the offshore location of the wintertime front between salty AW and fresher Surface Water in the ocean surface, (2) thermal convection of Atlantic Water over the shelf slope, likely enhancing vertical nutrient fluxes, and (3) the importance of ice melt derived upper ocean stratification for the spring bloom timing. Our findings strongly confirm the hypothesis that this “Atlantification,” as it has been called, of the shelf slope area north of Svalbard resulting from the advection of AW alleviates both nutrient and light limitations at the same time, leading to increased pelagic primary productivity in this region.

Keywords: Arctic Ocean, Atlantic water, hydrography, shelf slope, nutrients, carbon, fram strait, barents sea

1. INTRODUCTION

The rapid environmental changes occurring in the Arctic Ocean in recent decades include a process in the Atlantic sector sometimes referred to as “Atlantification.” Although it is currently not entirely clear whether this strengthened inflow of water from the North Atlantic is due to a climatic cycle, with data commonly going back to at most the late 1990s (e.g., Årthun et al., 2012; Polyakov et al., 2017), it is sometimes taken to express a fundamental shift of the Arctic Arctic to a new marine climate (Polyakov et al., 2017). In essence, “Atlantification” entails a replacement of water masses formed and advected from the central Arctic by water of Atlantic origin (Årthun et al., 2012), flowing northward along the shelf slope (West Spitsbergen Current, Fram Strait Branch)

as a boundary current, and through the Barents Sea (Barents Sea Branch), later joining the Fram Strait Branch at St. Anna Trough. Because the highly saline Atlantic Water (AW) is temperature-stratified, its weak water column stability is easily overcome by thermal convection. As opposed to the permanently salt-stratified central Arctic, this allows for efficient replenishment of upper-ocean nutrients early in winter over the shelf slope (Randelhoff et al., 2015). The release of large amounts of heat during winter exerts a strong control on the location of the ice edge (Untersteiner, 1988). This sea ice is usually advected from the Kara Sea (Pfirman et al., 1997), rather than formed locally. Reports of increasing AW temperatures throughout the Arctic (Polyakov et al., 2012) suggest that this heat has probably driven the bulk of the sea ice loss north of Svalbard in recent decades (Onarheim et al., 2014). When sea ice comes close to the heat stored in the AW, it melts and forms a near-surface layer of fresh, cold water, a crucial ingredient that shapes the planktonic ecosystem bustling and blooming in the summer months. One immediate implication is that near-surface AW penetrating further and further east has the capability to relieve both nutrient *and* light limitation on the shelf slope north-east of Svalbard, leading to increased productivity. Indeed, Slagstad et al. (2015) project that in the northern Barents and Kara seas, primary production might increase locally by up to 40–80 g C m⁻² year⁻¹ by 2,100.

Winter is traditionally undersampled in the Arctic Ocean. Only recently has the extreme loss of winter sea ice north of Svalbard mentioned above enabled research vessels to easily visit the area in the depth of winter, leading to new insights such as on ecosystem functioning during the longer polar night (Berge et al., 2015). Given the control Atlantic Water exerts on the heat (Rudels et al., 2015) and nutrient (Torres-Valdés et al., 2013) budgets of the Arctic Ocean, there is also the need for comprehensive and concurrent measurements of the key physical and biogeochemical elements in the AW inflow region. And even though the absence of light means no photosynthesis and thus no primary production, it is exactly in winter that the ecosystem is preconditioned for the next spring and summer, for example by setting up nutrient inventories. The Arctic ecosystem is therefore hinged on how these are modified through the annual cycle and as they travel from the Fram Strait and into the AO along the continental slope. In this study we summarize and discuss the key physical and biogeochemical changes occurring in the Fram Strait Atlantic Water inflow to the AO through a full annual cycle, and doing so form a basis for discussion and interpretation of the biological results obtained simultaneously during five field campaigns in 2014 and published in this special issue.

2. DATA AND METHODS

2.1. Data Set

The data presented here were collected during five cruises in January, March, May, August and November 2014 west and north of Spitsbergen as part of the CarbonBridge and MicroPolar projects. We discuss a total of five transects across the AW core (January, May, August) and six 30-h process stations (May and August), where comprehensive sampling of the

lower trophic level ecosystem in addition to biogeochemical and physical measurements were conducted. These observations are supplemented with observations of physical and biogeochemical parameters during March and November (sampled as part of the MicroPolar project) to increase temporal coverage and resolution of the region.

Parameters discussed in this study include:

- Conductivity-temperature-depth (CTD) profiles
- Inorganic nutrients: Nitrate+nitrite ($\text{NO}_2^- + \text{NO}_3^{2-}$), silicic acid ($\text{Si}(\text{OH})_4$, often called silicate and abbreviated as silica, Si), phosphate (PO_4^{3-}), and ammonium (NH_4^+)
- Chlorophyll-a concentration
- Fugacity of CO_2 ($f\text{CO}_2$)
- Photosynthetically available radiation (PAR)

It was desirable to sample as far east and north as possible (downstream the AW flow and into the ice), but unusually heavy ice cover around Svalbard during much of 2014 only allowed repetition of one May process station in August. The following is an overview over all occupied stations described and analyzed in this study (for a more detailed overview, see **Figure 1** and Table S1).

- Transect D (January, May and August): 79°N, 4–10°E
- Transect B (January): across the shelf slope north of Spitsbergen, approximately 20°E
- Process stations in May: P1, P3, P4
- Process stations in August: P5, P6, P7, where P6 and P7 were across the shelf slope north of Spitsbergen, approximately 15°E
- Supplemented by: One station north of Spitsbergen, March 2014, and three stations situated along the D transect in November 2014.

2.2. CTD System

Water samples were collected from 8-L Niskin bottles mounted on a General Oceanics 12-bottle rosette equipped with a Conductivity-Temperature-Depth sensor system (CTD, Seabird SBE-911 plus), including a Seapoint Fluorometer. Water was collected at a total of 11–14 depths during the first CTD profiles at each station. Samples were taken from surface to 1,000 m depth (or limited by station depth), with highest resolution in the upper 100 m. Subsamples for biological and chemical characterization such as Chlorophyll a (Chl-a) and nutrients were taken. Chl-a fluorescence was used to determine the depth of the chl-a maximum for bottle samples, and calibrated afterwards using chl-a bottle samples. Bottle samples were also collected to check conductivity cell drift. Salinity errors were small, on the order of 0.01, which agreed with the post-cruise slope correction. No corrections beyond standard SeaBird data processing routines were deemed necessary.

2.3. Water Masses

Water masses have been classified as follows (see also **Figure 2**). Atlantic Water (AW) is defined by salinity $S > 34.92$ and $T > 2^\circ\text{C}$, for straightforward comparison with other data sets from the Fram Strait area (Walczowski, 2013, and references therein). We further delineate cold Atlantic Water (cAW) with $0 < T < 2^\circ\text{C}$

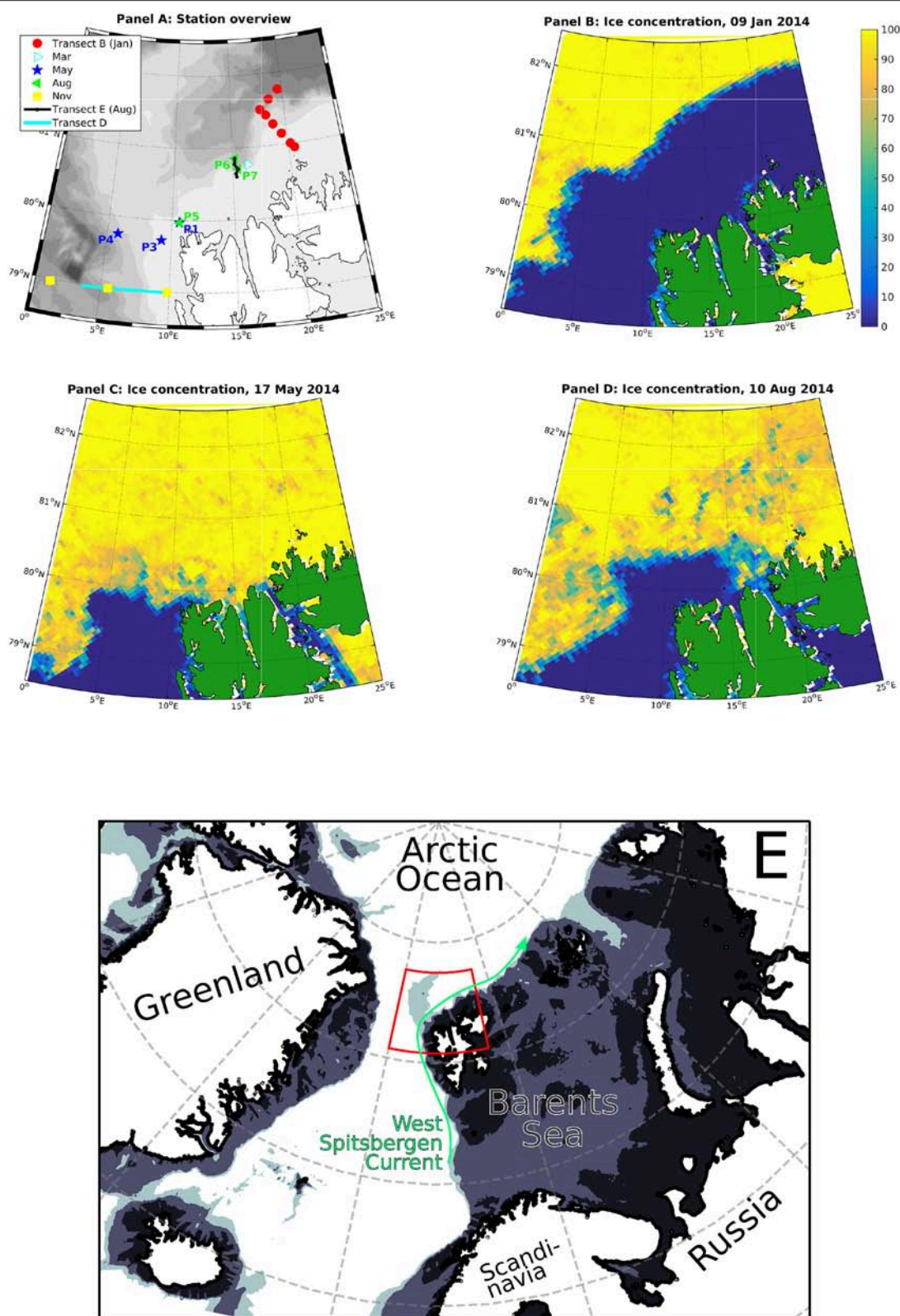


FIGURE 1 | Map of the study area (**A**) in its larger geographic context (**E**; red outline: study area), and ice charts for the January, May and August cruises (**B–D**). Transect D was sampled in January, May, August and November. Every cruise featured some additional stations further north, in particular transect B in January and transect E in August (which includes P6 and P7). All stations sampled in March and November were ice-free.

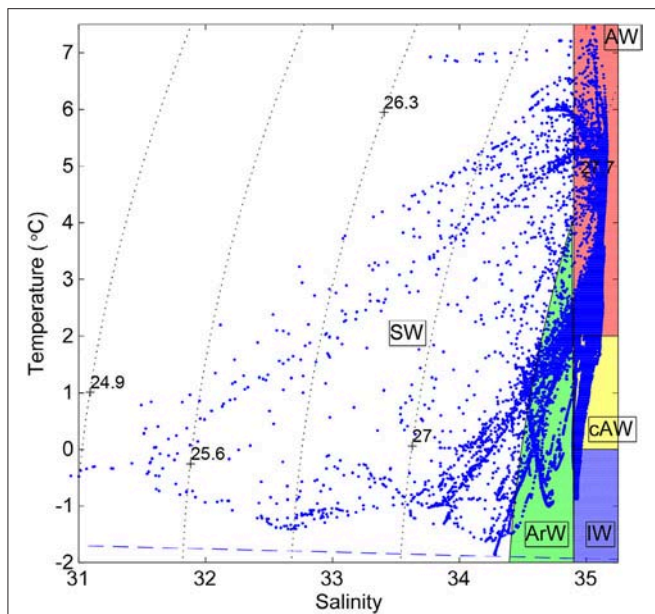


FIGURE 2 | Temperature plotted against salinity based on the full-depth profiles from the onboard CTD system (see Section 2.2) including water mass definitions: Atlantic Water (AW), Cold Atlantic Water (cAW), Intermediate Water (IW), Arctic Water (ArW), and Surface Water (SW). For definitions in terms of temperature-salinity properties, see Section 2.3.

and Intermediate Water (IW) $T < 0^{\circ}\text{C}$ (as in de Steur et al., 2014), both with $S > 34.9$ as the second defining limit. To identify water in the upper part of the column with characteristics typical of water that has undergone freshening and cooling inside the Arctic Ocean, we define Arctic Water (ArW) as having density $\rho_{\theta} > 27.7 \text{ kg m}^{-3}$ and $S < 34.92$ (or 34.9 when cooler than 2°C). It is important to note that not all water thus classified as ArW necessarily originates from the Arctic Ocean interior, but it has undergone similar modification processes and so deserves to be classified as such for easier comparison with earlier literature. Surface Water (SW) is delimited by density $\rho_{\theta} < 27.7 \text{ kg m}^{-3}$ (as in Marnela et al., 2013) and $S < 34.92$ to allow warm near-surface AW to remain in its original water mass (Beszczynska-Möller et al., 2012).

2.4. Sample Analysis and Data Processing

2.4.1. Calculation of Mixed-Layer Depth

For the purposes of this study, the depth of the mixed layer is defined as the depth where potential density (σ_{θ}) crosses 20% of the density difference between a surface layer density (3–5 m) and deeper (reference depth interval 50–60 m) values.

The reasoning behind this is that the upper ocean stratification observed during the summer cruises was often strong, yet shallow, not permitting the identification of a mixed layer in the classical sense of an actual well-mixed layer. Also note that whenever the density is homogeneous from the ocean surface to the bottom of the mixed layer, our algorithm gives results very similar to more standard methods, because all the density change happens in a rather thin pycnocline. Our method to study mixed

layer depths was developed in more detail by Randelhoff et al. (2017).

Mixed layer depths were derived from CTD profiles measured by a MSS-90L microstructure sonde (ISW Wassermesstechnik, Germany) that was deployed multiple times at all process stations. Ice cover permitting, the MSS was deployed from the ice at some distance from the ship, otherwise it was deployed from the ship and special care was taken to declutch the propeller and have the ship drift freely. Thus, these measurements permit resolving the upper 10 m of the water column more accurately than standard casts with a rosette, due to less disturbance of the measurements by the ship's presence, which is important in the summer marginal ice zone where melting is intense and can lead to strong near-surface stratification.

2.4.2. Nutrients

Water samples for analysis of nutrients ($\text{NO}_2^- + \text{NO}_3^-$, Si(OH)_4 , PO_4^{3-}) were frozen until analysis. They were analyzed by standard seawater methods using a Flow Solution IV analyzer from O.I. Analytical, USA. The analyzer was calibrated using reference seawater from Ocean Scientific International Ltd. UK. Three parallels were analyzed for each sample. Note that since NO_2^- levels are assumed to be low (see e.g., Codispoti et al., 2005), we use the sum $\text{NO}_2^- + \text{NO}_3^-$ instead of the NO_3^- concentration.

Ammonium (NH_4^+) concentrations were measured manually with the sensitive fluorometric method (Holmes et al., 1999). Reagents were added within minutes of sample collection.

2.4.3. Chlorophyll-a

For Chl-a analysis, triplicate subsamples (0.05–0.30 L) were filtered onto GF/F filters, and extracted by methanol over night in dark and cold conditions, before analysis using a Turner 10-AU fluorometer (calibrated using Chl-a, Sigma C6144) before and after acidification with 5 % HCl (Holm-Hansen and Riemann, 1978).

2.4.4. fCO_2

We used C_T , A_T (analysis described in the Supplementary Material), salinity, and temperature for each sample as input parameters in a CO_2 -chemical speciation model (CO2SYS program, Pierrot et al., 2006) to calculate CO_2 fugacity (fCO_2) in the water column. We used the HSO_4^- dissociation constant of Dickson (1990) and the CO_2 -system dissociation constants (K_1^* and K_2^*) estimated by Mehrbach et al. (1973), refit by Dickson and Millero (1987).

2.4.5. Calculation of the Euphotic Zone Depth

Continuous profiles of photosynthetically available radiation (PAR; radiation at wavelengths between 400 and 700 nm) in the upper ocean were measured at the process stations using a RAMSES radiometer (TriOS, Germany) with a wavelength spectrum of 190–575 nm. Because of data quality issues at wavelengths greater than 575 nm, an estimate of PAR was computed by integrating radiation data between 400 and 575 nm. The euphotic zone depth (Z_{eu}) was then defined as the depth at which downwelling PAR reached 1 % of its value just below the surface (Kirk, 2010). To derive Z_{eu} , the diffuse attenuation

coefficient of downwelling PAR (K_d) was first calculated by fitting an exponentially decreasing function to each profile,

$$E_z = E_0 \exp(-K_d z), \quad (1)$$

where E_0 is the irradiance below the surface, z corresponds to depth (positive downwards), and E_z is the irradiance at depth. K_d was then used to calculate the depth of the euphotic zone Z_{eu} by solving

$$Z_{eu} = \ln(0.01)/K_d. \quad (2)$$

2.4.6. Sea Ice Concentration Data

Sea ice concentration data were derived for AMSR-2 sea ice concentration data with grid cell size of 3.125 km (Spreen et al., 2008) were downloaded from http://www.iup.uni-bremen.de:8084/amr2data/asi_daygrid_swath/n3125/. Ice concentrations were gridded on a stereographic grid centered about the position of the ship at that time, and averaged over 6.25 km, i.e., over a radius of 2 grid cells, effectively. This scale is representative of the distance covered by ship or ice drift during a 24 h-process station and so can be regarded as a reasonable horizontal resolution.

3. RESULTS AND DISCUSSION

In general, our observations are consistent with what was known about the study area in that the large-scale inflow of AW dominates the picture (for a recent study focusing on the hydrography, see Koenig et al., 2017; Meyer et al., 2017), as we will show shortly. For instance, all nutrient samples showed a $\text{PO}_4^{3-}:\text{NO}_3^-$ slope and offset (Figure S1) consistent with the North Atlantic being the dominant source. This is not surprising since Pacific Water, the other major source of water in the Arctic Ocean, is not expected to be present in this area (Jones et al., 1998).

However, the warm Atlantic Water is obviously modified upon entering the cold Arctic Ocean, and the layering of the individual water masses crucially influences the timing and extent of primary production and other biogeochemical processes. Before going into seasonal dynamics and geographic distribution of sea ice meltwater, nutrient uptake, carbonate system and euphotic zone depth, we will therefore discuss the water masses in the purely physical hydrographic terms laid out in Section 2.3.

3.1. Hydrography

3.1.1. Water Masses

In both January and May 2014, AW was confined to the shelf slope and reached up to the surface between 6 and 8°E at transect

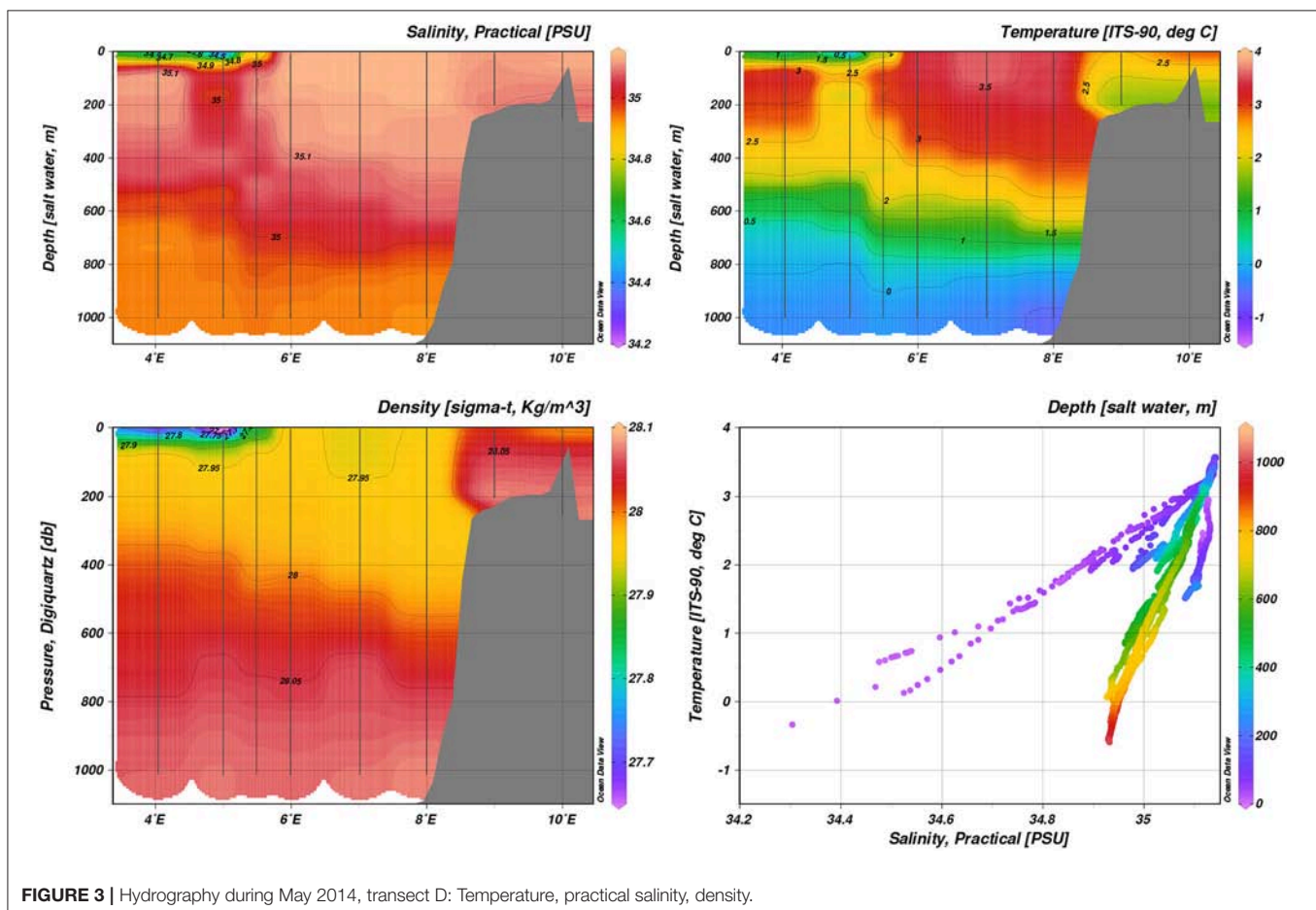


FIGURE 3 | Hydrography during May 2014, transect D: Temperature, practical salinity, density.

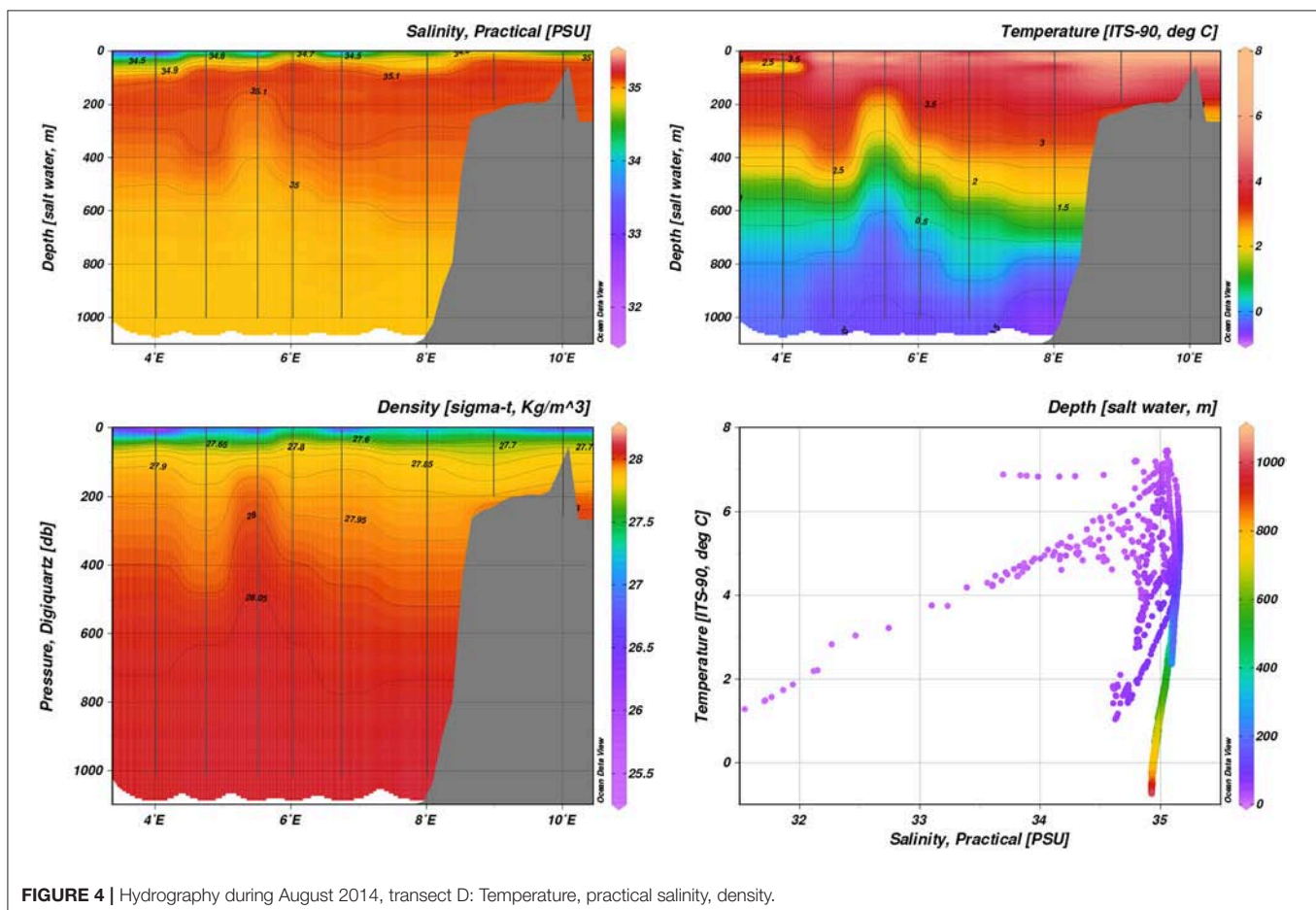
D, with maximum temperatures of 5 and 3.5°C in the surface 50 m, respectively (Figure 3 and Figure S2). Closer to the ice edge, colder, lower-salinity surface waters ($\sim 27.5 \text{ kg m}^{-3}$) were observed west of 5°E both in January and May. In August 2014, a fresher ($S < 34$) surface layer extended over most of transect D, with surface temperatures ranging from 7.5°C in the east to 1°C west of 4°E (Figure 4).

The AW core at transect D was much less well confined in temperature and salinity in August than in January and May. In January 2014, transect B at roughly 20°E showed subduction of the AW core below slightly colder and fresher water (Figure 5). Colder and fresher waters ($S = 34.4$, $T = -1^\circ\text{C}$, thus classified as SW) were present in the surface at bottom depths greater than 1000 m, indicating influence of polar water masses. May process stations repeated the pattern sampled on transect D during May (Figure 6). On-shelf (P1), surface waters were generally warmer and more saline ($S > 34.6$, $T > 1^\circ\text{C}$), as opposed to stations further off-shelf (P4, $S < 34.0$, $T < -0.5^\circ\text{C}$). Transect E and P6 and P7 showed warm AW of $T > 5^\circ\text{C}$ confined to the shelf slope at water depths $< 200 \text{ m}$ subducted under fresher, colder surface waters (Figure S3). Further off-shelf (water depths $> 200 \text{ m}$, north of 80.7°N), temperatures at intermediate depths (100–600 m) quickly dropped below 3°C, while still $S > 34.92$, indicating cooled AW.

The six process stations and the March station are shown in Figure 6 (see also Figure S4). The evolution of hydrographic properties from P1 to P5 exemplifies the evolution of the shelf water mass distribution during summer. While the salinity profile was virtually unchanged, presumably due to an approximate balance between ice melt and advection of saline waters, the water column at P5 was warmed due to less cooling during the northward transport. A similar evolution was mirrored in the evolution from the March station to P6 and P7. March showed a deeply-mixed winter profile with AW extending completely up to the surface. The August profiles, in comparison, showed a warmer AW core below approximately 20 m and a transition layer to the cold, fresh meltwater above.

3.1.2. Inorganic Nutrients and Chlorophyll-a

The distribution of nutrients along the D transect in January (Figure 7) reflected the water mass distribution, with maximum concentrations at depths larger than 800 m for nitrate (NO_3^-), phosphate (PO_4^{3-}) and silicate ($\text{Si}(\text{OH})_4$). Maximum concentrations of the different nutrients measured were $15.7 \mu\text{M}$ NO_3^- and $11.9 \mu\text{M}$ $\text{Si}(\text{OH})_4$ (both at 1,000 m, 8°E) and $1.07 \mu\text{M}$ PO_4^{3-} (1,000 m, 7°E). Also in May, maximum concentrations observed were $14.0 \mu\text{M}$ NO_3^- (1,000 m, 6°E), $1.10 \mu\text{M}$ PO_4^{3-} and $9.76 \mu\text{M}$ $\text{Si}(\text{OH})_4$ (both at 1,000 m, 5°E).



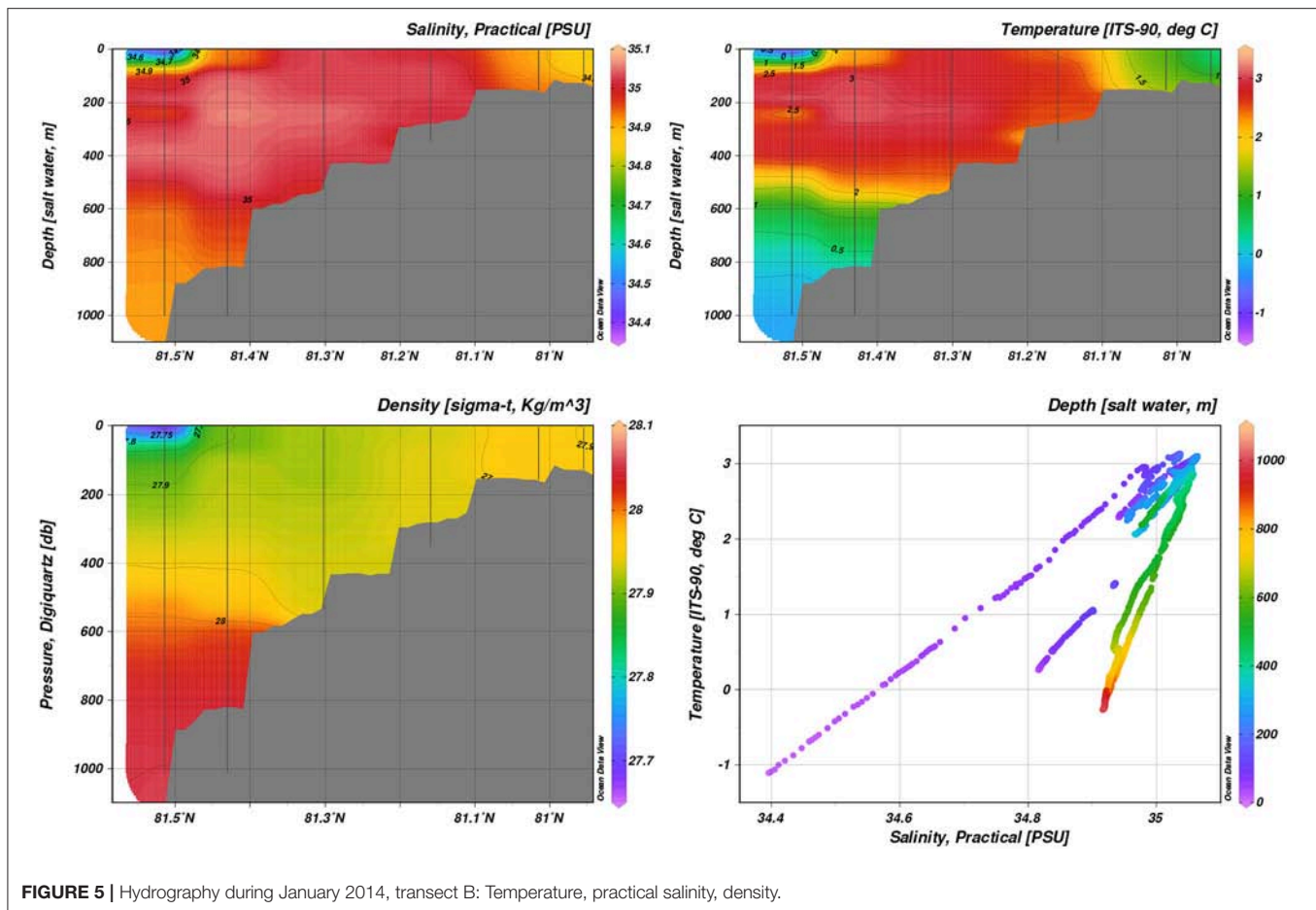


FIGURE 5 | Hydrography during January 2014, transect B: Temperature, practical salinity, density.

At transect B in January (see **Figure 8**), the nutrient distribution in January indicated low concentrations in the SW off the shelf, compared to the water masses on and along the shelf. Also north of the Svalbard shelf, maximum concentrations of nutrients were found at >800 m depth.

The nutrient data also revealed two distinct regimes in the water masses present (**Figure S1**). Water above the AW (S maximum, $\text{NO}_3^- \approx 10 \mu\text{M}$, $\text{Si(OH)}_4 \approx 4.5 \mu\text{M}$) followed a slope of approximately 1:2 in $\text{Si(OH)}_4:\text{NO}_3^-$, while water below the AW-associated salinity maximum continued from there with a slope rather close to 2:1, indicating a different stoichiometry in the remineralized nutrients accumulated in the deep.

3.2. Surface Layer Variability

3.2.1. Ice Cover and Mixed-Layer Evolution

Ice cover during the January, May and August cruises is plotted as ice concentrations in **Figure 1**. **Table 1** lists ice concentrations for the process stations. All process stations (except for the ice-free P5) were conducted in ice conditions typical of the Marginal Ice Zone over the AW inflow, with ice concentrations varying between 25 and 90 %. They were therefore subject to rapid ice melt, and there was no clearly defined surface mixed layer, but rather a thin layer of fresher water, separated from the underlying water by a shallow (~10–15 m) pycnocline (see **Table 1** and

Figure S5). Since the photic zone extended deeper than these freshwater layers, photosynthesis may occur across the whole seasonal pycnocline, as we will see in Section 3.4. Essentially, this decoupled mixed layer nutrient budgets from productivity (Randelhoff et al., 2016).

The temporal evolution of hydrographic properties at the D transect (**Figure 9**) demonstrates the contrast between the seasonality off and on the shelf slope. Off the shelf, seasonal stratification was stronger, had an earlier onset and was eroded later as distance from the shelf slope increases. A general pattern emerges where off-slope stations (e.g., the deeper parts of transect D and B) were stratified earlier and stronger than the stations on the upper shelf slope, which were unstratified even in January. Only in August a distinctly fresher surface layer was observed throughout the D transect. The relevant coordinate was the location with respect to both upper shelf slope (where the AW inflow lies) and the ice edge (where the meltwater input originates), seeing that a similar pattern was observed at P1-4.

3.2.2. Nutrient Uptake Dynamics

As expected, Chl-a concentrations in January were negligible at $<0.025 \text{ mg Chl-a m}^{-3}$. In May (see **Figure 10**), NO_3^- was depleted at $<0.5 \mu\text{M}$ in the surface waters at the western part of transect D (4°E), increasing to $\sim 2 \mu\text{M}$ at 7.5°E , reflecting a strong

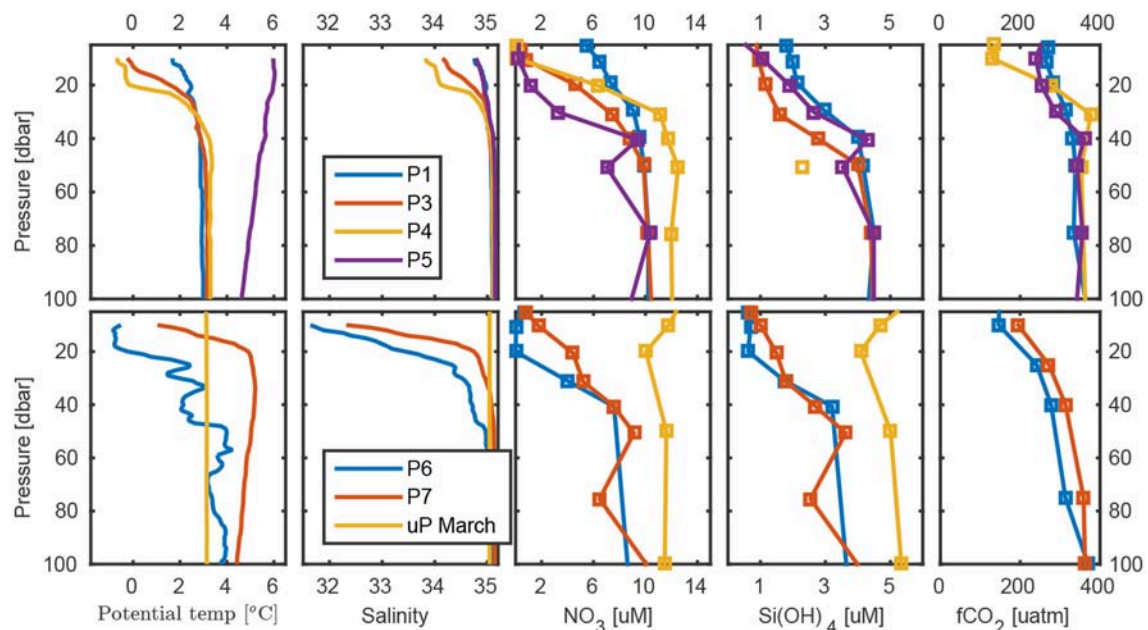


FIGURE 6 | Temperature, salinity, NO_3^- , Si(OH)_4 , and fCO_2 at process stations P1-P7 and the March station. The continental shelf is located toward the right (East), and Fram Strait to the left (West).

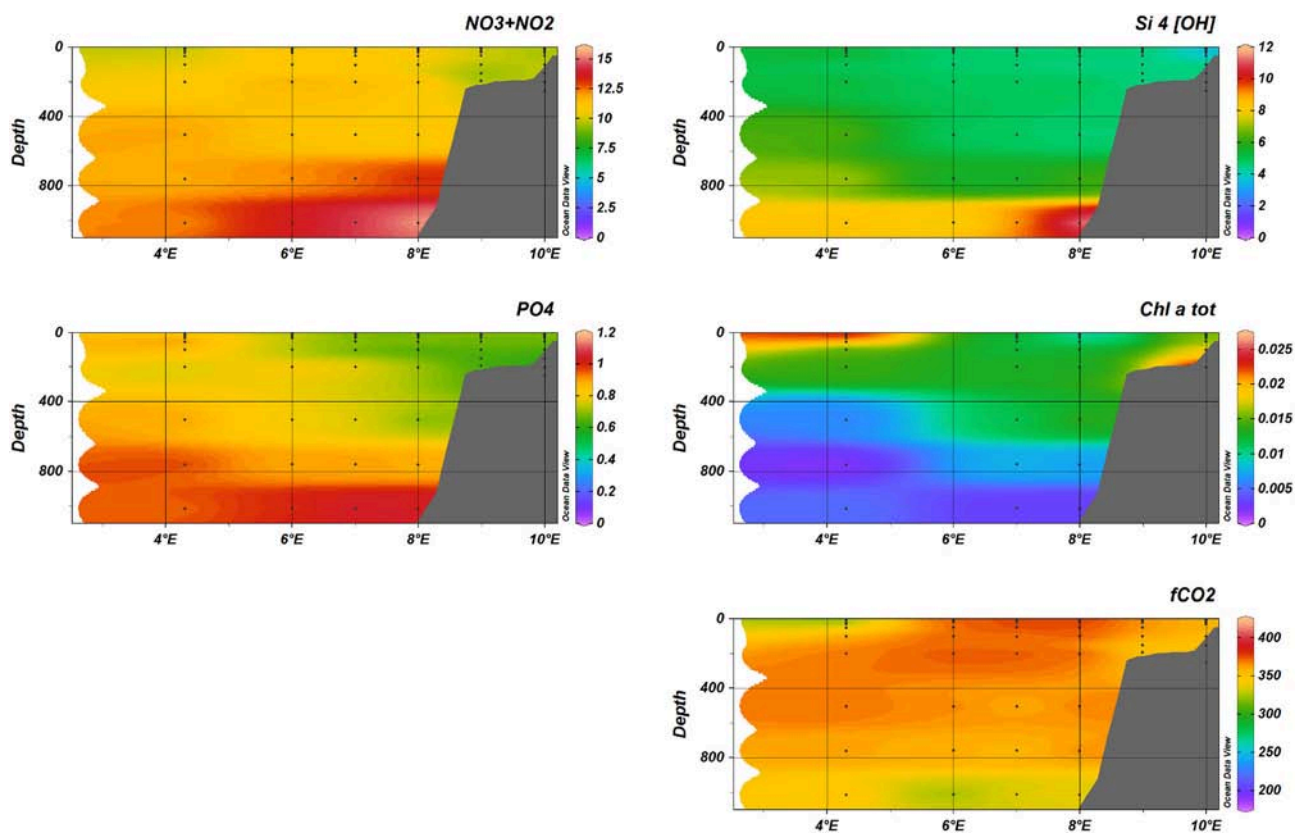


FIGURE 7 | Nutrients ($\text{NO}_3^- + \text{NO}_2^-$, Si(OH)_4 , PO_4^{3-}), fCO_2 , and total Chlorophyll-a during January 2014, transect D.

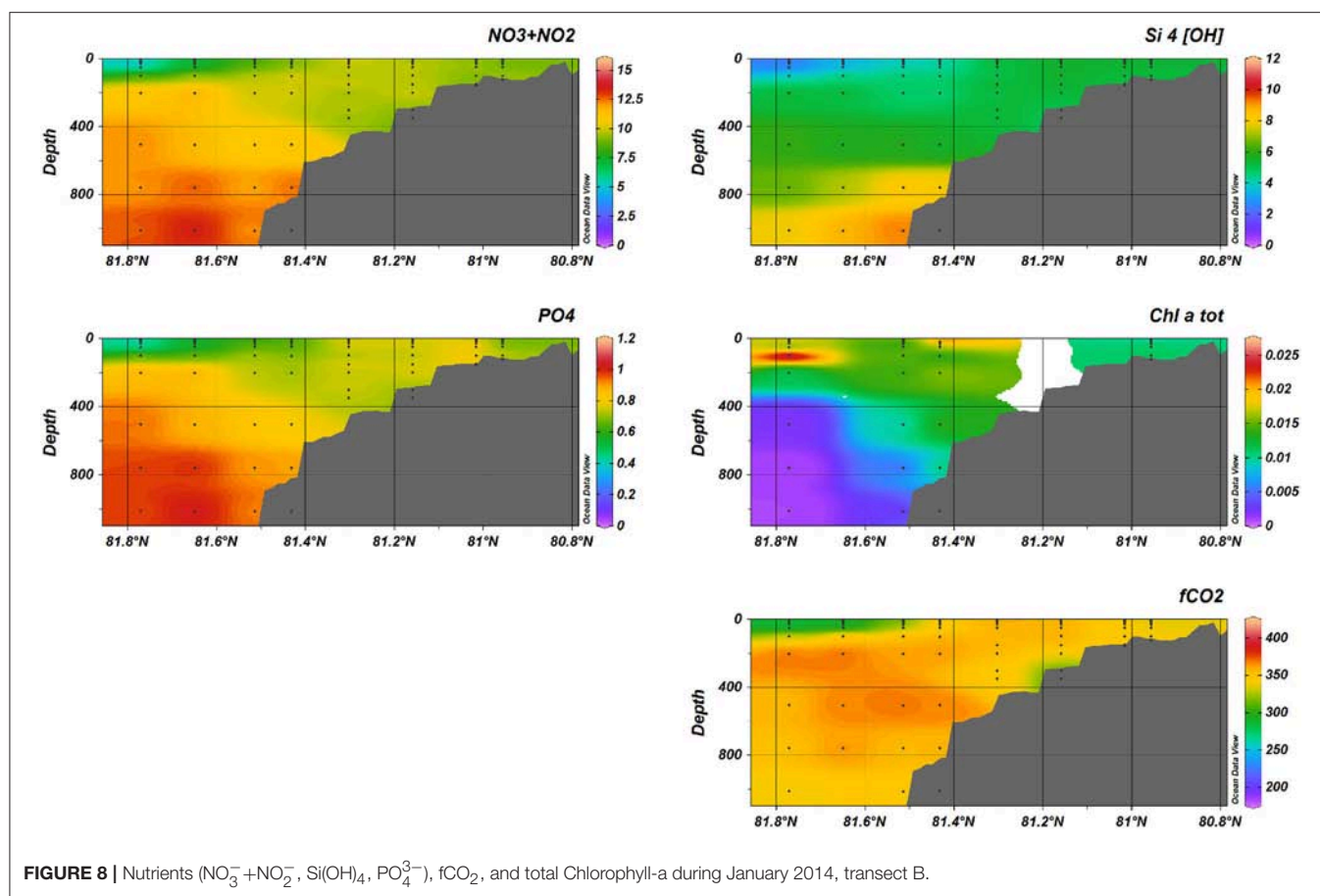


TABLE 1 | Process station data. $d_{\text{ML}}[\text{m}]$: Median mixed-layer depth (in parentheses: observed range).

	$d_{\text{ML}}[\text{m}]$	$d_{\text{N}}[\text{m}]$	$Z_{\text{eu}}[\text{m}]$	$K_d [\text{m}^{-1}]$	ice conc. [%]
P1	10 (7,12)	10–30*	23 ± 2	0.20	25
P3	10 (7,11)	15–30	19 ± 2	0.24	85
P4	11 (7,12)	20–30	22 ± 2	0.21	40
P5	15 (12,18)	25–40	22 ± 2	0.21	0
P6	10 (9,10)	26–40	48 ± 3	0.09	90
P7	9 (7,10)	10–40	45 ± 2	0.10	70

NB! these mixed-layer depths are nominal values following the definition employed here (see Section 2.4.1) and might not fulfill other criteria for a well-mixed layer (see text). d_{N} : nitracline depth (upper and lower extent), uncertainty $\pm 5 \text{ m}$ (*: nitrate not depleted in the surface layer), Z_{eu} : euphotic zone depth ($\pm$ uncertainty), K_d : diffuse attenuation coefficient of PAR, ice conc.: ice concentration, rounded to the closest multiple of 5%.

spring bloom with Chl-a concentrations $>11 \text{ mg Chl-a m}^{-3}$ in the surface waters. Chl-a concentrations $>1 \text{ mg Chl-a m}^{-3}$ were present to 50 m depth in this region. Further east ($>8^\circ\text{E}$), higher nutrient concentrations and lower Chl-a concentrations indicated that the bloom along and above the shelf started later compared to the central Fram Strait this year.

In August (see **Figure 11**), elevated chl-a concentrations were observed in the surface waters across transect D, but with maximum values of $6 \text{ mg Chl-a m}^{-3}$.

NH_4^+ levels in May were generally low, barely exceeding $0.5 \mu\text{M}$ under the pycnocline close to and in the MIZ (**Figure 12**, **Figure S6**). On-shelf on transect D, NH_4^+ levels were slightly elevated ($>0.3 \mu\text{M}$). August had a similar pattern, with elevated levels of NH_4^+ under the pycnocline ($>0.5 \mu\text{M}$) and increasing toward the shelf (P5, $>1.5 \mu\text{M}$ and on-shelf on transect D, $>2.5 \mu\text{M}$; **Figures S7, S8**). In winter, NH_4^+ levels were low (mostly $<0.2 \mu\text{M}$), apart from the (stratified) parts of transect B out into the basin, where values reached to a maximum of $0.75 \mu\text{M}$ at 10 m below the surface (data not shown).

The overall increase in ammonium values from May to August suggests that remineralization has started to take place and the community shifted toward a nutrient-recycling state. Notably, in the most stratified parts of transect B out into the basin, not all NH_4^+ has been removed. We hypothesize that this is related to the persisting stratification. To pinpoint the exact mechanism conclusively, further studies are needed; however, it seems plausible that the stratification inhibited downward mixing of the NH_4^+ left after the summer, possibly in concert with ongoing heterotrophic activity.

The timing of the mixed layer evolution coincides with the evolution of the water column nutrient inventory. All across the data set presented here we observe that the start of nutrient drawdown is closely tied to the development of a seasonal pycnocline. An interesting feature is that while

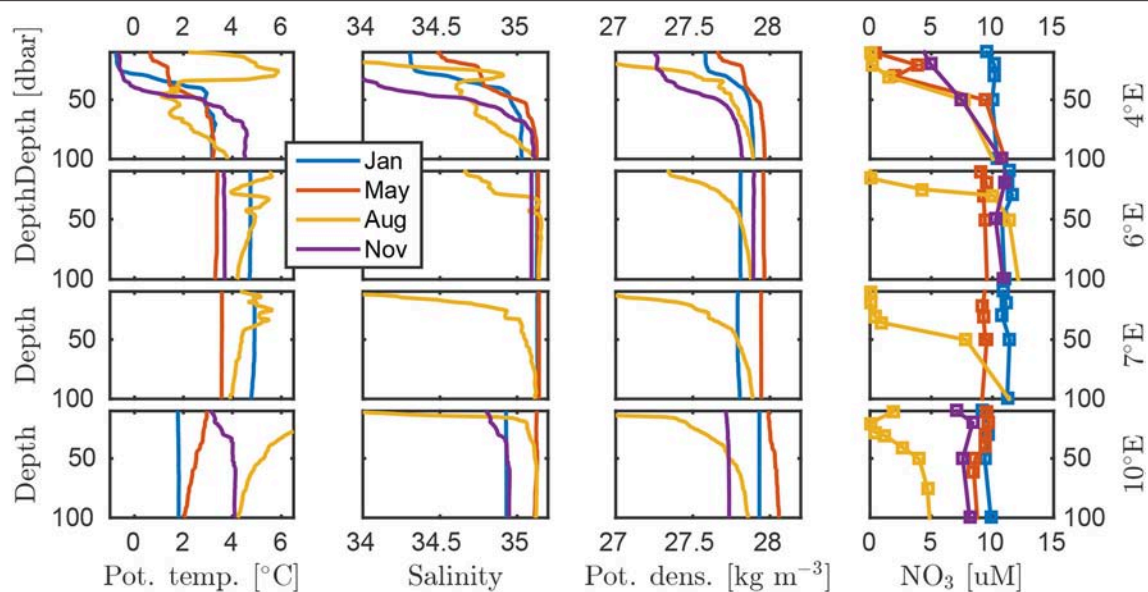


FIGURE 9 | Temporal evolution of the hydrography on the D transect. The AW core is located closest to the 7°E station. The 4°E profile in November is from 2°E. Full-depth profiles of these data are found in Figure S11.

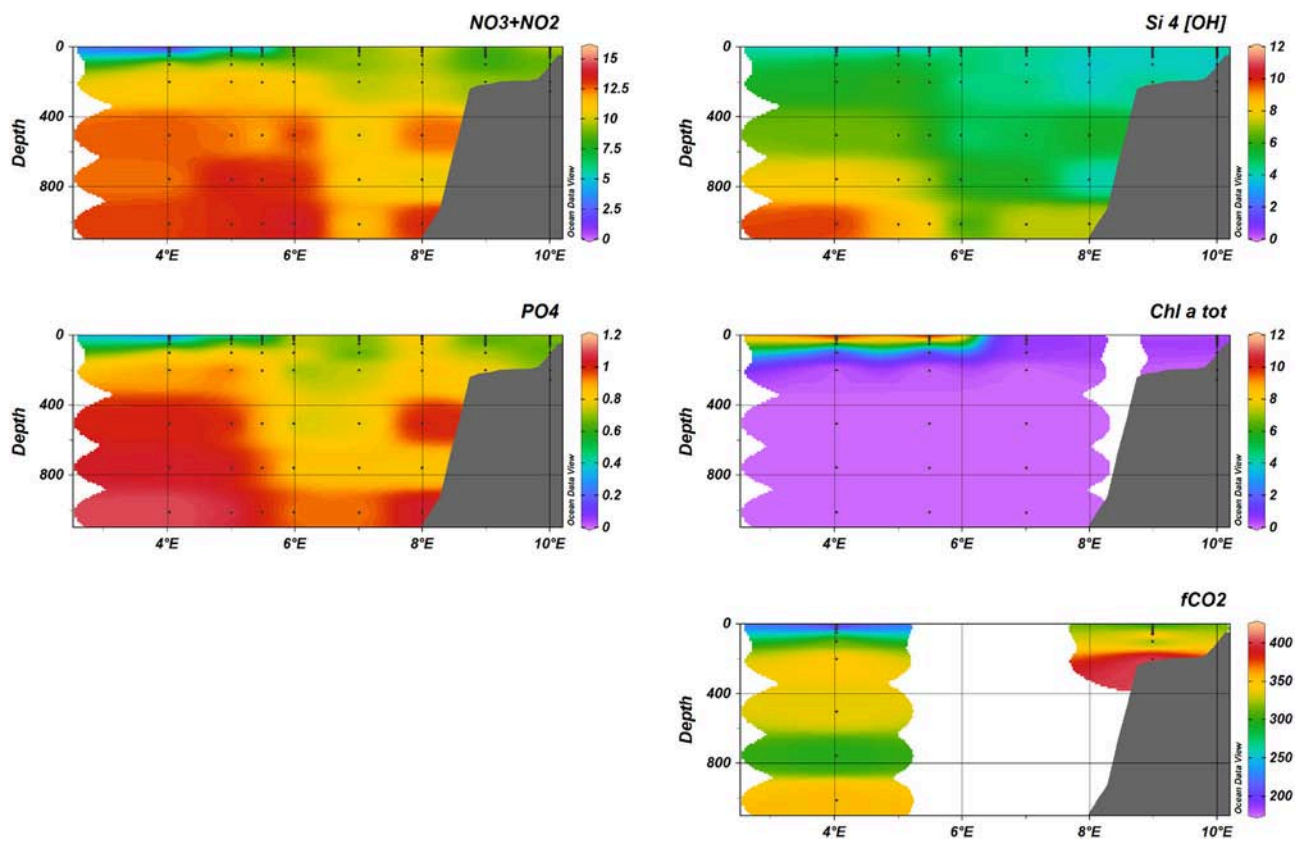


FIGURE 10 | Nutrients ($\text{NO}_3^- + \text{NO}_2^-$, $\text{Si}(\text{OH})_4$, PO_4^{3-}), fCO_2 , and total Chlorophyll-a during May 2014, transect D.

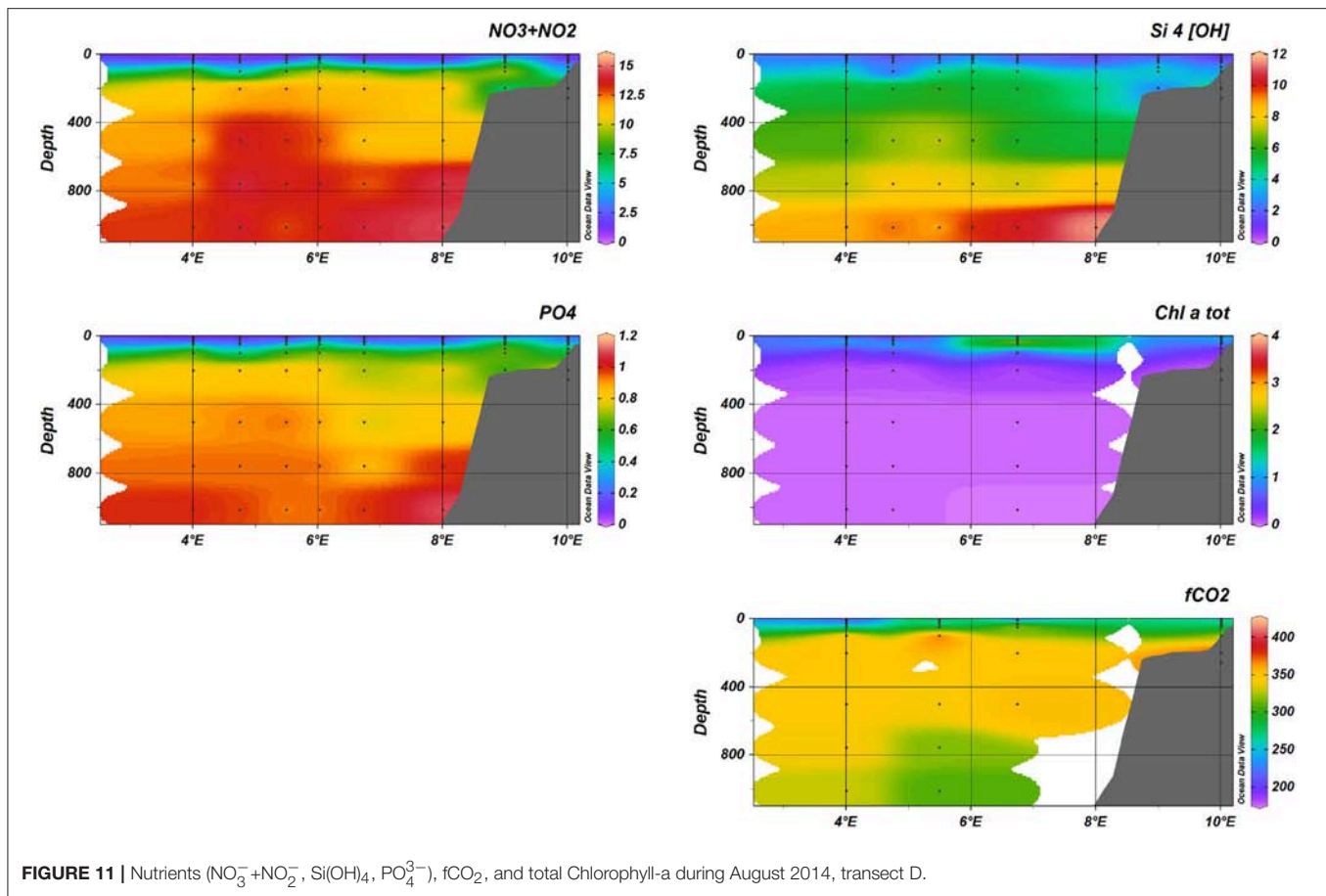


FIGURE 11 | Nutrients ($\text{NO}_3^- + \text{NO}_2^-$, Si(OH)_4 , PO_4^{3-}), fCO_2 , and total Chlorophyll-a during August 2014, transect D.

nutrient drawdown starts earlier off-shelf (May drawdown of nitrate larger off-shelf than on-shelf), the trend in August drawdown is reversed (**Figure 13**; see also Figure S11). With some modifications (a general intensification of both horizontal and vertical gradients in hydrography) due to the ice edge overlaying the shelf slope, this picture is valid across the inflow region (data not shown due to lack of measurements of winter profiles) – assuming a winter concentration equal to the “deep” concentration homogeneous with depth, the same is valid for P1 to P4 (**Figure 6**; see also Figure S4) and another transect slightly north of transect D that has not been presented in this study due to its similarity to D).

This is consistent with earlier reports of enhanced turbulent mixing over the shelf slope (Steele et al., 2012; Sarkar et al., 2015) which would ensure enhanced nutrient supply once the spring bloom is triggered, but we attempt no quantification beyond this qualitative observation.

Overall, Si was not entirely depleted in any of the samples, while NO_3^- frequently was limiting. The straight mixing line in Si: NO_3^- space between the AW core and the surface suggests that the surface area represents an end member (i.e., a water mass) with $\text{NO}_3^- = 0 \mu\text{M}$ and $\text{Si(OH)}_4 \approx 0 \mu\text{M}$. This would indicate a balance between overall drawdown of Si and N, that is an overall regional balance between the nutrient uptake of diatoms and of species that do not consume Si (like *Phaeocystis*), because Si:N

ratios commonly observed in marine diatoms (Brzezinski, 1985) are around twice to three times as much as the observed Si:N slope of approximately 0.5 observed here.

3.3. CO_2 Fugacity

The fugacity of CO_2 (fCO_2) showed a clear spatial and temporal variability going from the shelf in the East to the deeper part of the Fram Strait further west. In January (see **Figure 7**), fCO_2 was relatively uniformly distributed with highest values of about $375 \mu\text{atm}$ in the upper 300 meters between 6°E to 8°E . On the shelf ($9\text{--}10^\circ\text{E}$) and west of 6°E , values decreased likely due to colder water lowering fCO_2 . At 4°E , we encountered the ice edge and the lowest values of $320 \mu\text{atm}$ may have been influenced by a combination of low temperatures and sea-ice melt water. Surrounding this water of higher fCO_2 in the core of the Atlantic water were relatively uniform values of about $350\text{--}375 \mu\text{atm}$ and lower values in the surface at about 4°E which coincided with the location of the ice edge. In May (see **Figure 10**), the lowest fCO_2 values were observed extending across the whole water column except for the highest values of $375 \mu\text{atm}$ that persisted in the AW core waters. The surface water (upper 30 meters) showed the most pronounced decrease and reached fCO_2 minima of about $225 \mu\text{atm}$ in the top 30 meters extending close to the shelf (8°E).

At the process stations, the surface waters showed fCO_2 undersaturation of about $150 \mu\text{atm}$ relative to the atmospheric

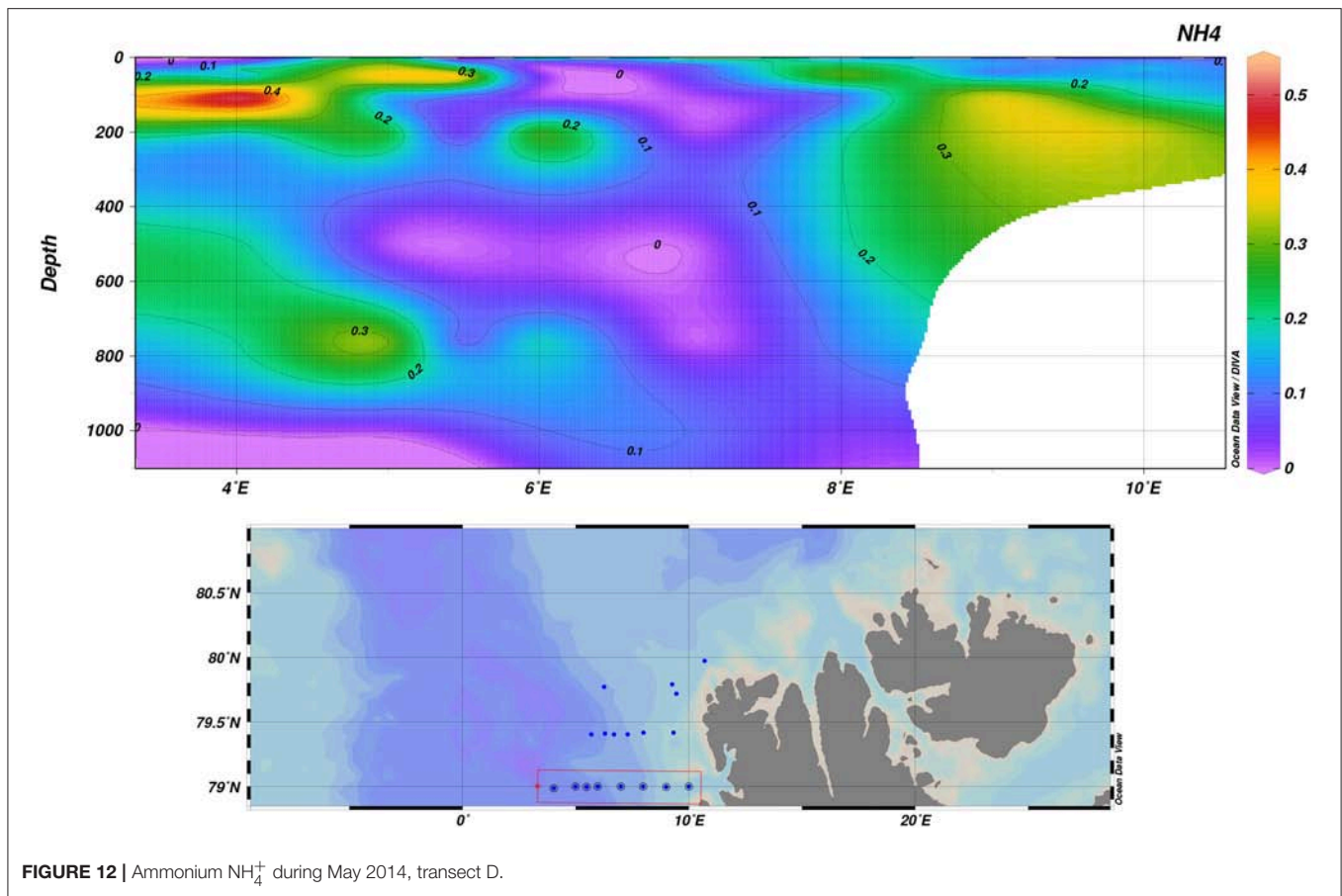


FIGURE 12 | Ammonium NH_4^+ during May 2014, transect D.

values of about $400 \mu\text{atm}$. We found large variability between 150 and $350 \mu\text{atm}$ in the upper 100 meters for all stations in May and August (Figure S9A). Below 200 meters, the fCO_2 showed similar values and little change between May and August. In the Intermediate Water (IW), below the core of the Atlantic Water, observed fCO_2 values were about $350 \mu\text{atm}$ (Figure S9B). The off shelf values (P4) were about $125 \mu\text{atm}$ lower compared to the shelf fCO_2 (P1) values in the upper 30 meters (Figure S9B). The lower surface water fCO_2 off the shelf may have been due to stronger CO_2 uptake by phytoplankton than on shelf production, since the temperature was about 2°C higher at P1 (Figure 6), which only accounts for about 20 % of the fCO_2 increase on-shelf relative to the off-shelf value. Seasonal variability on the shelf (P1 and P5) showed decreased fCO_2 of about $25 \mu\text{atm}$ from May to August in the upper 30 meters. Below that depth the fCO_2 values were similar (Figure 6).

The low values in the surface water from May decreased and extended throughout the whole transect in August. Since temperature increased, this was likely due to biological CO_2 drawdown during phytoplankton production. This is supported by the strong decrease in nitrate and the increase in chlorophyll a between January and May in the same area and depth range. In August, increasing fCO_2 values were likely due to warming and a decline in the phytoplankton bloom. The increase may also partly have been due to net fCO_2 production from respiration of organic

matter. In the Fram Strait, the strongest seasonal fCO_2 variability was not observed on the shelf (near Svalbard) but near the area of seasonal sea ice cover.

The range of fCO_2 levels in the surface water from this study can be compared with locations further east in the Arctic Ocean using data from ACSYS96 expedition (M. Chierici, unpublished data) and publicly available data from the Surface Ocean Carbon Dioxide Atlas (SOCAT, Bakker et al., 2016). In August in the northern Kara Sea at St. Anna Trough, fCO_2 ranges between $250 \mu\text{atm}$ to $390 \mu\text{atm}$, which is similar to the fCO_2 levels we found both north and west of Svalbard. This is also similar to the values reported by SOCAT for the Laptev Sea. However, fCO_2 values are substantially lower in the surface waters in the East Siberia Sea and on the Chuckhi Sea shelf. Here, fCO_2 values were lower than $100 \mu\text{atm}$ in August 2005, which was explained to be due to substantial CO_2 uptake by phytoplankton (Fransson et al., 2009).

3.4. Depth of the Euphotic Zone

Euphotic zone depth (Z_{eu}) at spring 2014 stations were shallow, ranging between 19 and 23 m (Table 1, Figure S10). While a shallow Z_{eu} was also encountered in the summer at station P5 ($Z_{\text{eu}} = 222 \text{ m}$, Table 1), euphotic zone depth at stations occupied north of Svalbard were overall deeper, ranging between 45 and 48 m. Calculated diffuse attenuation coefficients (K_d) showed a

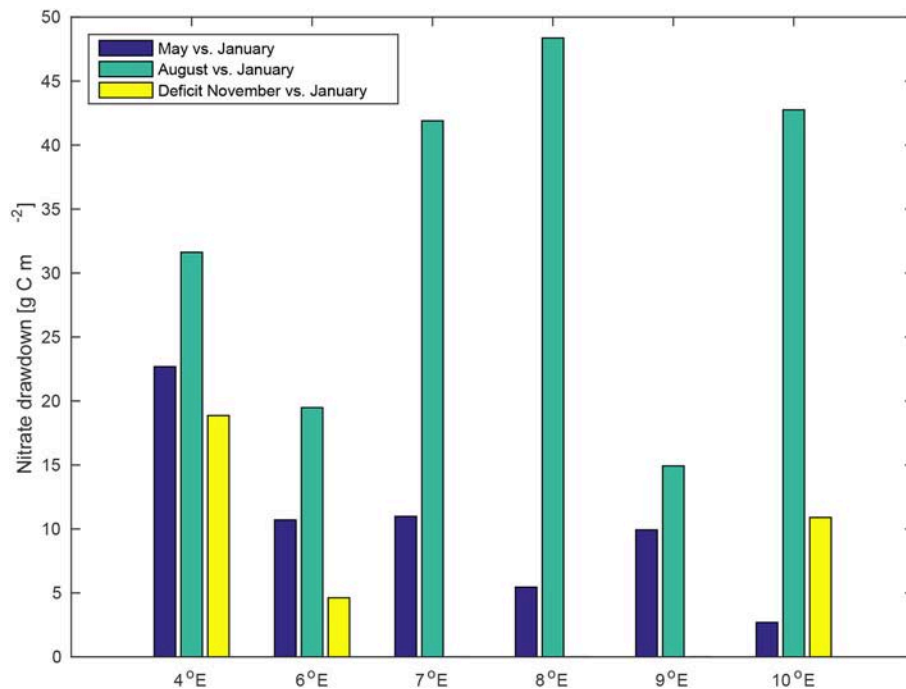


FIGURE 13 | Temporal evolution of the upper ocean nitrate deficit (converted to carbon mass using the Redfield ratio) relative to the January values. The November deficit at 4°E was calculated using the 2°E November profile (cf. **Figure 9**). Note that advection is not taken into account here.

moderate positive relationship with mean water column chl-a concentration across all sampling stations ($r^2 = 0.69$; Figure S10);

The depth of the euphotic zone, where 1% of the incident radiation reaches the phytoplankton, was always deeper than the shallow meltwater lens that defines the mixed layer (**Table 1**). The vertical distribution of phytoplankton was also deeper than the mixed layer depth, with highest concentrations at the surface and starting to decrease at Z_{eu} . In this way, the irradiance profiles, and in particular Z_{eu} , reflected the seasonal phytoplankton development. Stations P1, P3, and P4 had shallow Z_{eu} with high surface chlorophyll concentrations; the euphotic zone deepened in the late summer coinciding with lower phytoplankton biomass, with the exception of P5 that maintained high chlorophyll at the surface. Lower chlorophyll concentrations translated to deeper Z_{eu} , twice as deep as in the spring, both in Arctic waters (P6) and Atlantic waters (P7) north of Svalbard. These latter two stations had similar optical properties and chlorophyll profiles than those reported by Granskog et al. (2015) for Atlantic Waters and the ice edge in the Fram Strait at 79°N, sampled a few weeks later in the same season. The Atlantic waters showed a broad subsurface chlorophyll maximum between 20 and 30 m depth, while the Ice Edge stations have a sharp and pronounced chlorophyll maximum at 25 m. This similarity indicates that the phytoplankton distribution in the Atlantic waters is maintained from West to North of Svalbard in late summer (i.e., from approximately 79°N, 0 to 9°E to 80° 41.12N, 14° 14.53E).

The diffuse attenuation coefficient (K_d), ranging from 0.09 to 0.24 m^{-1} across the sampling stations, reflects the clarity

of upper ocean waters. In our stations the magnitude of this parameter increases as the average euphotic zone chl-a concentration increases: $K_d = 0.1229 + 0.0099 \cdot (\text{chl-a})$, $r^2 = 0.691$ (**Table 1**, Figure S12A), with chl-a concentrations in turn significantly positively correlated with optical measured of turbidity (Figure S12B). While confirming the impact of phytoplankton on ocean optical properties, the positive intercept in Figure S12A also provides evidence for absorption by non-algal particles.

Previous sampling of the region by Pavlov et al. (2015) showed that absorption in the West Spitsbergen Current at 79°N in late summer (September) is dominated by particles, of which phytoplankton constituted a significant component. The K_d values of 0.15 and 0.17 m^{-1} reported for the WSC, and euphotic depths of 37.4 and 41.9 m, indicate that waters upstream of the Carbon Bridge study area had somewhat higher phytoplankton concentration than the Atlantic inflow north of Svalbard (station P7).

3.5. Thermal Convection in Winter

The surface mixed layer over the shelf-slope was replete with nitrate on all stations in January 2014. Mooring data from earlier years at the shelf slope further downstream (30°E) confirm that this is part of a larger pattern, whereby the seasonal expansion of AW inflow along the shelf (Ivanov et al., 2009) slope breaks down the summer stratification as early as in December (Randelhoff et al., 2015), and preconditions deep-reaching (150–200 m) convection events, as was suggested by Aagaard et al. (1987) on the basis of a rather limited observational data set. The

section B is located about 100 nautical miles upstream from those moorings, and therefore this specific feature of winter vertical thermohaline structure could be expected to be more pronounced here. However, in January 2014 the warming impact of AW on local hydrographic conditions was anomalously strong. In fact, AW reached the ocean surface over a distance of approximately 35 nautical miles across the shelf-slope (**Figure 5**). The warm water (with maximum temperature over 3°C) at the ocean surface contributed to keeping ice-free conditions (see **Figure 1**) and air temperature between zero and a few degrees below zero (data not shown). During the January survey, vertical thermal convection was still developing at the deep stations, while at the shallow stations (less than 200 m) convection had already reached the seabed. This is indicated by depth-uniform vertical distributions of temperature and salinity on shelf. Intensive vertical mixing aided replenishment of the nutrient pool in the photic zone, cf. Randelhoff et al. (2015).

Some reports claim evidence for wintertime, wind-driven upwelling in this area, and link this to primary productivity (e.g., Falk-Petersen et al., 2014). We have not found any indications to that effect during our sampling campaigns. For a more detailed description of the issue of wind-driven upwelling in Arctic shelfbreak areas, see Randelhoff and Sundfjord (2018). All else aside, even actual upwelling in winter would not enhance productivity in our study area since, as we have shown, the surface mixed layer is already replete by that time and well before the onset of the next spring bloom.

Vertical homogeneity in oxygen saturation also suggests a possible oxygenation of intermediate waters. However, attempts at answering this issue using our data set remain inconclusive since the difference between values of oxygen saturation at the surface and at 400 m depth inferred from a CTD-mounted SBE43 dissolved oxygen sensor (transect E, summer: approximately 75%, transect B, winter: approximately 79%) was small, and because we lack sufficiently precise Winkler oxygen measurements. In a more general context, the large heat content of inflowing AW in combination with depleted ice cover in the fall of 2013 provided a long-living anomaly of ice concentration north and north-east of Svalbard in winter 2014 (Ivanov et al., 2016). This anomaly in ice cover might have impacted both processes in the ocean and in the atmosphere.

4. SYNTHESIS AND CONCLUSIONS

The Atlantic inflow area west and north of Svalbard is a dynamic one, where warm, saline AW meets Arctic Water and sea ice, leading to an influx of fresh and cold meltwater. Both sea ice and Atlantic Water are continually being advected into the area. This tug of war leads to a fine balance in the development of the shallow, strongly stratified seasonal pycnocline in summer and its erosion in winter. Seasonal, light-dominated biological processes therefore take place at the fringes of the large-scale hydrography and are not easily represented by large-scale, long-time averages. Understanding seasonal and local aspects of stratification and mixing processes is thus necessary in order to correctly couple biology and biogeochemistry to their physical drivers.

Based on the data presented in this study, we make the following conclusions: (1) Atlantic Water (AW) and cold Atlantic Water (cAW) are the dominant water masses in the area. While this finding is hardly new, it is worth keeping in mind that most samples acquired during the CarbonBridge campaign are taken from waters of Atlantic origin that are cooled and freshened on a seasonal basis as opposed to originating from the central Arctic Ocean. (2) Northward penetration of temperature-stratified AW permits thermal convection in winter and thus high heat fluxes, potentially keeping the area ice-free in winter. The AW influence documented here and elsewhere thus permits rapid replenishment of nutrients around the shelf slope. (3) The timing of nutrient and fCO_2 drawdown is closely linked to the development of a seasonal pycnocline (see also Marit Reigstad et al., “Bloom stage characteristics in an Atlantic-influenced Arctic marine ecosystem and implications for future productivity pathways,” this issue). However, for nitrate, the seasonally integrated drawdown can depend on other parameters and tends to be larger on than off the shelf.

Ice extent in our study area is notoriously dominated by the wind field from seasonal to interannual scales (e.g., Koenigk et al., 2009), and we do therefore not assume that the exact distribution (i.e., based on latitude-longitude-referenced maps) of the parameters that we found in our data set is exactly reproduced during other years. However, patterns should be similar interannually when referenced to the relative positions

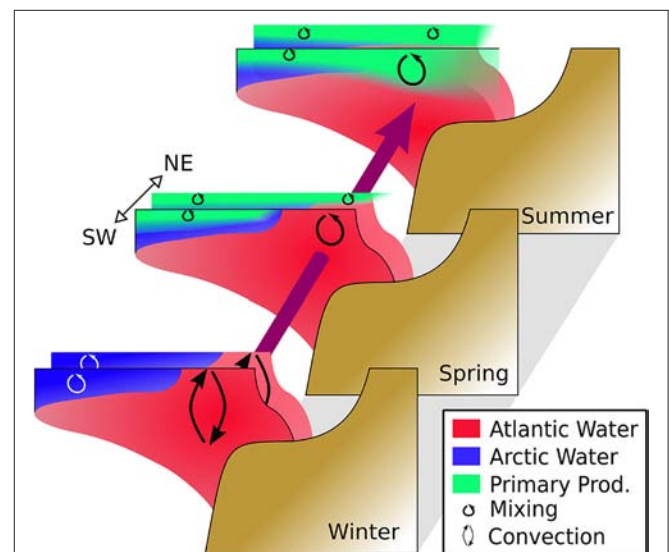


FIGURE 14 | Schematic summarizing the major seasonal and spatial hydrographic patterns described in this study. Shown are the water masses, mixing processes, and primary production in six conceptual cross-shelf transects. For each season (in our data represented by the months January, May, August), there are two transects, one further south and west (in our data: transect D) and one further north and east (our transects B, E, and various process stations; see **Figure 1**). Further northeast, more ice is present, stratifying the Atlantic inflow earlier, with a concomitant earlier bloom. Once the Atlantic inflow is stratified and the spring bloom has started also further southwest (see the “Summer” transect), the nutrient consumption even reaches deeper, presumably due to weaker stratification, hence deeper mixing.

of the AW core, the ice edge and the seasonal freshwater layer, which in our data set are tightly coupled to the biogeochemistry.

We summarized our central conclusions about the seasonal and geographic distribution of hydrography, mixing, and consequently biogeochemistry in a schematic: see **Figure 14**.

All of these findings indicate that under a scenario of increased “Atlantification” of the shelf slope north of Svalbard, this area will indeed likely become a regional hotspot with increased primary production due to efficient transport and vertical supply of nutrients coupled with decreased light limitation due to oceanic heat.

AUTHOR CONTRIBUTIONS

AR: led the overall data analysis and writing of the paper; MR: led the analysis of the nutrient and chlorophyll-a data; MCh: led the analysis of the $f\text{CO}_2$ data; MCa: led the analysis of the radiation profiles; MR, MCh, AS, VI, MCa, MV, J-ÉT, and GB: contributed to the writing; MR, MCh, AS, and MCa: helped produce the figures. All authors contributed to data analysis.

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All data are made available to the public, see PANGAEA (<https://www.pangaea.de>), the Norwegian Polar Data Centre (<https://data.npolar.no>) (for hydrographic data), the Norwegian Marine Data Centre (<https://www.nmdc.no>) and GLODAP (Global Ocean Data Analysis Project for Carbon, <https://climatedataguide.ucar.edu/climate-data/glodap-global-ocean-data-analysis-project-carbon>), the latter two for carbonate system data.

SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: <https://www.frontiersin.org/articles/10.3389/fmars.2018.00224/full#supplementary-material>

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Properties of Sediment Trap Catchment Areas in Fram Strait: Results From Lagrangian Modeling and Remote Sensing

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Vertical particle fluxes are responsible for the transport of carbon and biogenic material from the surface to the deep ocean, hence understanding these fluxes is of climatic relevance. Sediment traps deployed in Fram Strait within the framework of the Arctic long-term observatory FRAM provide a time-series of vertical particle fluxes in a region of high CO₂ uptake. Until now the source area (catchment area) of trapped particles is unclear; however, lateral advection of particles is supposed to play an important role. This study presents a Lagrangian method to backtrack the origin of particles for two Fram Strait moorings equipped with sediment traps in 200 and 2,300 m depth by using the time-dependent velocity field of a high-resolution, eddy-resolving ocean-sea ice model. Our study shows that the extent of the catchment area is larger the deeper the trap and the slower the settling velocity. Chlorophyll-a concentration as well as sea ice coverage of the catchment area are highest in the summer months. The high sea ice coverage in summer compared to winter can possibly be related to a weaker across-strait sea level pressure difference, which allows more sea ice to enter the then well-stratified central Fram Strait where the moorings are located. Furthermore, a backward sea ice tracking approach shows that the origin and age of sea ice drifting through Fram Strait, partly responsible for vertical particle fluxes, varies strongly from year to year, pointing to a high variability in the composition of particles trapped in the moorings.

Keywords: lagrangian modeling, particle trajectories, sediment trap, catchment area, fram strait

1. INTRODUCTION

The oceans play a critical role in the global carbon cycle through regulating the exchange of carbon dioxide between atmospheric and oceanic reservoirs. There are numerous interconnected mechanisms involved in this exchange: the biological carbon pump (Volk and Hoffert, 1985), the solubility pump, the microbial carbon pump (Jiao et al., 2010) and the lipid pump (Jónasdóttir et al., 2015). The biological carbon pump is perhaps the most widely studied and traditionally refers to the gravitational settling of particles produced in the surface to the ocean interior (Sarmiento and Gruber, 2006). It is comprised of two components: the soft-tissue pump (Volk and Hoffert, 1985) and the carbonate counter pump (Heinze and Maier-Reimer, 1991). The soft-tissue pump is

the vertical transfer of photosynthetically fixed carbon dioxide into the ocean interior as organic particles (Sarmiento et al., 1988), that may be associated with inorganic ballast minerals (Klaas and Archer, 2002; Salter et al., 2010). The carbonate counter pump is related to the precipitation of calcium carbonate minerals that act as a source of CO₂ to the atmosphere over climatically-relevant timescales (Zeebe, 2012). The balance of these two processes thus governs the net sequestration of atmospheric CO₂ into the ocean interior (Antia et al., 2001; Salter et al., 2014) and thus has an important impact on global climate (Sarmiento and Toggweiler, 1984; Sabine et al., 2004; Kwon et al., 2009). In addition, through pelagic-benthic coupling (Graf, 1998), the biological carbon pump acts as the principal source of energy and nutrients to abyssal ecosystems (Billett et al., 1983; Rembauville et al., 2018). A good understanding of the mechanisms transferring biogenic particles from the surface to the deep-ocean and sediments is critical.

Early studies attempting to link surface properties like primary productivity to particle flux have provided evidence for fast one dimensional coupling (Deuser and Ross, 1980; Alldredge and Chris, 1988; Asper et al., 1992). However, it has been subsequently shown that horizontal advection of water may displace particles significantly from their place of production during sinking (Siegel and Deuser, 1997; Waniek et al., 2000, 2005). Lateral advection and variable settling velocities thus have the potential to significantly modify the spatial pattern of transmission of a surface signal to the ocean interior. Significant inputs of particles can be laterally advected from ocean margins and shelf systems and can be important for balancing regional biogeochemical budgets (Anderson and Ryabchenko, 2009; Burd et al., 2010). Mesoscale eddies have also been shown to shape planktonic particle distribution and influence export to the deep-ocean (Waite et al., 2016). Interpretation of flux data measured by moored sediment traps therefore relies on resolving these physical processes (Waniek et al., 2005).

In addition to horizontal fluid velocities, the consideration of particle settling velocities is critical to determine particle export trajectories from the surface ocean (e.g., Siegel et al., 1990; Waniek et al., 2000). Ballasting of particles by biogenic and lithogenic minerals can effect the transfer of organic material to the deep-ocean (Armstrong et al., 2001; Klaas and Archer, 2002). Laboratory experiments and field studies have indicated that mineral ballast can increase the density and settling velocity of particles (Fischer and Karakaş, 2009; Iversen and Ploug, 2010; Lombard et al., 2013). Lithogenic minerals in particular may modify the transfer of organic material to the bathypelagic (Ittekkot, 1993; Salter et al., 2010) and could be particularly important in the Arctic if aluminosilicate clays are entrained in the ice through suspension freezing over shallow topography. A wide variety of techniques has been used to determine particle settling velocities including laboratory settling columns, *in-situ* settling columns and imaging systems (Asper and Smith, 2003), temporal peak matching of particle flux profiles (Armstrong et al., 2009) and particle gel traps (McDonnell and Buesseler, 2010). These methods have generated a large range of settling velocities that vary between 5 and 2,700 m/d (McDonnell and Buesseler, 2010). Typically marine particles are considered to settle in the

range of one to some meters per day for phytoplankton cells, hundreds of meters per day for aggregates and upwards of hundred to several thousand meters per day for fecal material (Waniek et al., 2000; Turner, 2002; Armstrong et al., 2009; McDonnell and Buesseler, 2010; Turner et al., 2014). Quantitative partitioning across different sinking fractions shows that both large, fast sinking particles and small, slow sinking particles can be important contributors to total organic matter flux (Peterson et al., 2005; Trull et al., 2008; Riley et al., 2012; Durkin et al., 2015) and is unsurprisingly related to planktonic ecosystem structure. Variability in sinking velocity classes and particle flux size-spectra has important implications for calculating particle trajectories.

Estimating the catchment area (according to Deuser et al., 1988 defined as the surface domain that contains all likely positions where particles entering the trap might come from) is not a trivial task, and a range of different methods and simplifications have been applied previously. Due to lack of availability of a full time-dependent 3D velocity field, several studies used the time dependent velocity profile measured by instruments attached to moorings to calculate particle trajectories (v. Gyldenfeldt et al., 2000; Waniek et al., 2000, 2005; Bauerfeind et al., 2009). This results in so called progressive vector diagrams, which are based on the assumption of spatial homogeneity of the horizontal velocity field around the trap. In these studies the resulting catchment area is described in terms of distance to the trap (e.g., Waniek et al., 2005, their Figure 5), but does not indicate the geographical location. Another approach was followed by Siegel et al. (2008), using a combination of geostrophic velocities derived from satellite altimetry, shipboard ADCP data and satellite-tracked surface drifters. Abell et al. (2013) used surface geostrophic currents derived from satellite altimetry and reconstructed a time dependent 3D velocity field by assuming that currents decrease linearly from the surface to 15% at 1,500 m depth to backtrack particles in time starting at the trap. Qiu et al. (2014) performed backward particle tracking for sediment traps located in the Ligurian Sea by using the time dependent 3D velocity field of an ocean model.

The FRontiers in Arctic Monitoring observatory (FRAM; Soltwedel et al., 2013) aims to establish a long-term observing infrastructure that is capable of detecting changes in the physical, chemical and biological properties of a rapidly changing Arctic Ocean. It is comprised of numerous observing components that include fixed point mooring arrays and seafloor observations, and also numerical ocean modeling. The instrumentation and autonomous sampling devices deployed on the observational components aim to provide continuous data-flow on the organic flux rates to the seafloor and the resulting impact on deep-sea communities. To link the variability in these phenomena to changes occurring in the surface ocean, it is necessary to take advantage of ocean models that realistically represent the circulation and hydrography of the region, as well as remote-sensing data products that can provide information on chlorophyll-a and ice-cover dynamics. The objectives of the present study are to (i) develop a particle tracking model to define catchment areas of sediment traps and (ii) constrain the temporal variability of sea ice coverage

and chlorophyll-*a* distribution within the defined catchment areas.

2. STUDY AREA, METHODS, AND MATERIAL

2.1. Study Area

The Fram Strait, located between Greenland and Svalbard (**Figure 1A**), is characterized by contrasting water masses. Warm and salty waters of Atlantic origin are carried northward by the West Spitsbergen Current (WSC, e.g., von Appen et al., 2016). A fraction of the Atlantic Water (AW) carried by the WSC recirculates in Fram Strait at around 79°N and continues to flow southward, forming the Return Atlantic Water (RAW), whereas the remaining part enters the Arctic Ocean via the Svalbard and Yermak branches. Along the Greenland continental shelf break, the East Greenland Current (EGC, e.g., de Steur et al., 2009) carries cold and fresh Polar Water (PW) as well as RAW southward. Sea ice is exported with the Transpolar Drift out of the Arctic through the Fram Strait. The sea ice export occurs at the western side of the strait, which is thus ice-covered year-round. The eastern part of the Fram Strait is ice-free year-round due to the presence of warm AW.

In this study, we focus on moorings HG-IV and HG-N which are part of the FRAM Observatory (**Figure 1A**). HG-IV and HG-N are located in the central Fram Strait, southeast and northeast, respectively of the Molloy Deep, the deepest depression of Fram Strait. They are located in a region where warm AW recirculates westward.

2.2. Ocean-Sea Ice Model

Model output from the Finite-Element Sea-ice Ocean Model (FESOM) version 1.4 is used to calculate backward trajectories. FESOM is an ocean-sea ice model which solves the hydrostatic primitive equations in the Boussinesq approximation and is discretized with the finite element method (Wang et al., 2014; Danilov et al., 2015). Details on the coupling of the ocean and sea ice model can be found in Timmermann et al. (2009). In this study, we use a FESOM configuration that was optimized for Fram Strait, applying a mesh resolution of 1 km in this area (Wekerle et al., 2017). By comparing with the local Rossby radius of deformation (around 4–6 km in Fram Strait, e.g., von Appen et al., 2016) which is an indication of eddy size, this configuration can be considered as “eddy-resolving.” A snapshot of the simulated velocity in 100 m depth is shown in **Figure 1B**, revealing strong eddy activity. The simulation covers the time period 2000 until 2009. It is forced with atmospheric reanalysis data from COREv.2 (Large and Yeager, 2008), which includes sea surface wind and temperature, precipitation and snow, and longwave and shortwave radiation. River runoff is taken from the interannual monthly data set provided by Dai et al. (2009). A comparison with observational data (hydrography and velocity measured by a mooring array in Fram Strait) showed that the model performs well in reproducing circulation

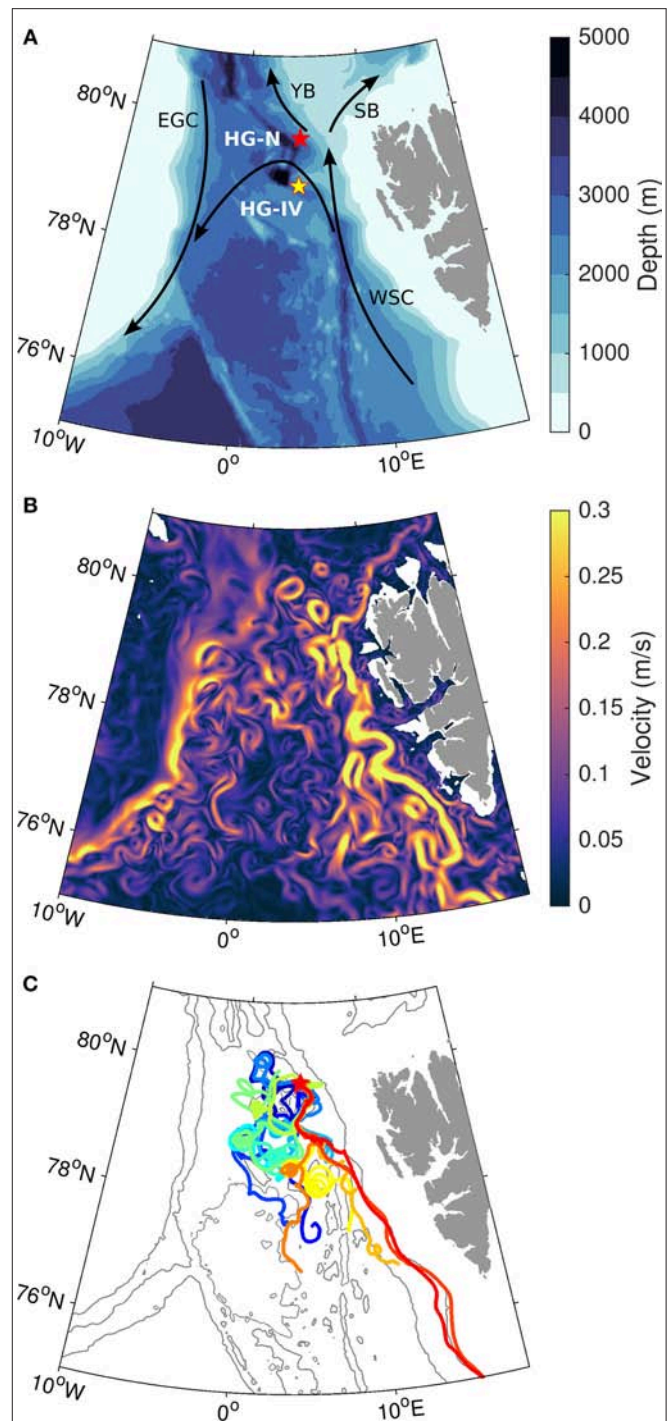


FIGURE 1 | (A) Bathymetry in the Fram Strait region. Shown are the locations of the two moorings, HG-N (red star) and HG-IV (yellow star). Indicated are also major currents in the Fram Strait: West Spitsbergen Current (WSC), East Greenland Current (EGC), Yermak Branch (YB) and Svalbard Branch (SB). **(B)** Snapshot of simulated velocity in 100 m depth on 1 July 2009. **(C)** 115-day long backward trajectories of particles calculated with a settling velocity of 20 m/d released at HG-N in 2,300 m depth in the time period 1–14 July 2009. Each color indicates a different release date. Gray contours show the bathymetry at 1,000 m intervals.

TABLE 1 | Settings of 12 experiments performed in this study.

Sediment trap locations	HG-N (4°30.36'E / 79°44.39'N, water depth 2,620 m) HG-IV (4°19.92'E / 79°0.43'N, water depth 2,540 m)
Depth of sediment traps	200 and 2,300 m
Settling velocities	120, 60, and 20 m/d

For each experiment, particle trajectories were started once per day during the time period 2002–2009.

structure, eddy kinetic energy and hydrography (Wekerle et al., 2017).

2.3. Calculation of Backward Ocean Trajectories

To determine the catchment area of sediment traps deployed in Fram Strait, we used a Lagrangian particle tracking algorithm (see **Appendix** for details) and computed backward particle trajectories. This was done by reversing the flow field, i.e., particles were treated as if they were rising from the mooring location to the surface with a negative settling velocity, being horizontally displaced with the reversed horizontal velocity (vertical ocean velocities were neglected). Particles were advected with daily averaged horizontal model velocities from the FESOM simulation described above and a constant settling velocity¹ of either 120, 60, or 20 m/d. They were released at either 200 or 2,300 m depth (which is relatively close to the bottom), and tracked until they reached the surface. Thus, the duration of trajectories released at e.g., 2,300 m depth was 19, 38, and 115 days for settling velocities of 120, 60, and 20 m/d, respectively. The computation of backward particle trajectories was performed for two locations of moorings equipped with sediment traps in central Fram Strait, HG-N and HG-IV (indicated by stars in **Figure 1A**). Note that other starting positions or settling velocities can be implemented easily. Particles were released once per day during the time period 2002–2009, resulting in 2,920 trajectories. Considering the 12 experiments (two mooring positions, two depths of release, three settling velocities, see **Table 1**), altogether 35,040 trajectories were calculated. A time step of 1 h was used for the trajectory calculation, and thus hourly positions and corresponding temperature and salinity values were stored. A sensitivity test with smaller time steps revealed that a time step of 1 h is sufficient.

With this procedure, some assumptions and simplifications are made. By using the daily averaged velocity field, fluctuations on time scales less than a day are neglected. Note also that tides are not explicitly simulated in the FESOM configuration used in this study. Some Lagrangian codes include sub-grid scale turbulence by either adding a random velocity or by adding a random displacement of the particle position (e.g., Döös et al., 2011, 2017). This was not done in our study, which adds to the uncertainty in our experiments. Nonetheless, meso-scale variability is well reproduced in the ocean-sea ice model, as

¹Since we perform a backtracking particle method, the term “rising speed” would be more appropriate. However, in the literature, the term “sinking velocity” or “settling velocity” is commonly used.

shown by Wekerle et al. (2017). Using constant settling velocities also increases the uncertainties in our calculations, which will be further discussed in section 4.4.

To quantify the spatial structure of the simulated catchment area, particle positions at the sea surface were binned into a spatial grid and then divided by the total number of particles to determine the fraction of collected particles originating from each grid box.

2.4. Measurements of Settling Velocities

During expedition PS99.2 with RV Polarstern to Fram Strait in summer 2016, intact aggregates were sampled using a marine snow catcher (MSC). On board, their settling velocities as well as size and composition were measured. The aggregates were individually transferred to a vertical flow chamber (Ploug et al., 2010) that was filled with GF/F filtered seawater collected from the same MSC and kept at *in situ* temperature. The x-, y-, and z-axis of each aggregate was measured in the vertical flow system using a horizontal dissection microscope and an ocular. The volume was thereafter calculated assuming an ellipsoid form, which was used to calculate the equivalent spherical diameter. To measure the sinking velocity, aggregates were placed in the middle of the flow chamber and upward flow was increased until the aggregate was floating one diameter above the net. The sinking velocity was thereafter calculated by determining the flow speed three times, and dividing the average of these measurements by the area of the flow chamber.

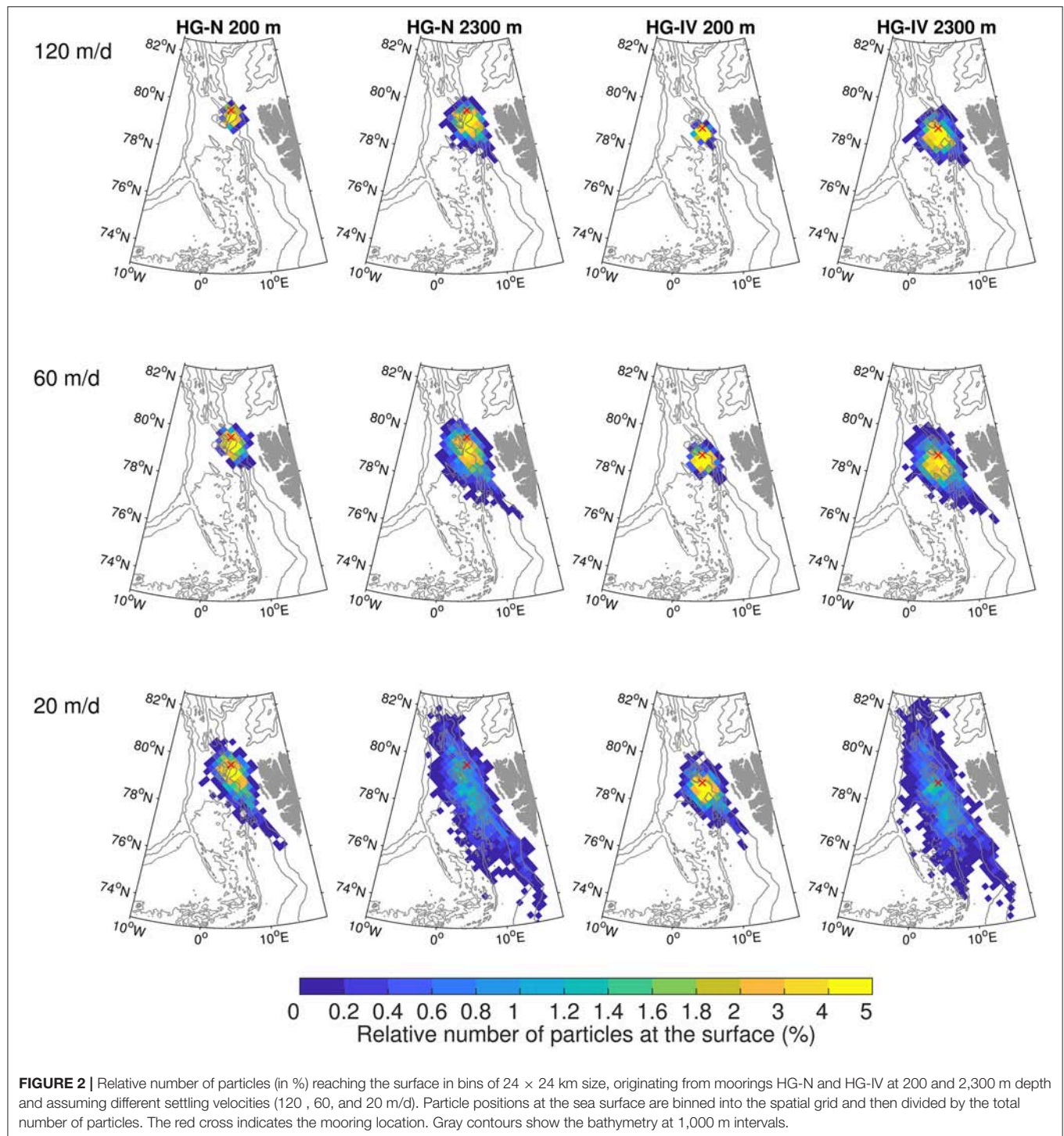
2.5. Calculation of Backward Sea Ice Trajectories

To determine sea ice source area and age of sea ice arriving in Fram Strait, a Lagrangian approach (ICETrack) was used that tracks sea ice backward in time using a combination of satellite-derived low resolution drift products. ICETrack has been used in a number of publications to examine sea ice sources, pathways, thickness changes and atmospheric processes acting on the ice cover (Krumpen et al., 2016; Damm et al., 2018; Peeken et al., 2018). The tracking approach works as follows: An ice parcel is tracked backward in time on a daily basis starting at Fram Strait. Tracking is stopped if (a) ice hits the coastline or fast ice edge, or (b) ice concentration at a specific location drops below 20% and we assume the ice to be formed.

2.6. Sea Ice Concentration Data

A sea ice concentration product provided by CERSAT is used in this study. It is based on 85 GHz SSM/I brightness temperatures, applying the ARTIST Sea Ice (ASI) algorithm. The product is available on a 12.5 × 12.5 km grid (Ezraty et al., 2007).

We use a weighted mean approach to estimate the sea ice coverage of the simulated catchment area. First, particle positions at the sea surface of all trajectory calculations conducted daily for the time period 2002–2009 are binned into the 12.5 × 12.5 km grid. As described in section 2.3, this amounts to altogether 2,920 trajectories per experiment, resulting in a climatological two-dimensional probability distribution for particle origin. Second, the ice coverage



of the catchment area for each month of the time period 1998–2016 is computed by weighting the ice concentration of a grid box with the number of particles that reach the surface in that box. Using these probability distributions for calculating weighted means for sea ice coverage provides a more realistic estimate than simply integrating the surface

property evenly over the areal extent of the catchment area.

2.7. Chlorophyll Concentration Data

Ocean color technique exploits the electromagnetic radiation emerging from the sea surface at different wavelengths of

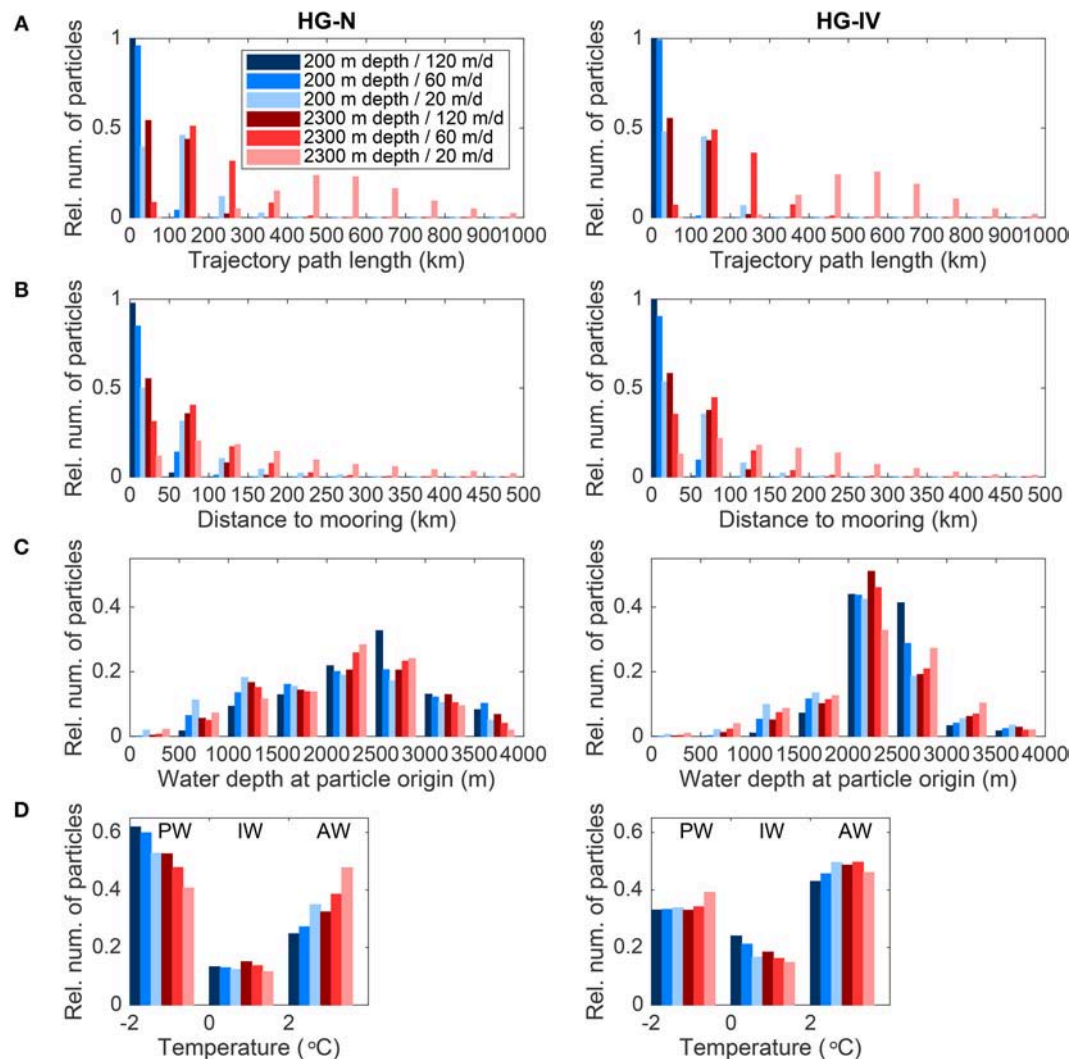


FIGURE 3 | Histograms of (A) travel path length in km, (B) distance in km between particle location at the surface and sediment traps, (C) water depth at the particle origin and (D) temperature at the particle surface position for sediment traps (left) HG-N and (right) HG-IV, different depths of particle release (200 and 2,300 m) and settling velocities (120, 60, and 20 m/d). Abbreviations PW, IW, and AW stand for water masses Polar Water ($T < 0^{\circ}\text{C}$), Intermediate Water ($0^{\circ}\text{C} < T < 2^{\circ}\text{C}$) and Atlantic Water ($T > 2^{\circ}\text{C}$), respectively.

the visible wavelength region. The spectral variability of this signal defines the so called ocean color which is affected by the presence of phytoplankton. By comparing reflectances at different wavelengths and calibrating the result against *in-situ* measurements, an estimate of chlorophyll content can be derived. The Climate Change Initiative (CCI) of the European Space Agency (ESA) is a 2-part program aiming to produce “climate quality” merged data records from multiple sensors. The Ocean Color project within this program has a primary focus on chlorophyll in open oceans, using the highest quality of radiation measurements and merging process to date. This uses a combination of band-shifting to a reference sensor and temporally-weighted bias correction to align independent sensors into a coherent and minimally-biased set of reflectances.

These are derived from standard level 2 products, calculated by the best-in-class atmospheric correction algorithms.

For the Arctic Ocean, the ESA Ocean Color CCI Remote Sensing Reflectance (merged, bias-corrected) data are used to compute surface chlorophyll-a concentration with a spatial resolution of 1 km^2 using the regional OC5ci chlorophyll algorithms. The Remote Sensing Reflectance data are generated by merging the measurements from SeaWiFS, MODIS-Aqua and MERIS sensors and realigning the spectra to that of the SeaWiFS sensor. The chlorophyll-a concentration is estimated from the OC5ci algorithm, a combination of the Case 1 OCI (Hu et al., 2012) and the Case 2 OC5 (Gohin et al., 2008) algorithms, developed at PML (Plymouth Marine Laboratory) within the Copernicus Marine Environment

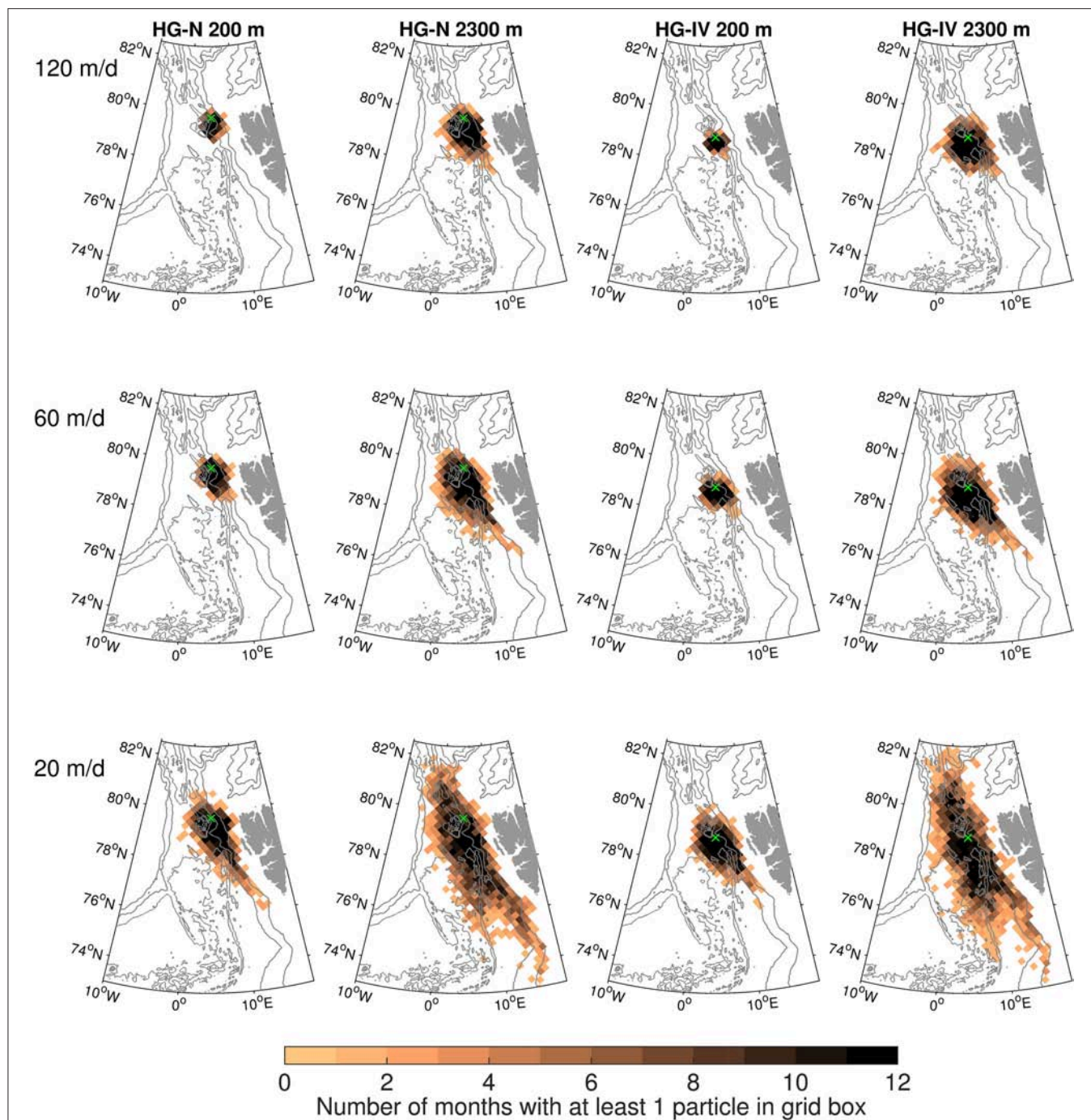


FIGURE 4 | Seasonal distribution of the catchment area for sediment traps HG-N and HG-IV, different depths of particle release (200 and 2,300 m) and settling velocities (120, 60, and 20 m/d): For each grid box of size 24×24 km, the number of months is shown in which at least one particle reaches the surface. The green cross indicates the mooring location. Gray contours show the bathymetry at 1,000 m intervals.

Monitoring Service (CMEMS). Units are expressed in mg m^{-3} .

As in the case of sea ice coverage described above, we compute the chlorophyll-a content of the simulated catchment area as a weighted mean. Again, the catchment area computed

from all trajectories calculated daily for the time period 2002–2009 is used. First, the chlorophyll-a data is interpolated to the sea ice grid (12.5×12.5 km resolution). Second, the chlorophyll-a concentration of a grid box is weighted with the number of particles that reach the surface in that box. As

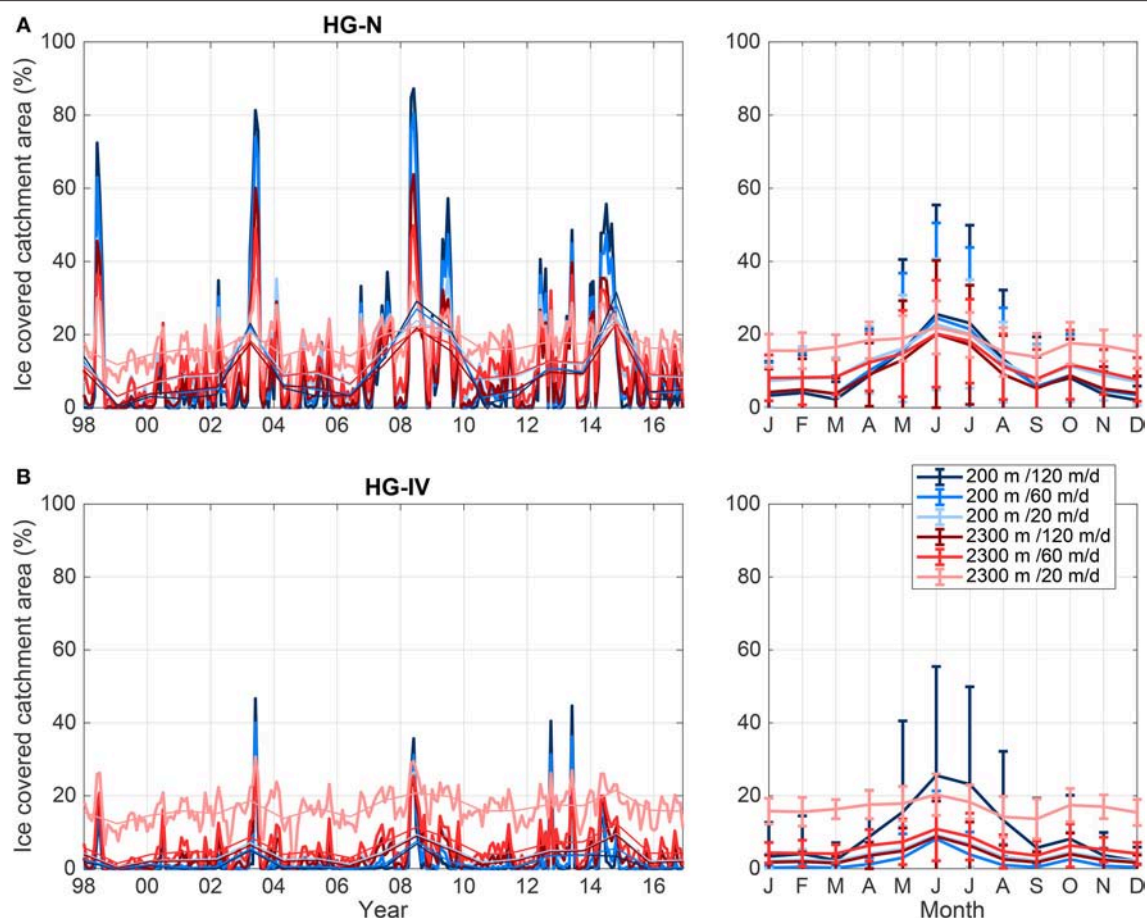


FIGURE 5 | Monthly mean (thick lines) and annual mean (thin lines) ice coverage of the catchment area (in %) of sediment traps **(A)** HG-N and **(B)** HG-IV for the time period 1998–2016 (left) and its seasonal cycle (right). Error bars in the right panel show the standard deviation of the monthly mean values.

monthly means of chlorophyll-a concentration is available for the time period 1998–2016, we obtain a 19-year long time-series.

3. RESULTS

3.1. Catchment Area of Particles Advected by Ocean Currents

Pathways of 14 particles released at HG-N ($4^{\circ}30.36'E/79^{\circ}44.39'N$) in 2300 m depth from 1 to 14 July 2009 sinking with a speed of 20 m/d are shown in **Figure 1C**. Particles travel distances between 540 and 950 km, and some of them reach the surface as far south as $\sim 74.4^{\circ}N$. Most particles originate from south of the mooring position, indicating that they are carried by the northward flowing WSC. The particle trajectories exhibit strong eddying motions driven by the eddying velocity field, as seen in a snapshot of simulated velocity from 1 July 2009 (**Figure 1B**).

All particle positions at the sea surface are binned into a grid with a spacing of 24×24 km. The percentage of particles originating from each grid box for each of the 12 experiments

listed in **Table 1** is shown in **Figure 2**. For both moorings, HG-IV and HG-N, the simulated catchment area (here defined as the area where at least one particle reaches the surface) is larger the deeper the trap and the slower the settling velocity. This is expected since particles stay in the water column for a longer time period and are thus exposed to a greater extent to the currents. For all experiments, most particles originate from southeast of the mooring locations, which shows that they were carried by the northward flowing WSC. Particularly in the experiment with the deep trap and slow sinking rate (2,300 m depth and 20 m/d), the pattern of particle distribution reveals the two branches of the WSC, the inshore WSC located mainly between the 1,000 and 2,000 m isobaths, and the offshore branch that mainly follows the Knipovich Ridge. This is even more distinct for particles released at mooring HG-IV than at HG-N. Some of the particles originate from north of the mooring location, indicating the influence of the EGC and of the dynamic eddy field that leads to random movement of particles.

The trajectory path length is, as expected, highest in experiments 2,300 m depth/20 m/d, and reaches up to 1,000 km (**Figure 3A**). The mean/median path length in these experiments amounts to 560/550 km and 540/530 km in the case of HG-IV and

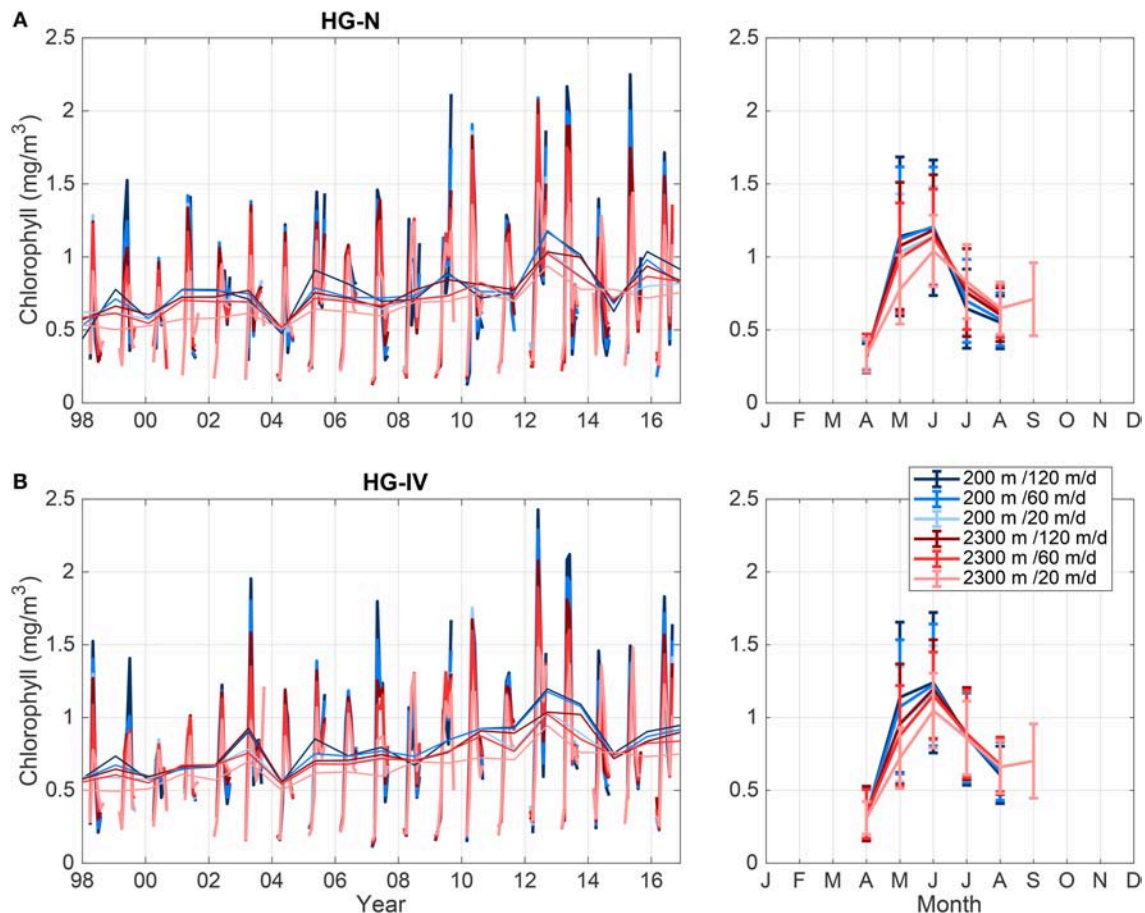


FIGURE 6 | Monthly mean (thick lines) and summer mean (thin lines) chlorophyll-a distribution of the catchment area (mg m^{-3}) of sediment traps **(A)** HG-N and **(B)** HG-IV for the time period 1998–2016 (left) and its seasonal cycle (right). Error bars in the right panel show the standard deviation of the monthly mean values. Note that data coverage is limited to the summer months.

HG-N, respectively. Particles reach the surface as far as $\sim 74^\circ\text{N}$ and $\sim 82^\circ\text{N}$, with distances to the mooring locations of more than 400 km (**Figure 3B**). Mean / median distances to the mooring locations HG-IV and HG-N are 160/140 and 190/150 km, respectively. With a faster settling velocity of 60 m/d, trajectory path lengths up to 400 km are reached, and mean/median values amount to 200/190 km (HG-IV) and 190/180 km (HG-N). In the experiments with the shallow trap (200 m depth) and fast sinking rate of 120 m/d, the trajectory path length does not exceed 100 km, and mean / median trajectory path lengths of 18/15 km (HG-IV) and 22/19 km (HG-N) are reached.

For mooring HG-IV, most particles (the range is 69–90% in all 6 experiments) originate from areas with water depth deeper than 2,000 m, whereas for mooring HG-N, the percentage of particles originating from shallower regions is higher. It is noticeable, however, that for both moorings, almost no particles originate from shallow areas with depths between 0 and 500 m (**Figure 3C**).

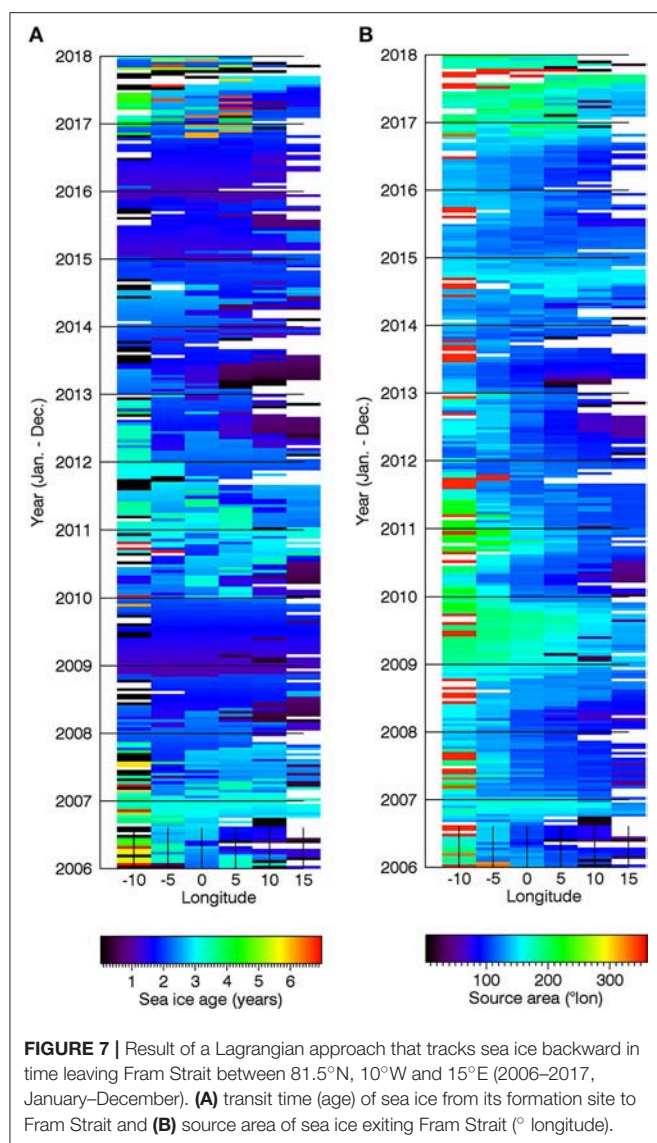
A large fraction of particles trapped in mooring HG-N originates from areas characterized by PW (defined as waters with $T < 0^\circ\text{C}$) at the surface (39–63% in all 6 experiments), and a smaller fraction of particles originates from areas with

AW (defined as waters with $T > 2^\circ\text{C}$) at the surface (24–49%) (**Figure 3D**). This is opposite for mooring HG-IV with less particles originating from areas with PW (34–41%), and more particles originating from areas with AW (42–49%). Note that mooring HG-N is only located ~ 80 km northwest of HG-IV, but this difference already leads to differences in surface water mass properties of particles.

The seasonal variation in the particle distribution at the surface is rather low for all 12 experiments (**Figure 4**). Moreover, the spatial extent of the simulated catchment area does not vary strongly during the year and also on inter-annual timescales (**Figures S1, S2**). In fact, in terms of spatial extent, the amplitude of the seasonal cycle is lower than the difference between the 12 experiments.

3.2. Sea Ice Coverage and Chlorophyll-A Distribution in the Catchment Area

The ice coverage of the simulated catchment area shows significant inter-annual variability (**Figure 5**). In most years, it reaches values of up to $\sim 20\%$ for mooring HG-N and slightly lower values for mooring HG-IV. This rather low ice coverage



indicates that large parts of the simulated catchment area of both moorings are located in the marginal ice zone characterized by low ice concentration or in areas characterized by Atlantic Water. However, in some years a particularly high ice coverage occurs (years 1998, 2003, 2008, 2009, 2012, 2013, and 2014). The seasonal cycle reveals a maximum in June, which will be further discussed in section 4.3.

In addition to sea ice coverage, we also investigate the chlorophyll-a content of the simulated catchment area (Figure 6). Since ocean color measurements depend on light, they only provide values for open water and for the summer period (May to August). The catchment area obtained in the experiment with 2300 m water depth and 20 m/d settling velocity extends further to the south than all other experiments, and thus values up to September are available. The maximum chlorophyll-a concentration in the catchment area occurs in June in all experiments. The summer mean time series shows

that there is significant inter-annual variability. For the HG-IV and HG-N catchment areas, chlorophyll-a concentration has increased in the recent years. The trend in summer chlorophyll-a concentration ranges between 0.014 and 0.02 mg/m³/year in the six HG-IV experiments, and between 0.017 and 0.022 mg/m³/year in the six HG-N experiments. This is consistent with the studies by Nöthig et al. (2015) and Cherkasheva et al. (2014). In particular, Cherkasheva et al. (2014) found a positive trend in Fram Strait chlorophyll-a concentration of 0.015 mg/m³/year for the years 1998–2009, and explained this with an increase in sea surface temperature and a decrease in Svalbard coastal ice.

The annual time series shows that years with high chlorophyll-a content in the simulated catchment area do not coincide with years with high sea ice coverage. This is expected since chlorophyll-a measurements are only available for ice-free waters. However, concerning the seasonal cycle, the maximum in sea ice coverage and chlorophyll-a concentration both occurs in June.

3.3. Catchment Area of Particles Carried by Sea Ice

The ice coverage of the simulated catchment areas of moorings HG-N and HG-IV is ~20%, indicating that both moorings are located in the marginal ice zone. Hence, sea ice plays an important role for vertical particle fluxes. Sea ice melting rates in Fram Strait are high due to the interaction of sea ice with warm Atlantic Water, and thus particles trapped by sea ice or organisms growing underneath sea ice contribute to vertical particle fluxes. How much sea ice contributes to sedimentation in Fram Strait depends on age, source area and thickness of sea ice leaving the Arctic Ocean (Eicken et al., 2000; Wegner et al., 2017). In particular, ice formed in the shallow waters of the Siberian Shelf Sea can contain large fractions of biogeochemical material taken up by suspension freezing (Dethleff and Kempema, 2007).

Figure 7 shows the inter-annual and seasonal variability in age (a) and source area (b) of sea ice exiting Fram Strait between 10° W and 15° E from 2006 to 2017, calculated by tracking sea ice backward in time (section 2.5). During some years, sea ice export is characterized by ice originating from the Laptev Sea (100°E–140°E) only. During other years, Fram Strait outflow is fed by the Beaufort Gyre (>160°E) or Kara Sea (60°E–100°E). Also the age of sea ice differs significantly between years. In addition, there is a strong gradient across Fram Strait: Ice leaving Fram Strait near Svalbard originates more likely from the Kara or Barents Sea and is younger. In contrast, ice that exits through western Fram Strait comes more likely from the Laptev and Beaufort Sea and contains a higher fraction of Multi-Year Ice.

4. DISCUSSION

4.1. Origin of Particles

The particle trajectory experiments showed that particles originate mostly from areas south and southeast of the moorings. They originate mostly from deep areas, with almost no particles originating from shallow areas with depths between 0 and 500 m (Figure 3C). Regarding the simulated catchment areas, this shallow area corresponds to the Svalbard and Barents Sea shelf

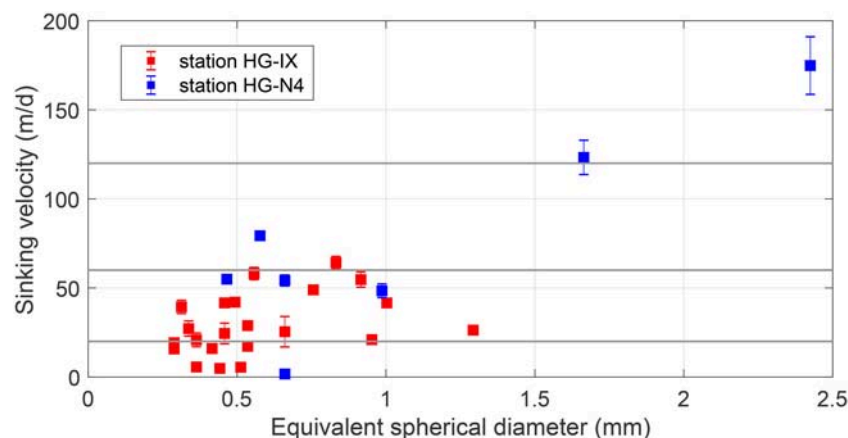


FIGURE 8 | Sinking velocity, its standard deviation and the associated equivalent spherical diameter of aggregates, measured during RV Polarstern expedition PS99.2 in summer 2016 at stations HG-IX (close to the Molloy Deep) in 80 m depth and HG-N4 in 20 m depth. Gray lines indicate settling velocities of 20, 60, and 120 m/d used in this study.

region. Thus, the strong WSC appears to present a barrier that prevents particles from the shelf to reach central Fram Strait.

However, particles are not only advected by ocean currents, but also carried by sea ice. The ice coverage of the simulated catchment area is not negligible (**Figure 5**), hence both moorings are located in the marginal ice zone. Hebbeln and Wefer (1991), based on mooring measurements, observed maximum particle fluxes in the marginal ice zone of Fram Strait. The ice tracking analysis revealed that sea ice transported particularly through eastern Fram Strait originates mostly from the Siberian Shelf Seas. Since sea ice formation can occur close to the sea floor in these regions, it can entrain sediments which strongly contribute to particle fluxes in Fram Strait. This is supported by high sea ice melting rates in the Fram Strait marginal ice zone, which results from the interaction with warm AW. Another, indirect way to reveal the origin of particles is the analysis of their composition, e.g., the seasonal and regional variability of clay minerals, as done by Berner and Wefer (1994). In the Fram Strait marginal ice zone / WSC area, the authors found both a high / medium lithogenic content, pointing to the release of ice-rafted material by melting, and koalinite/illite ratios related to high plankton productivity, respectively.

4.2. Seasonality of Particle Catchment Areas

The particle trajectory calculation revealed that the seasonal variation in the particle distribution at the surface is rather low for all 12 experiments (**Figure 4** and **Figures S1,S2**). As shown by observations and model studies, the WSC is stronger in winter than in summer, with higher eddy activity during winter season (Beszczynska-Möller et al., 2012; von Appen et al., 2016; Wekerle et al., 2017). This might lead to a compensating effect, with more particles trapped in eddies despite stronger currents during winter time, overall resulting in a weak seasonal variation of the catchment area.

However, by starting one trajectory calculation per day, we cannot inherently account for differences in particle production

rate, which varies considerably during the year. First, the sea ice coverage of the simulated catchment area is highest in summer (the reason for this will be discussed in the next section), and also melting of sea ice is highest during this season. As described above, sea ice can originate from the shallow Siberian shelf seas, carrying sedimentary material that contributes to vertical particle fluxes. Second, the chlorophyll-a concentration of the simulated catchment area reaches its maximum in summer as well ². We suppose that the timing of the maximum bloom is correlated with the highest export efficiency. Although knowing that secondary effects (e.g., ingestion by zooplankton) play a dominant role on particle fluxes, we can expect high particle fluxes measured by the sediment traps in summer and early autumn (depending on the settling velocities, it takes days or even up to months until particles reach the trap). In fact, a sedimentation study conducted in the central Fram Strait during the years 2000–2005 revealed increased vertical particle fluxes in August/September and May/June (Bauerfeind et al., 2009).

4.3. Summer Sea-Ice Maxima of the Simulated Catchment Area

The ice coverage of the simulated catchment areas shows strong seasonal variability (**Figure 5**). Surprisingly, the highest ice coverage of the catchment area of both HG-N and HG-IV occurs in the summer months, particularly in June. What is the reason for this summer maximum? Tsukernik et al. (2010) showed that anomalies in ice export through Fram Strait can be explained by an east-west dipole pattern of sea level pressure anomaly with centres located over the Barents Sea and Greenland, associated with anomalous meridional winds across Fram Strait. Moreover, Smedsrud et al. (2017) used mean sea level pressure anomalies across Fram Strait to compute geostrophic winds, and a comparison with sea ice drift speed obtained from satellite measurements revealed a high correlation. An almost

²Note that the satellite measurements cover only the surface layers, a deep chlorophyll-a maximum would not be detected.

linear relationship of sea ice export through Fram Strait and wind speed was also shown by Harder et al. (1998) in model experiments. This relationship between sea level pressure and ice export is significant in the winter months, but not in the summer months (Tsukernik et al., 2010). Thus, in the summer, sea ice can move more freely into central Fram Strait (where HG-N and HG-IV are located) and is not as strongly restricted to the western part of Fram Strait as in the winter months. Potentially also the seasonal difference in the strength of the AW recirculation can play a role. The stronger westward flow of AW in winter may inhibit sea ice eastward motion.

4.4. What Is a Realistic Estimate of Settling Velocities?

In our study, we apply a range of constant settling velocities for the trajectory calculation, ranging between 20 and 120 m/d. Settling velocities commonly used in particle trajectory studies range from 50 to 200 m/d (Siegel and Deuser, 1997; Waniek et al., 2000; Siegel et al., 2008; Abell et al., 2013). The choice of values used in this study stems from field measurements conducted in Fram Strait in summer 2016, described in section 2.4. **Figure 8** shows settling velocities and associated equivalent spherical diameter measured for *in situ* collected marine snow at locations HG-IX (close to the Molloy Deep) at 80 m depth and HG-N at 20 m depth. At the Molloy Deep, 22 samples were analyzed, revealing minimum and maximum settling velocities of 5 and 64 m/d, with a mean value of 30 m/d. At location HG-N, the spread of measured values is larger. 7 samples were analyzed, and settling velocities ranged between 2 and 175 m/d, with a mean value of 77 m/d. Particle trajectory experiments conducted in this study with settling velocities of 20 and 60 m/d are thus more realistic than the case with 120 m/d.

A more realistic approach than using constant settling velocities is the application of the Stokes Law. It relates the particle sinking velocity to the density difference of particle and sea water as well as particle size, as e.g., done in a study by Qiu et al. (2014). However, particle density and size are parameters that are difficult to measure in practice, and furthermore a wide range of particles with different size and density classes occurs in the water column. Processes like fragmentation, aggregation, consumption, and microbial activity can also change the sinking velocity as particles descent through the water column (Siegel et al., 1990). In particular, field observations by Berelson (2001) and Fischer and Karakaş (2009) showed that settling velocities increase with depth. This was explained by carbon loss during degradation in the epi- and mesopelagic which increases particle densities, and by an increase in ballast minerals with depth. Furthermore, the vertical ocean velocity can impact the pathway of the sinking particle. In general, vertical velocities are much smaller than the particle settling velocities used in this study, and are hence neglected. However, vertical velocities associated with sub-mesoscale eddies or filaments can be significantly larger (>50 m/d, von Appen et al., 2018). Moreover, Fram Strait is characterized by a deep mixed layer in the winter months, associated with strong convection events. This also leads to high vertical velocities.

To conclude, settling velocities vary with depth, regionally, seasonally and inter-annually. Dedicated studies are required to analyse these processes.

5. CONCLUSIONS

In this study we developed a Lagrangian model to determine the catchment area of sediment traps attached to two moorings operated in central Fram Strait. The time-dependent velocity field of a high resolution, eddy resolving sea ice-ocean model was used to compute backward trajectories starting at the trap locations once per day for the time period 2002–2009. Remote sensing products (sea ice concentration and chlorophyll-a distribution) were used to characterize the simulated catchment area.

Our study shows that the extent of the catchment area is larger the deeper the trap and the slower the settling velocity. Particles advected with ocean currents originate mostly from south of the mooring sites, and show a wide spread (45–88% originate from distances larger than 50 km), indicating the influence of the northward flowing WSC, but also of the vigorous eddy field leading to random motion of particles. Particles trapped in mooring HG-N originate from surface areas mostly characterized by Polar Water. In contrast, the simulated catchment area of mooring HG-IV, which is located around 80 km south of HG-N, is mostly characterized by Atlantic Water. For both moorings, particles mostly originate from areas deeper than 500 m, and thus the Svalbard shelf does not play a major role as a source region. Sea ice concentration over the catchment area reaches up to 20%, and is highest in the summer months when the surface air pressure difference between Greenland and Svalbard is low, allowing sea ice to move more freely into central Fram Strait. Thus, particles carried by sea ice could potentially contribute to vertical particle fluxes measured by moorings HG-IV and HG-N. A sea ice backtracking method allowed us to determine the source area and age of sea ice advected through Fram Strait. Chlorophyll-a distribution over the simulated catchment area reaches its maximum in June, indicating that highest vertical particle fluxes are expected in the summer months. The catchment areas and integrated remote-sensing products defined in this study will provide a valuable time-series to interpret ongoing changes in pelagic-benthic coupling processes in the Fram Strait.

DATA AVAILABILITY

The backward particle trajectories are available at Pangaea (<https://doi.pangaea.de/10.1594/PANGAEA.895078>). All datasets used for sea ice tracking are compiled here: http://epic.awi.de/45411/1/AWI_ICETrack_ver2017Sep.pdf. Sea ice concentration data is available at <ftp://ftp.ifremer.fr/ifremer/cersat/products/gridded/psi-concentration/data/arctic/daily/netcdf/>. Chlorophyll-a data is available at http://marine.copernicus.eu/services-portfolio/access-to-products?option=com_csw&view=details&product_id=OCEANCOLOUR_ARC_CHL_L3_REP_OBSERVATIONS_009_069.

AUTHOR CONTRIBUTIONS

CW contributed the particle trajectory analysis and wrote most of the manuscript, TK contributed the sea ice tracking and ice coverage analysis, TD contributed the analysis of chlorophyll-a, MI contributed the analysis of measured settling velocities. CW, WJvA, and IS designed this study. All authors discussed the content of the manuscript and contributed to the interpretation of data and writing of the manuscript.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: <https://www.frontiersin.org/articles/10.3389/fmars.2018.00407/full#supplementary-material>

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APPENDIX: PARTICLE TRACKING ALGORITHM

The Lagrangian particle-tracking algorithm is based on the following equation:

$$\frac{d\mathbf{x}}{dt} = \mathbf{u}(\mathbf{x}, t), \quad (1)$$

where $\mathbf{x}$ is the 3D particle position and $\mathbf{u}$ is the 3D velocity field at the particle position. If we knew the particle position at time n , the position at time $n + 1$ will be

$$\mathbf{x}(t_{n+1}) = \mathbf{x}(t_n) + \int_{t_n}^{t_{n+1}} \mathbf{u}(\mathbf{x}, t) dt. \quad (2)$$

We use the Euler method to compute the particle position at time $t_{n+1} = t_n + \delta t$:

$$\mathbf{x}(t_{n+1}) = \mathbf{x}(t_n) + \mathbf{u}(\mathbf{x}(t_n), t_n) \delta t. \quad (3)$$



Net Community Production and Carbon Exchange From Winter to Summer in the Atlantic Water Inflow to the Arctic Ocean

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The eastern Fram Strait and area north of Svalbard, are influenced by the inflow of warm Atlantic water, which is high in nutrients and CO₂, influencing the carbon flux into the Arctic Ocean. However, these estimates are mainly based on summer data and there is still doubt on the size of the net ocean Arctic CO₂ sink. We use data on carbonate chemistry and nutrients from three cruises in 2014 in the CarbonBridge project (January, May, and August) and one in Fram Strait (August). We describe the seasonal variability and the major drivers explaining the inorganic carbon change (C_{DIC}) in the upper 50 m, such as photosynthesis (C_{BIO}), and air-sea CO₂ exchange (C_{EXCH}). Remotely sensed data describes the evolution of the bloom and net community production. The focus area encompasses the meltwater-influenced domain (MWD) along the ice edge, the Atlantic water inflow (AWD), and the West Spitsbergen shelf (SD). The C_{BIO} total was 2.2 mol C m⁻² in the MWD derived from the nitrate consumption between January and May. Between January and August, the C_{BIO} was 3.0 mol C m⁻² in the AWD, thus C_{BIO} between May and August was 0.8 mol C m⁻². The ocean in our study area mainly acted as a CO₂ sink throughout the period. The mean CO₂ sink varied between 0.1 and 2.1 mol C m⁻² in the AWD in August. By the end of August, the AWD acted as a CO₂ source of 0.7 mol C m⁻², attributed to vertical mixing of CO₂-rich waters and contribution from respiratory CO₂ as net community production declined. The oceanic CO₂ uptake (C_{EXCH}) from the atmosphere had an impact on C_{DIC} between 5 and 36%, which is of similar magnitude as the impact of the calcium carbonate (CaCO₃, C_{CALC}) dissolution of 6–18%. C_{CALC} was attributed to be caused by a combination of the sea-ice ikaite dissolution and dissolution of advected CaCO₃ shells from the south. Indications of denitrification were observed, associated with sea-ice meltwater and bottom shelf processes. C_{BIO} played a major role (48–89%) for the impact on C_{DIC}.

Keywords: Atlantic water, sea ice melt water, Fram Strait and Svalbard shelf, ocean CO₂ sink, denitrification, primary production, ocean acidification

INTRODUCTION

The Arctic Ocean is changing, where warming, decreasing sea-ice extent, thinning of ice and increased freshwater addition have been reported recently (e.g., IPCC, 2007; Rabe et al., 2009; Morrison et al., 2012; Pachauri et al., 2014). The characteristics of the Arctic ice cover has changed from thick multi-year sea ice to thinner first- or second-year sea ice (e.g., Serreze et al., 2007;

Rabe et al., 2009; Granskog et al., 2016; Rösel et al., 2018). As a result of all these changes, surface-water stratification, primary production, carbon export and ocean CO₂ uptake are expected to change (e.g., ACIA, 2005; AMAP, 2013, 2018; Slagstad et al., 2015; Fransson et al., 2017).

Part of the changes within the Arctic Ocean originates from trends already observed in the Pacific and Atlantic inflow waters (e.g., Jones et al., 2003; Shadwick et al., 2011b). One of the main deep gateways to the Arctic Ocean is the Fram Strait, where the inflow (eastern Fram Strait) into the Arctic consists of the relatively warm and salty Atlantic water (AW; e.g., Schauer et al., 2008). Recent findings show warming of the inflowing Atlantic water into the Arctic Ocean (e.g., Schauer et al., 2008; Beszczynska-Möller et al., 2012). The warmer inflowing water also affects the Arctic Ocean, and waters around Svalbard and in the Barents Sea, where less sea ice in summer has been reported (e.g., Årthun et al., 2012; Onarheim et al., 2014; Carmack et al., 2015), which will have implications for the biogeochemical processes and greenhouse-gas exchange (Damm et al., 2011; Fransson et al., 2017). The inflowing Atlantic water supplies nutrients, which is favorable for primary production, with consequences for the marine ecosystem (e.g., Fransson et al., 2001; Torres-Valdés et al., 2013; Haug et al., 2017). Moreover, the Atlantic water also transports inorganic carbon into the Arctic Ocean (e.g., Anderson et al., 1998; Fransson et al., 2001). Most of the atmospheric CO₂ uptake occurs as the Atlantic water is cooled, during its way north along the Norwegian coast, and consequently the AW contains high anthropogenic CO₂ content (e.g., Sabine et al., 2004; Olsen et al., 2006; Vázquez-Rodríguez et al., 2009). In addition, Chierici (1998) found that although most of the CO₂ uptake occurred before the AW enters the Arctic Ocean, it was due to processes within the Arctic, such as transport by brine shelf plumes that acted to sequester CO₂ into deep waters.

Ocean CO₂ uptake, as an effect of increased atmospheric CO₂ due to the increased emission of CO₂ from human activities (e.g., burning of fossil fuel, deforestation), is causing ocean acidification (OA) in the Arctic Ocean (e.g., AMAP, 2013, 2018). In addition, reported release of methane and CO₂ from the Siberian shelves may also contribute to OA in the Arctic (e.g., Semiletov et al., 2012; Anderson et al., 2017; Qi et al., 2017). With continued warming, freshening and changes to primary production, the rate of ocean acidification is expected to increase (AMAP, 2013, 2018). This will have consequences for the carbon export, ocean CO₂ uptake, anticipated consequences for the marine organisms and ecosystems around the Svalbard Archipelago. For example, several studies suggest that increased CO₂ in the Arctic Ocean would increase and stimulate spring bloom production (Holding et al., 2015; Sanz-Martin et al., 2018).

The seasonal variability in physical variables (salinity, temperature, and water masses), nutrients and chlorophyll a concentrations is well known and thoroughly described from the CarbonBridge cruises in Randelhoff et al. (2018). In this study, we focus on the seasonal variability of the carbonate chemistry parameters from surface to 800 m, such as dissolved inorganic carbon (DIC), total alkalinity (AT), pH, fugacity of

CO₂ ($f\text{CO}_2$), and aragonite saturation (Ω_{Ar}). Especially, little is known about the seasonal variability of these parameters as well as the ocean acidification state and change in the Atlantic water inflow to the Arctic Ocean. In addition, we use the semi-conservative tracer N*, which indicates deviations from a conservative nitrogen to phosphate behavior during photosynthesis and gives an indication of effects due to denitrification and nitrogen fixation in our study area. Here, we explore the components explaining the DIC change, such as biological DIC (e.g., CO₂) uptake (by the nitrate loss from pre-bloom values in January), the net DIC exchange with the surrounding environment, such as the air-sea CO₂ flux, and the formation and dissolution of calcium carbonate in three domains: the ice-melt affected domain, the Atlantic core-water domain, and the shelf domain. Our estimates are compared with other studies in the same area and polar regions in general.

STUDY AREA

The study area (79°N–80°N, 4°E–10°E) that includes the eastern Fram Strait, west and north of Svalbard and main surface currents are shown in **Figure 1**. The eastern Fram Strait and western shelf off Spitsbergen are affected by the warm and saline Atlantic water (AW), transported in the West Spitsbergen Current (WSC; e.g., Cottier et al., 2005). This current brings heat, nutrients, and carbon into the Arctic Ocean and the Svalbard area (e.g., Randelhoff et al., 2018; Renner et al., 2018). In the western part of the WSC, sea ice forms in winter and seasonal heating creates a surface layer of meltwater. In 2014, the area north of Svalbard was covered by sea ice throughout the study (**Figures 2A–D**). In our main study region between 79 and 79.5°N, and 4–10°E, the sea-ice boundary (>10% of sea ice) was found at about 4°E (**Figure 2A**). This limited the ship's ability to move further west in January and May 2014. In the area close to Svalbard, shelf water and shelf processes dominated, resulting in a mixture of AW, coastal water and locally formed water such as transformed Atlantic water (e.g., Cottier et al., 2005; Randelhoff et al., 2018).

Three different domains are defined based on the surface-water characteristics in January and on topography. The meltwater domain (MWD) includes the western and northern parts of the study area that are influenced by fresher surface water in spring and summer due to sea-ice melt from the sea ice formed the previous winter. The Atlantic core-water domain (AWD) is dominated by the AW and the shelf domain (SD) is located on the shelf near West Spitsbergen (**Figure 1**).

MATERIALS AND METHODS

Sampling

The data of carbonate chemistry and inorganic nutrients were collected during four cruises in 2014 (**Figure 1** and **Supplementary Table S1**). Three cruises were conducted as

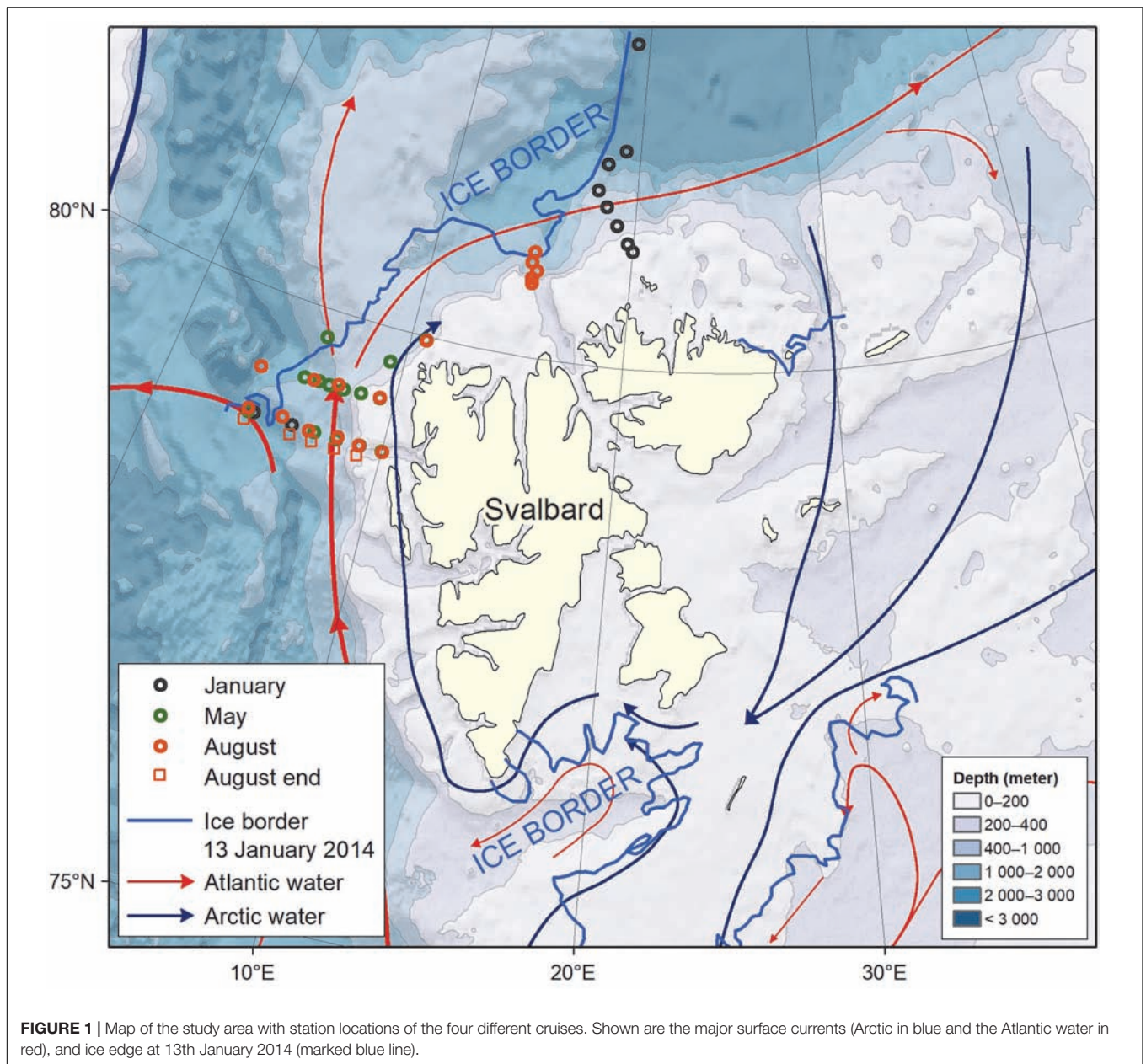


FIGURE 1 | Map of the study area with station locations of the four different cruises. Shown are the major surface currents (Arctic in blue and the Atlantic water in red), and ice edge at 13th January 2014 (marked blue line).

part of the CarbonBridge project (January, May, and August). A Fram Strait cruise was conducted in late August 2014, to obtain information on the Atlantic water inflow. The data analysis concentrates on two sections with the largest seasonal coverage on the eastern shelf of the Fram Strait (January, May, beginning of August and end of August) between ~ 79 – 79.5°N and 4 – 10°E .

Water samples were collected from 8-L Niskin bottles mounted on a General Oceanics 12-bottle rosette equipped with a Conductivity-Temperature-Depth sensor system (CTD, Seabird SBE-911 plus). Water samples were collected at a total of 11 to 14 depths, from surface to 800 m depth (or at bottom) at each station, with the highest resolution in the upper 100 m. From these samples inorganic nutrients, nitrate (NO_3^-), phosphate

(PO_4^{3-}), silicic acid [$\text{Si}(\text{OH})_4$], and total DIC and total AT were determined.

Section figures and surface interpolation from weighted-gridding were performed in Ocean Data View software version 4.7 (Schlitzer, 2015).

Chemical Analyses

The DIC and AT were analyzed after the cruises at the Institute of Marine Research (IMR Tromsø, Norway) following the method described in Dickson et al. (2007). DIC was determined using gas extraction of acidified samples followed by coulometric titration and photometric detection using a Versatile Instrument for the Determination of Titration carbonate (VINDTA 3D, Marianda, Germany). The AT was

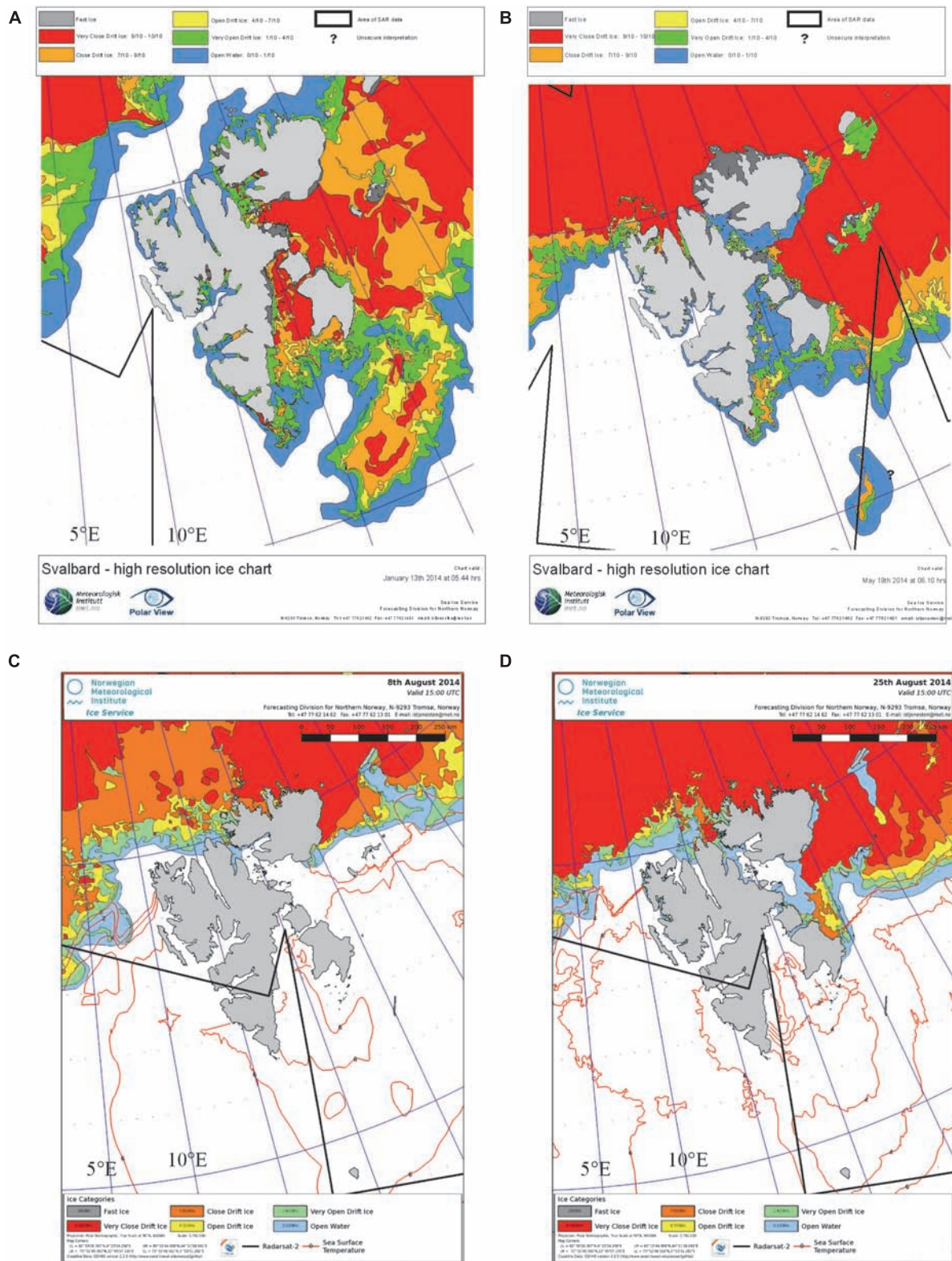


FIGURE 2 | Sea ice cover around Svalbard for selected dates during the four cruises: **(A)** 13th of January, **(B)** 19th of May, **(C)** 8th of August, and **(D)** 25th of August in 2014. Data is obtained from the Ice Service of the Norwegian Meteorological Institute (MET, <http://polarview.met.no/>) and use their ice chart color scheme for very open drift ice (1–4/10ths), open drift ice (4–7/10ths), close drift ice (7–10/10ths), and fast ice (10/10ths).

determined by potentiometric titration with 0.1 N hydrochloric acid using a Versatile Instrument for the Determination of Titration Alkalinity (VINDTA 3S, Marianda, Germany). Routine analyses of Certified Reference Materials (CRM, provided by A. G. Dickson, Scripps Institution of Oceanography, United States) ensured the accuracy of the measurements, which was better than ± 1 and $\pm 2 \mu\text{mol kg}^{-1}$ for DIC and AT, respectively.

Water samples for analysis of nutrients [$\text{NO}_2^- + \text{NO}_3^-$, Si(OH)_4 , PO_4^{3-}] were frozen until post-cruise analysis by standard methods (Grasshoff et al., 2009) using a Flow Solution IV analyzer from O.I. Analytical, United States. The analyzer was calibrated using reference seawater from Ocean Scientific International Ltd., United Kingdom. Three replicates were analyzed for each sample. Note that we refer to the NO_3^- concentration throughout the study, but it is actually the sum of $\text{NO}_2^- + \text{NO}_3^-$, since NO_2^- levels are considered to be low in this area (Codispoti et al., 2005).

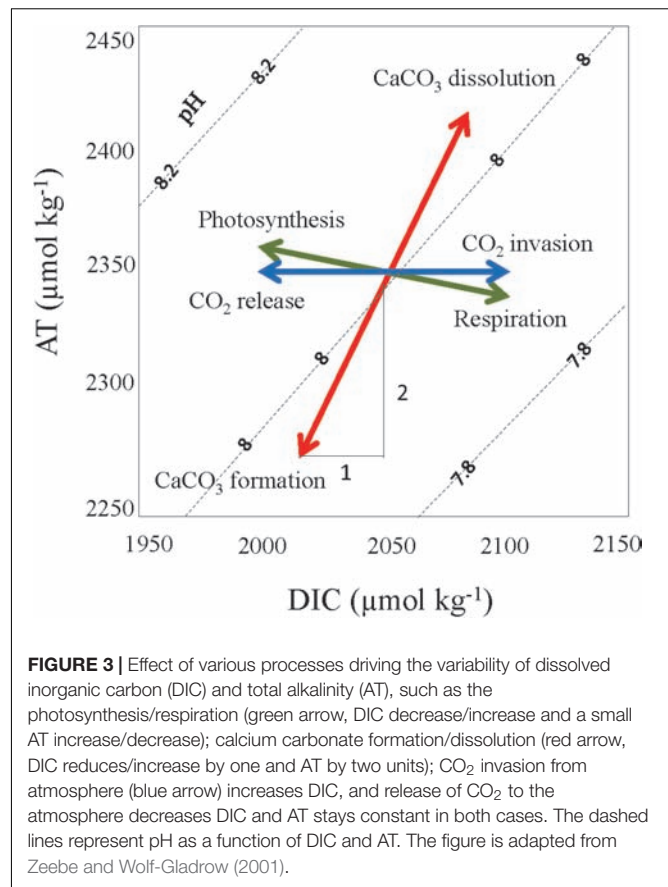
Calculations of the Carbonate System

We used AT, DIC, and nutrient concentrations as input parameters in a CO₂-chemical speciation model (CO2SYS program, Pierrot et al., 2006) to calculate other variables describing the carbonate chemistry, such as pH, fugacity of CO₂ ($f\text{CO}_2$), saturation state of calcium carbonate (Ω) for the two most common forms of aragonite (Ω_{Ar}) and calcite (Ω_{Ca}). The calculations are based on the carbonate system dissociation constants (K^*1 and K^*2) estimated by Mehrbach et al. (1973), modified by Dickson and Millero (1987) and the HSO_4^- dissociation constant from Dickson (1990).

Calcium carbonate (CaCO_3) saturation state (Ω) is commonly used to indicate a change in the CO₂ chemistry and the ocean acidification state, and indicates the dissolution potential for solid CaCO_3 , such as calcareous shells and skeleton of marine organisms. When $\Omega < 1$, solid CaCO_3 is chemically unstable and prone to dissolution (i.e., the waters are undersaturated with respect to the CaCO_3 mineral). In the Arctic Ocean, increased freshwater supply from sea-ice melt and river runoff have shown to decrease Ω (and provide a positive feedback on OA; Chierici and Fransson, 2009; Fransson et al., 2013, 2015). However, Ω is a chemical parameter showing the dissolution potential; most organisms require higher saturation state to grow due to the high energy demand of calcification. For example, the aragonite forming pteropod *Limacina helicina*, showed decreased calcification at Ω_{Ar} value of < 1.4 and that lower values had negative effects on the shell density and thickness (e.g., Comeau et al., 2009; Lischka and Riebesell, 2012; Bednaršek et al., 2014).

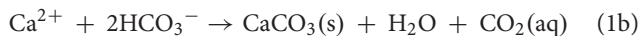
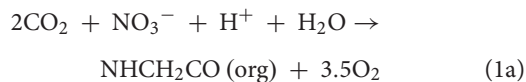
Calculation of Seasonal Drivers of the Carbonate System

The strength of the effects and direction of different drivers of the change of DIC are schematically summarized in Figure 3. Earlier studies have shown that biological processes, such as photosynthesis and respiration explain much of the observed seasonal changes of the carbonate system in the Arctic Ocean as well as on the air-sea CO₂ exchange (Fransson et al., 2001, 2017;



Chierici et al., 2011; Tynan et al., 2016). During photosynthesis, DIC and $f\text{CO}_2$ decrease, and pH and CaCO_3 saturation (Ω) increase. AT increases slightly during photosynthesis as a result of nitrate and hydrogen ion consumption when proteins are formed (Eq. 1a) but is less affected by photosynthesis than DIC (Figure 3). However, the AT change is twice as much as DIC during the production of calcium carbonate (Eq. 1b). This means that if CaCO_3 production occurs simultaneously with photosynthesis, both AT and DIC change, but if no CaCO_3 production takes place, only DIC changes. Thus, AT can give indications on the presence of CaCO_3 -forming organisms and the contribution of CaCO_3 formation in sea ice. Sea-ice melting and formation cause changes to the carbonate chemistry where CaCO_3 is formed inside the ice (Assur, 1958) producing high CO₂-rich brine, which is rejected to underlying water (e.g., Rysgaard et al., 2007; 2013; Fransson et al., 2013, 2017). The solid CaCO_3 can be trapped in the ice until ice melting when it dissolves in the water (e.g., Rysgaard et al., 2012, 2013). The CO₂-rich brine is considered an important process for transport and sequestering of CO₂ in the Arctic Ocean to depth (e.g., Chierici, 1998; Fransson et al., 2013; Rysgaard et al., 2013). In our study area, sea ice is formed in the western part of the Fram Strait and in the area north of Svalbard while the AW inflow keeps the West Spitsbergen shelf ice free. Precipitation of CaCO_3 from the brine produces CO₂ (aq) and reduces AT

in the brine (Eq. 1b), where Ca^{2+} and HCO_3^- denote the concentration of the calcium ions (Ca^{2+}) and the bicarbonate ions (HCO_3^-) that are consumed as solid $\text{CaCO}_3(\text{s})$, CO_2 , and water (H_2O) are produced.



Physical processes such as mixing of sub-surface water, usually high in CO_2 (low pH), play a large role for transferring CO_2 to the surface water, especially in fall due to increased wind-induced mixing and water column cooling. The DIC, $f\text{CO}_2$, and pH values also change with air-sea CO_2 exchange (C_{EXCH}). When the ocean $f\text{CO}_2$ is lower than the atmospheric, CO_2 is added to the water CO_2 (ocean sink, referred as invasion in **Figure 3**), and if ocean $f\text{CO}_2$ is higher, it loses CO_2 to the atmosphere during ocean outgassing (ocean CO_2 source, referred to as release in **Figure 3**). Since AT describes the ion-charge balance in the water, changes in the uncharged CO_2 will not affect AT (**Figure 3**). Seasonal warming and cooling affect the CO_2 solubility and explain part of the $f\text{CO}_2$ and pH variability.

The full inorganic carbonate system is used together with nutrient data from the seasonal cruises, to estimate the different components causing a change in DIC (C_{DIC}) from pre-bloom situation in January, to May, August to the end of August, described in Eqs 2–5. The January values of a salinity >35 in the upper 50 m were considered representative for concentrations before the onset of photosynthesis (**Supplementary Table S2**). In order to eliminate the change in concentrations due to salinity changes (i.e., dilution), all data were salinity-normalized to 35.1 (January salinity in the Atlantic water), after $35.1/S \times C$, where S refers to the observed salinity and C refers to the concentration of either DIC, AT, or NO_3^- . Since the area is considered to be nitrogen limited (Smith et al., 1987; Kattner and Becker, 1991; Randelhoff et al., 2018), we used the change in salinity-normalized nitrate concentrations from January to May/August (ΔNO_3^- , $\mu\text{mol kg}^{-1}$) converted to carbon using the carbon-to-nitrate (C:N) stoichiometric ratio based on 106:16 (Redfield et al., 1963), to estimate the biological component (C_{BIO} , mol C m^{-2}) of the total DIC change (C_{DIC} , mol C m^{-2}). Similar C:N ratios were found in the particulate organic matter during nitrogen consumption in May and August based on data collected in the same study (Paulsen et al., 2018). The difference between C_{DIC} , C_{BIO} , and C_{CALC} gives an estimate of the ocean's role as an atmospheric CO_2 sink or source, C_{EXCH} (mol C m^{-2}) according to Eq. 5. C_{BIO} , C_{EXCH} , and C_{CALC} were integrated in the top 50 meters. This assumption was valid because that was the maximum depth of nitrate drawdown observed in Randelhoff et al. (2018). Following from the discussion above, the change in total alkalinity (ΔAT , mol C m^{-2}) corrected for the effect of photosynthesis by subtracting the NO_3^- change, was used to estimate the change in the calcification component of the

C_{DIC} (mol C m^{-2}), referred to as C_{CALC} , mol C m^{-2} . The mean concentrations for each parameter in January at $S > 35$ were used to represent the pre-bloom state (**Supplementary Table S2**).

$$C_{\text{DIC}} = C_{\text{BIO}} + C_{\text{EXCH}} + C_{\text{CALC}} \quad (2)$$

$$C_{\text{BIO}} = \Delta\text{NO}_3^- \times \text{C:N} \quad (3)$$

$$C_{\text{CALC}} = 0.5(\Delta\text{AT} + \Delta\text{NO}_3^-) \quad (4)$$

$$C_{\text{EXCH}} = C_{\text{DIC}} - C_{\text{BIO}} - C_{\text{CALC}} \quad (5)$$

Calculation of N^*

The semi-conservative tracer N^* ($\mu\text{mol L}^{-1}$) allows us to easily identify high and low anomalies relative to the global mean concentration of fixed nitrogen lost relative to the phosphate concentration (PO_4^{3-} , $\mu\text{mol L}^{-1}$, Eq. 6). Deviations from conservative behavior are meaningful in identifying regions of denitrification and nitrogen fixation but only give indications for either nitrogen loss or replenishment, which are not always caused by nitrification. This means that negative (positive) values of N^* cannot be directly associated with denitrification (nitrogen fixation). The distribution and seasonal change in N^* in our study area was calculated using the relationship described in Eq. 6 (Deutsch et al., 2001). This relationship includes processes leading to deviations in the entire water column and not only in the euphotic zone as described in Gruber and Sarmiento (1997).

$$\text{N}^* = \text{NO}_3^- - 16 \times \text{PO}_4^{3-} + 2.9 \quad (6)$$

In the equation, the constant 16 refers to the stoichiometric relationship between NO_3^- and PO_4^{3-} based on linear regression of world ocean nutrient data, and 2.9 is the constant derived by setting the global mean values to zero (Gruber and Sarmiento, 1997). The change in N^* reflects the net effect of denitrification and N_2 fixation, thus negative N^* values suggests a deficit of nitrogen relative to the global mean, whereas positive values denotes larger than the world mean thus suggesting a nitrogen excess possibly linked to nitrogen fixation. In this study N^* is used to study the seasonal change of the deficit or source that may be explained by denitrification or nitrogen fixation, but also by advection of waters of different N^* .

Remotely Sensed Data

To obtain information on the timing and development of the phytoplankton bloom in our study area we used data on chlorophyll (Chl_{sat}) and particulate inorganic carbon (PIC, **Figure 12**) from the Moderate Resolution Imaging Spectroradiometer (MODIS) onboard Aqua spacecraft downloaded from NASA Goddard Space Flight Center, Ocean Ecology Laboratory, Ocean Biology Processing Group. Level 3, 8-day binned, 9×9 km resolution arrays were further sampled into grid cells limited by 1° longitude and 0.5° latitude (Børshiem et al., 2014).

Estimates of net primary production from the Vertically Generalized Production Model (VGPM, Behrenfeld and Falkowski, 1997) were downloaded from www.science.oregonstate.edu. Annual primary production was estimated by integrating the production time series from each grid cell throughout the productive season (Børsheim et al., 2014).

The information on sea-ice coverage for the Svalbard area during part of our field periods displayed in **Figure 2** was obtained from ice charts of the Ice Service of the Norwegian Meteorological Institute (MET)¹ where the ice chart color scheme shows for very open drift ice (1–4/10ths), open drift ice (4–7/10ths), close drift ice (7–10/10ths), and fast ice (10/10ths).

RESULTS

Seasonal Variability in the Atlantic Water Inflow and Shelf Water

Hydrography

Salinity and temperature in January, May, and August showed large variability between months (**Figures 4–6**). In January, there were clear longitudinal differences in the water-mass characteristics in the upper 100 m, which defined our study domains. At 4–5°E, there was a relatively thin surface layer in the upper 20 m, with lower salinity (<34.5) and temperature (<0°C) than in the surface water further to the east (**Figures 4A,B**). Between 5 and 8°E, the upper 100 m was more saline (>35) and warmer (4–6°C) than the other domains, while on the shelf (8–10°E) the salinity and temperature were intermediate, 34.8–35 and 2–4°C, respectively (**Figures 4A,B**). In January and May, a relatively warm (>2°C) water off shelf, with high salinity (>35), reached from >600 m depth to the surface. The warm (>4°C) core in the upper 150 m in January was not observed in May (**Figures 4B, 5B**). The low-salinity (<34.5) and cold water (<2°C) in January in the upper 50 m observed in the western part of the study area (3–5°E), was located further to the east, closer to the slope (5–8°E) in May (**Figures 4–6**). In August, this low-salinity upper-50 m layer had spread eastward to the slope and shelf, where increased temperature (>6°C) was observed, compared to in January and May (**Figures 6A,B**). The relatively low salinity and relatively high temperature contributed to a water stratification in the upper 50 m.

Carbonate Chemistry and Ocean Acidification State

The AT, DIC, and *f*CO₂ values varied between the months. The AT values were lowest (about 2270 μmol kg⁻¹) in the upper 50 m at 4–5°E (MWD) in January (**Figure 4C**) and at 5–8°E (AWD) in May (**Figure 5C**), similar to the pattern observed in salinity (**Figures 4A, 5A, 6A**). The highest AT values of approximately 2325 μmol kg⁻¹ were observed in the locations of AWD and SD in the upper 50 m. In August, this low-alkalinity water was spread in the upper 50 m over the entire study area 4–10°E (**Figure 6C**), coinciding with low salinity (**Figure 6A**). The linear relationship between AT and salinity in the upper 50 m ($AT = 57.07 \times S + 315$,

$R^2 = 0.95$, $N = 99$), indicated a freshwater end-member of 315 μmol kg⁻¹. The DIC values in January and May were also low in the upper 50 m, coinciding with observations of low salinity and AT in the upper 50 m (**Figures 4A,D, 5A,D**). In August, the DIC trends were different than those observed in January and May, with the lowest DIC (<2100 μmol kg⁻¹), coinciding with both the lowest salinity and the highest temperature, in the upper 50 m (**Figures 6A,B,D**). At a few depths on the slope at 50–400 m depth, DIC was elevated compared to the same depth off the slope and on the shelf during all three cruises: in January (**Figure 4D**), May (**Figure 5D**) and August (**Figure 6D**). The *f*CO₂ values were undersaturated relative to the atmospheric *f*CO₂ levels of about 406 μatm (Fransson et al., 2017), with the lowest *f*CO₂ values in the upper 50 m in May (<200 μatm) and August (about 250 μatm), following a similar pattern to DIC (**Figures 5D,F, 6D,F**). In the water column on the shelf at about 9°E, the DIC and *f*CO₂ values were higher than the surrounding water. This was most evident in the *f*CO₂ that reached near atmospheric concentration of 406 μatm. The pH, Ω_{Ar} and Ω_{Ca} values also showed temporal variability, highest in May (**Figures 5E,G,H**) and August (**Figures 6E,G,H**) in the upper 50 m, coinciding with low DIC and *f*CO₂ values, in the stratified upper 50 m due to changes in salinity and temperature (**Figures 5C,D, 6C,D**). In May, the Ω_{Ar} and Ω_{Ca} values reached values up to a maximum of 2.5 and 4, respectively (**Figures 5G,H**), coinciding with low-salinity water (**Figure 5A**). The minimum Ω_{Ar} and Ω_{Ca} values of approximately 1.3 and 2.05, respectively, were observed at depths below 600 m in January (**Figures 4G,H**).

Nutrients, N*, and Chlorophyll

In the AWD, the water column had high concentrations of NO₃⁻, PO₄²⁻, and Si(OH)₄ in January throughout the water column with values of 11, 0.8, and 5 μM, respectively (**Figures 4I–K**). Interestingly, the PO₄²⁻ concentrations were higher near the ice edge (MWD) in the upper 200 m relative to the concentrations in AWD, whereas NO₃⁻ and Si(OH)₄ concentrations were lower in this region, relative to those in the AWD. In the upper 50 m, nutrient concentrations changed from relatively high (values) in January to depleted or near-depleted values in May (**Figures 4, 6I–K**). The Si(OH)₄ concentration had the largest decrease from January to May in the AWD, whereas PO₄²⁻ and NO₃⁻ concentrations showed largest decrease in the low-salinity water. This was where high pH and high Ω_{Ar} and Ω_{Ca} values were observed (**Figures 5E,G,H**). By August, Si(OH)₄ concentrations in the upper 50 m, were low (<2 μM) from off shore to the shelf (**Figure 6K**). The ratio between ΔNO₃ and ΔPO₄ over the period of maximum observed nutrient decrease (i.e., January to May), based on data in upper 50 m was 15.2 ± 0.5 μM, similar to the N:P ratio of 16 reported by Redfield et al. (1963).

In January, N* values were generally positive, in excess of >3 μmol kg⁻¹ throughout the water column in the Atlantic-water influenced domain (**Figure 4L**). Similar values were also found on the shelf. Negative values of less than <-1 μmol kg⁻¹ were observed in the upper 100 m and below 650 m in the MWD (**Figure 5L**). By May, negative N* remained in the MWD (**Figure 5L**). The most striking difference from January to May was the change of N* in the western part of the

¹<http://polarview.met.no/>

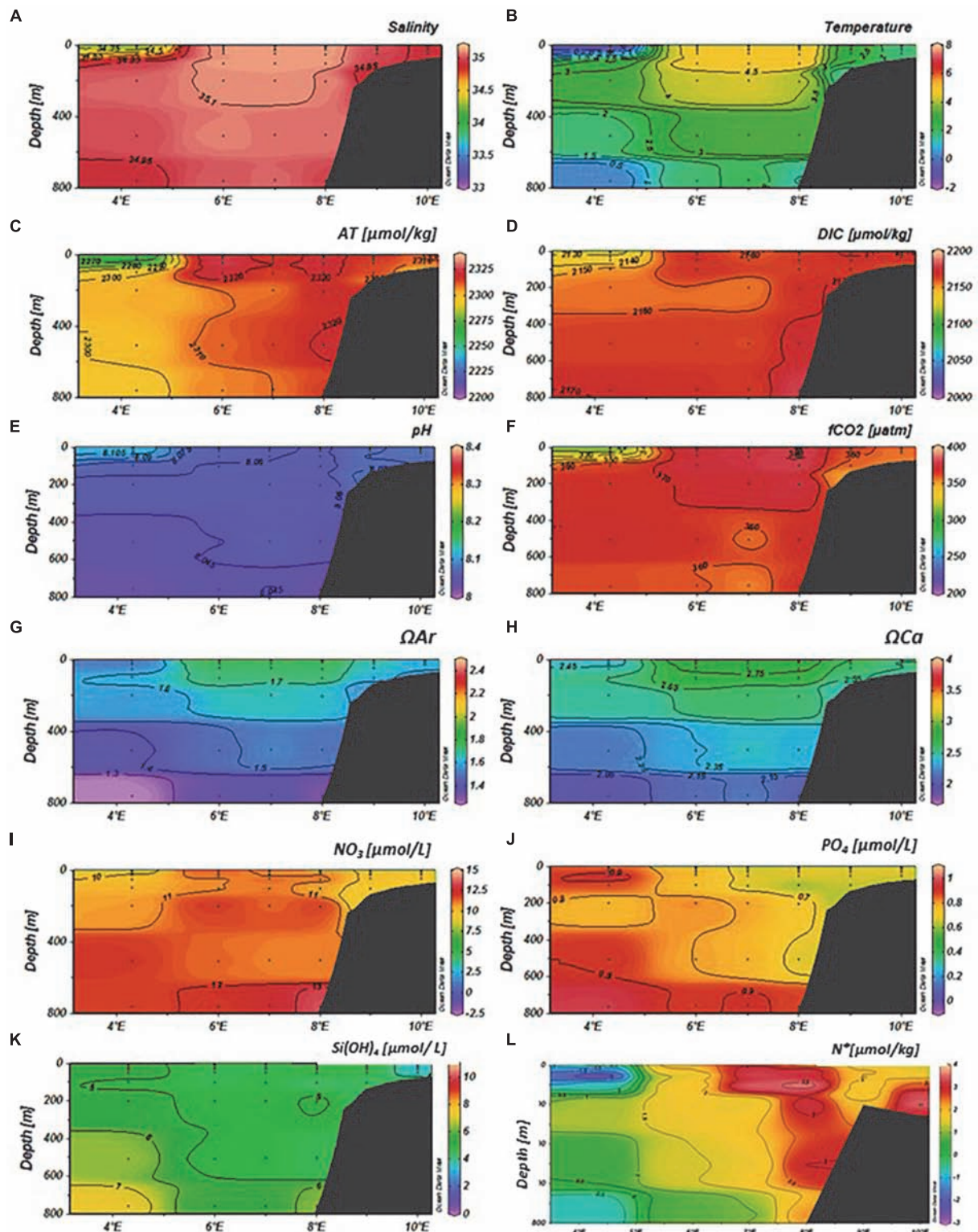


FIGURE 4 | Variability of physical and chemical parameters in the eastern Fram Strait (latitude: 79–79.5°N, longitude: 4–10°E) in January 2014 from top; **(A)** salinity, **(B)** temperature (°C), **(C)** total alkalinity (AT, $\mu\text{mol kg}^{-1}$), **(D)** total dissolved inorganic carbon (DIC, $\mu\text{mol kg}^{-1}$), **(E)** pH, **(F)** fugacity of carbon dioxide ($f\text{CO}_2$, μatm), **(G)** aragonite saturation (Ω_{Ar}), **(H)** calcite saturation (Ω_{Ca}), **(I)** nitrate (NO_3 , $\mu\text{mol L}^{-1}$), **(J)** phosphate (PO_4 , $\mu\text{mol L}^{-1}$), **(K)** silicic acid (Si(OH)_4 , $\mu\text{mol L}^{-1}$), and **(L)** N^* ($\mu\text{mol kg}^{-1}$, negative values denote denitrification, and positive values show nitrification). The sampling locations and depths are denoted as black dots. The section plot and interpolation were performed by the Ocean Data View program (Schlitzer, 2015).

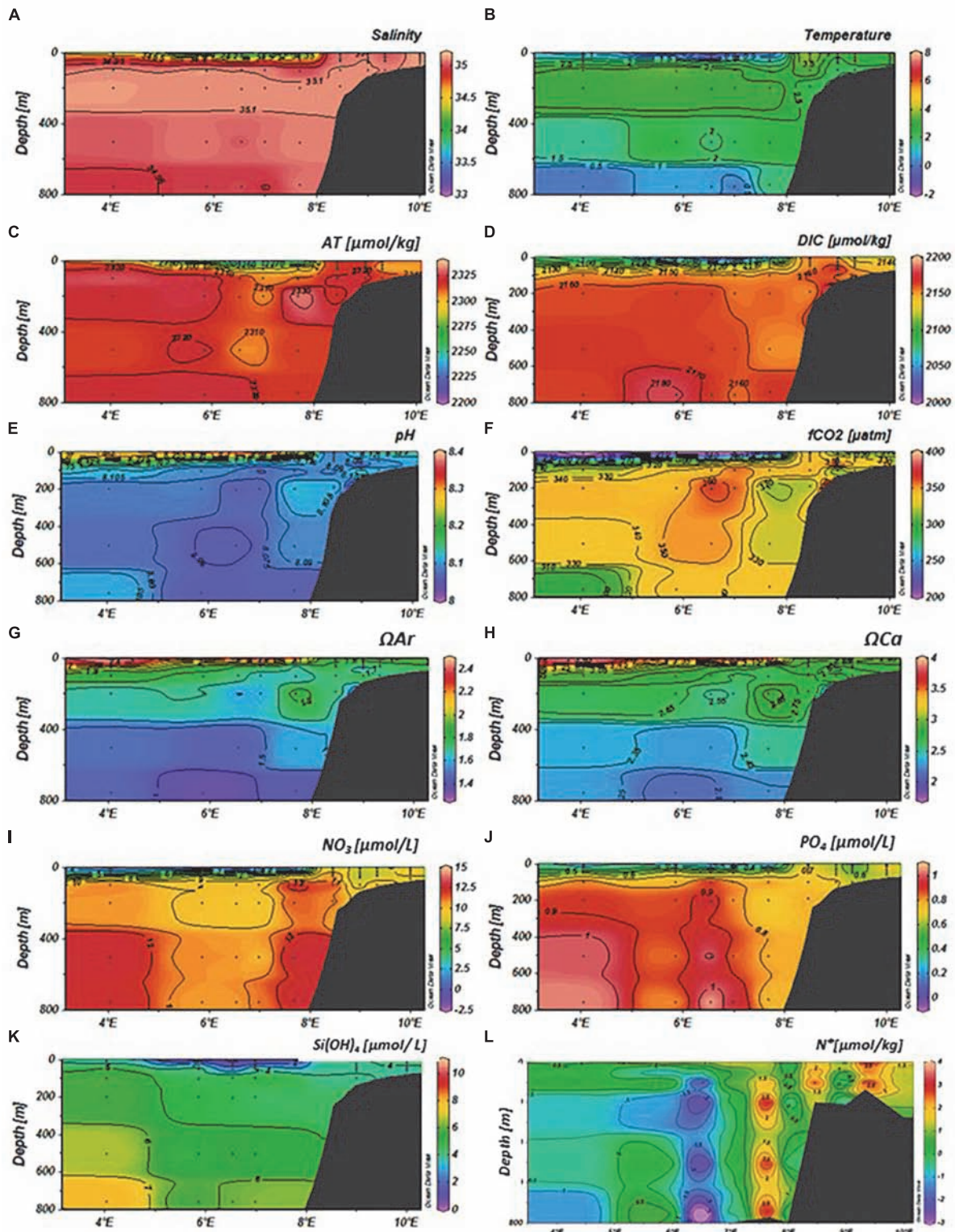


FIGURE 5 | Variability of physical and chemical parameters in the eastern Fram Strait (latitude: 79–79.5°N, longitude: 4–10°E) in May 2014 from top; **(A)** salinity, **(B)** temperature (°C), **(C)** total alkalinity (AT, $\mu\text{mol kg}^{-1}$), **(D)** total dissolved inorganic carbon (DIC, $\mu\text{mol kg}^{-1}$), **(E)** pH, **(F)** fugacity of carbon dioxide ($f\text{CO}_2$, μatm), **(G)** aragonite saturation (Ω_{Ar}), **(H)** calcite saturation (Ω_{Ca}), **(I)** nitrate (NO_3 , $\mu\text{mol L}^{-1}$), **(J)** phosphate (PO_4 , $\mu\text{mol L}^{-1}$), **(K)** silicic acid (Si(OH)_4 , $\mu\text{mol L}^{-1}$), and **(L)** N^* ($\mu\text{mol kg}^{-1}$, negative values denote denitrification, and positive values show nitrification). The sampling locations and depths are denoted as black dots. The section plot and interpolation were performed by the Ocean Data View program (Schlitzer, 2015).

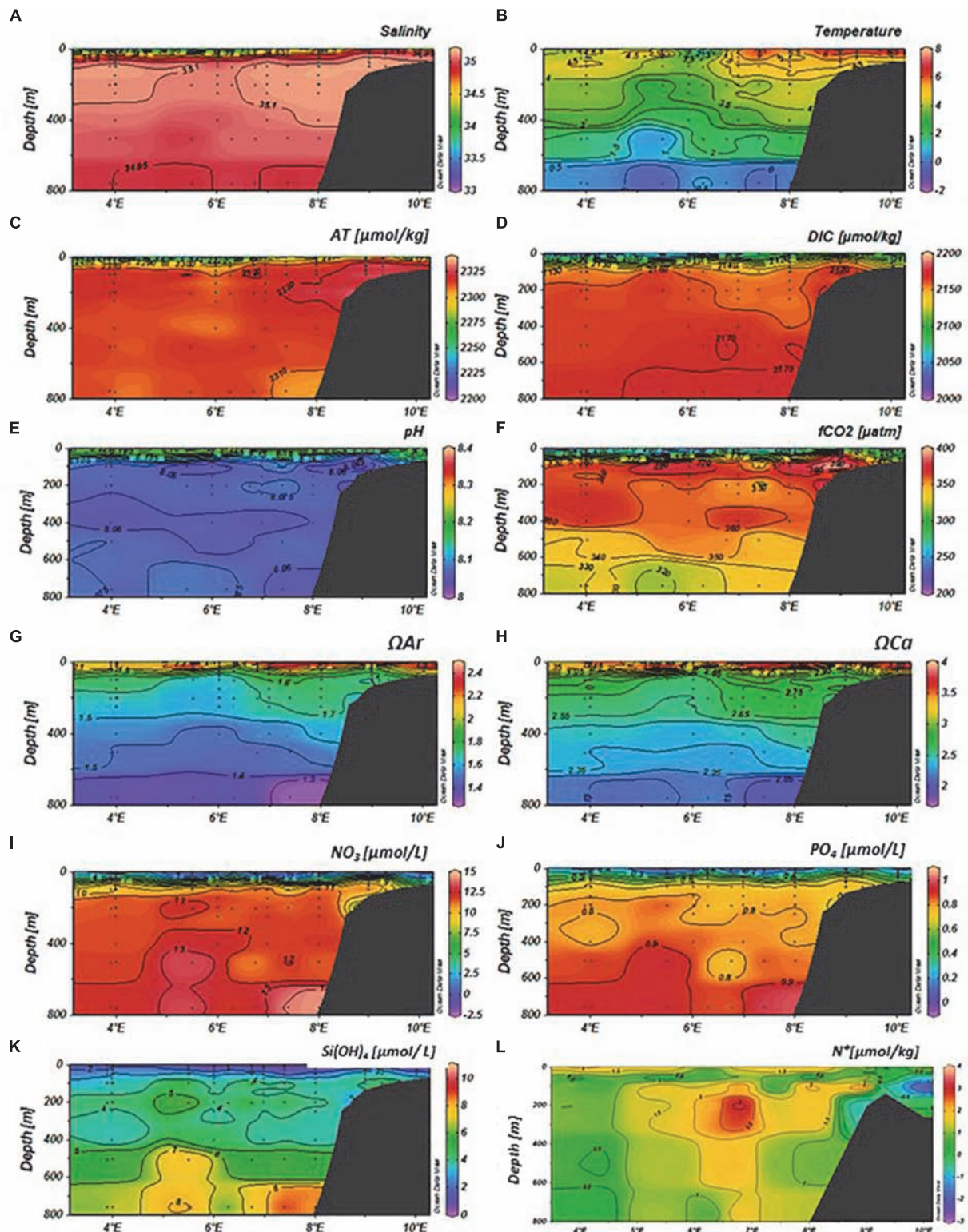


FIGURE 6 | Variability of physical and chemical parameters in the eastern Fram Strait (latitude: 79–79.5°N, longitude: 4–10°E) in August 2014 from top: **(A)** salinity, **(B)** temperature (°C), **(C)** total alkalinity (AT, μmol kg⁻¹), **(D)** total dissolved inorganic carbon (DIC, μmol kg⁻¹), **(E)** pH, **(F)** fugacity of carbon dioxide (fCO₂, μatm), **(G)** aragonite saturation (ΩAr), **(H)** calcite saturation (ΩCa), **(I)** nitrate (NO₃, μmol L⁻¹), **(J)** phosphate (PO₄, μmol L⁻¹), **(K)** silicic acid (Si(OH)₄, μmol L⁻¹), and **(L)** N* (μmol kg⁻¹, negative values denote denitrification, and positive values show nitrification). The sampling locations and depths are denoted as black dots. The section plot and interpolation were performed by the Ocean Data View program (Schlitzer, 2015).

AWD, which shifted from high positive N^* values in January, to negative values of less than $-2 \mu\text{mol kg}^{-1}$ at 7°E (Figure 5L). The change from positive to negative values were also observed on the slope (8°E), and on parts of the shelf at 9°E (Figure 5L). In August, the negative N^* values remained only in the intermediate water on the shelf, while the rest of the study area showed positive N^* values with a maximum of $2.8 \mu\text{mol kg}^{-1}$ in the AWD (Figure 6L).

Remotely sensed chlorophyll data (Chl_{sat}) gives an overview of the succession of the phytoplankton bloom and clearly shows the onset of a bloom near the ice edge (Figures 7B,C, white areas show ice cover). In the first week of May (Figure 7A), the bloom increased around the ice edge (Figure 7C), continuing until late June (Figure 7D), when the Chl_{sat} decreased. At the end of July, Chl_{sat} increased again in our study area and persisted through August (Figures 7E,G) until the beginning of September after which the bloom ceased completely and reached undetectable values (Figure 7H). Largest values were observed in between May and mid-June (Figures 7B,C).

Seasonal Drivers of DIC Change

Negative values of C_{BIO} signify loss of DIC in the surface water (i.e., CO₂) through net photosynthesis, whereas positive C_{BIO} values signify DIC release through net respiration. The C_{BIO} between January and May was between 1.9 and 2.2 mol C m^{-2} (23 – 26 g C m^{-2}) in the MWD at about 4 – 6°E (Figure 8A). In the AWD, further east (>6 and 8°E) and along 79°N , the C_{BIO} averaged between $-0.7 \text{ mol C m}^{-2}$ and near 0 mol C m^{-2} at the shelf break (Figure 8A). On the West Spitsbergen shelf, C_{BIO} was $-0.8 \text{ mol C m}^{-2}$. The C_{BIO} between January and August was $-3.0 \text{ mol C m}^{-2}$ (-36 g C m^{-2}) in the AWD (Figure 8B), implying a 0.8 mol C m^{-2} net community production in summer (between May and August).

Negative C_{EXCH} indicates an ocean loss, for example through CO₂ outgassing to the atmosphere (loss, negative values), while positive values denote an oceanic uptake of atmospheric CO₂ (Figure 9, Eq. 4). Between January and May, C_{EXCH} ranged from being a net oceanic CO₂ sink of about 0.5 mol C m^{-2} on the SD, northern MWD and the northeast Svalbard, to become a net atmospheric CO₂ source (loss) between 0.5 and 0.2 mol C m^{-2} in the southern MWD (Figure 9A). By August, the southern part of the study area (around 79°N), especially evident in the AWD, C_{EXCH} changed from an insignificant ocean CO₂ sink to a larger CO₂ sink of about 2.3 mol C m^{-2} (Figure 9B). In the northern part, C_{EXCH} values were changed from a net sink to a net CO₂ source reaching a maximum release of 0.5 mol C m^{-2} . This was particularly pronounced in the area north of Svalbard (Figure 9B).

The influence of calcification or dissolution of CaCO₃ on the DIC change (C_{CALC}) was investigated following Eq. 4, where positive values signify a gain in DIC through CaCO₃ dissolution and negative values a loss through CaCO₃ formation/precipitation. Equation 4 is based on the salinity-normalized AT, corrected for photosynthesis using the nitrate change. Since AT is not affected by air-sea CO₂ exchange, it is only CaCO₃ dissolution that explains the increase in AT and ultimately the increase in C_{CALC} . Generally, the area showed a

DIC gain (positive C_{CALC}) for the whole region, except for the small loss of 0.1 mol C m^{-2} found in the SD between January and May (Figure 10A). At this time, the largest DIC gain of up to 0.5 mol C m^{-2} was found in the MWD and the lowest DIC gain of less than $0.10 \text{ mol C m}^{-2}$ in the area north of Svalbard (Figure 10A). In the AWD, the largest C_{CALC} values were 0.3 mol C m^{-2} . Between January and August, the DIC gain derived from C_{CALC} had generally increased throughout the study area except in the MWD and north of Svalbard compared to the change between January and May. The largest DIC gain derived from C_{CALC} was observed in the AWD to a maximum of 0.7 mol C m^{-2} between January and August, hence an increase between May and August of about 0.4 mol C m^{-2} (Figure 10B).

Figure 11 shows a composite of the seasonal change of C_{BIO} , C_{EXCH} , and C_{CALC} focusing on variability of the area between 79 – 79.5°N and 4 – 10°E between January and May (Figure 11A), May and August (difference in the DIC between January and August, Figure 11B), and between beginning August and the end of August (Figure 11C). Figure 11 clearly shows a large biological DIC uptake, C_{BIO} in the MWD between January and May (Figure 11A). C_{BIO} DIC uptake increased (more negative C_{BIO}) in the SD and AWD from May to August to a maximum C_{BIO} DIC change of $-3.0 \text{ mol C m}^{-2}$ (Figure 11B). By the end of August, C_{BIO} showed a net DIC gain in the AWD and MWD of up to 2.3 mol C m^{-2} , sustaining biological DIC uptake (negative C_{BIO}) in part of the MWD and SD of about 0.2 mol C m^{-2} (Figure 11C). Between January and May, C_{EXCH} showed that the ocean generally acted as a small net oceanic sink of atmospheric CO₂ of about 0.4 mol C m^{-2} (Figure 11A). By beginning of August, the CO₂ sink increased in the AWD of up to 2.3 mol C m^{-2} (Figure 11B). At the end of August, the CO₂ sink decreased greatly and changed C_{EXCH} by $-3.8 \text{ mol C m}^{-2}$ from a sink to become a CO₂ source, releasing CO₂ to the atmosphere in the AWD (Figure 11C). In January to May and May to August, throughout the study area, the C_{CALC} resulted in a DIC gain of maximum of 0.5 mol C m^{-2} in the MWD in January to May (Figures 11A,B). In the SD, C_{CALC} showed less importance than the other domains (Figures 11A–C). By the end of August, the C_{CALC} changed from a DIC gain to a DIC loss (Figure 11C) of a maximum of about $-0.5 \text{ mol C m}^{-2}$.

The large C_{CALC} values in May and August were found in the area influenced by sea-ice formation and melt, such as in the MWD in May, and in the AWD in August. In our study area and time of year, the remotely sensed data on particulate inorganic carbon (PIC_{sat}) showed a clear seasonal trend (based on data in the area 78.5 – 79.5°N and 4 – 10°E) from values less than $0.1 \mu\text{mol kg}^{-1}$ in May to maximum PIC values of up to $0.6 \mu\text{mol kg}^{-1}$ in August (Figure 12). The seasonal trend agrees with our C_{CALC} estimates for the AWD, but the values are too low to explain the C_{CALC} in the AWD of up to 0.5 mol C m^{-2} between May and August (Figure 11B). Part of the difference between the PIC_{sat} and C_{CALC} are based on the methodological difference. The C_{CALC} values are integrated to 50 m and PIC_{sat} values are based on the surface ocean.

The succession of C_{BIO} from May to end of August was also observed from the remotely sensed chlorophyll data (chl_{sat}). The

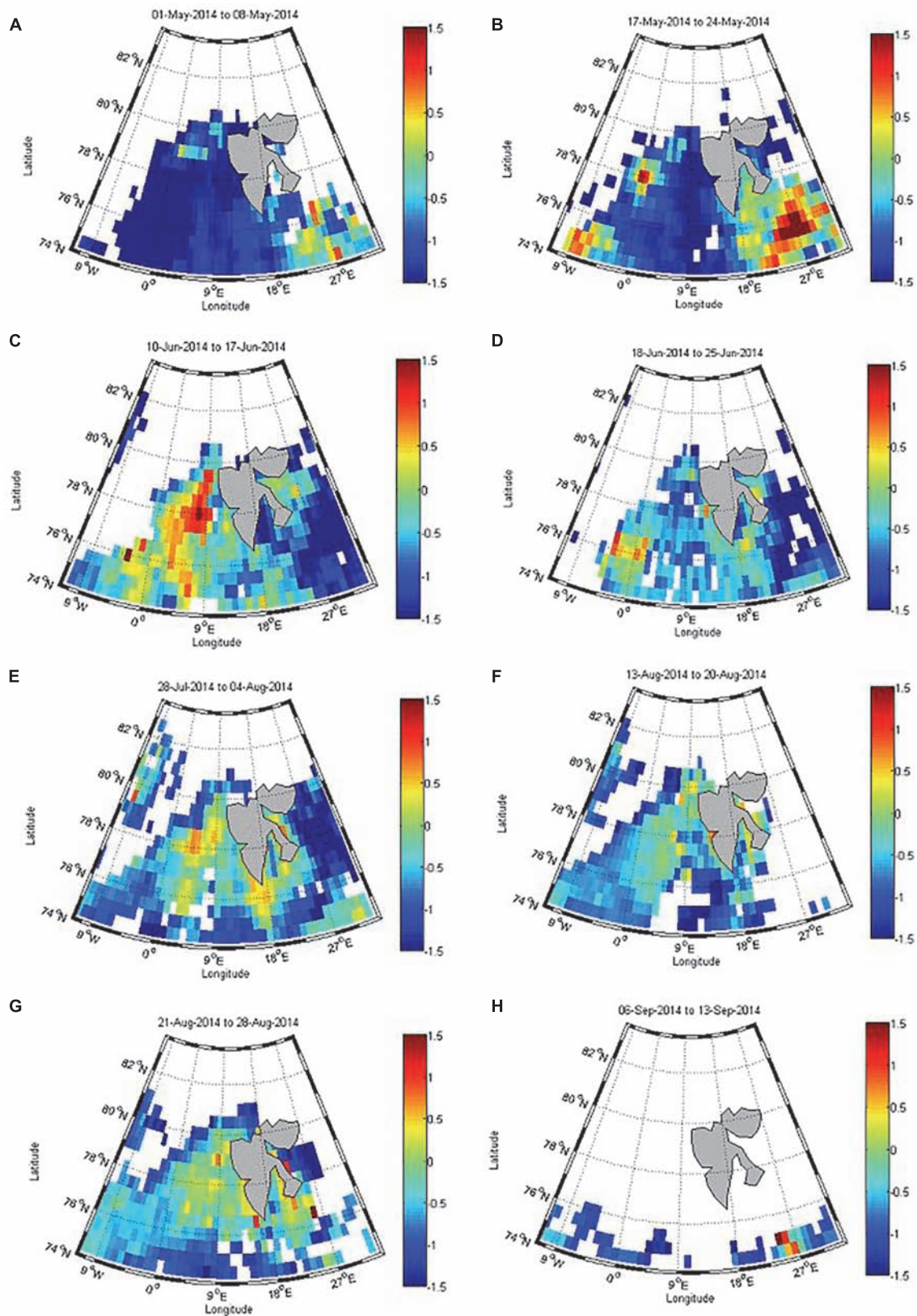
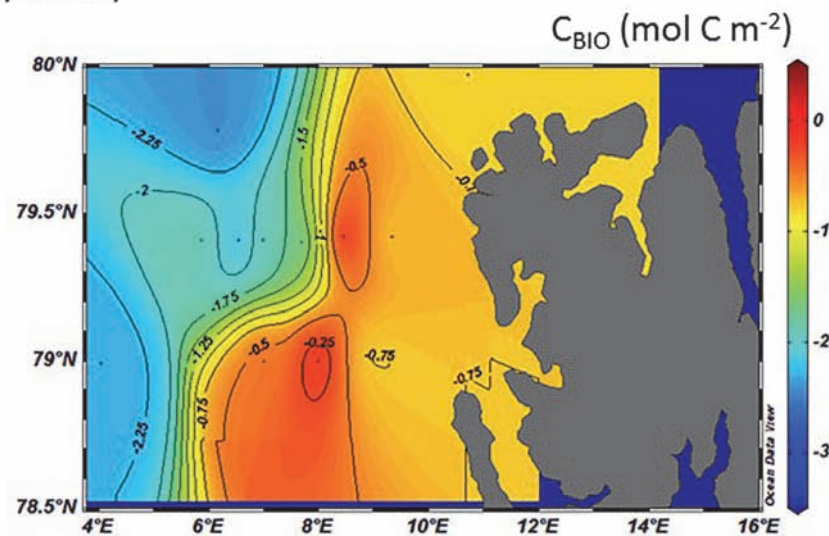


FIGURE 7 | Remotely sensed chlorophyll *a* (Chl_{sat}, 8-day average) in May (A,B), June (C,D), July (E), August (F,G), and September (H), in 2014. Red values show the highest concentration and blue the lowest values on a logarithmic scale in mg m⁻³.

A January to May



B January to August

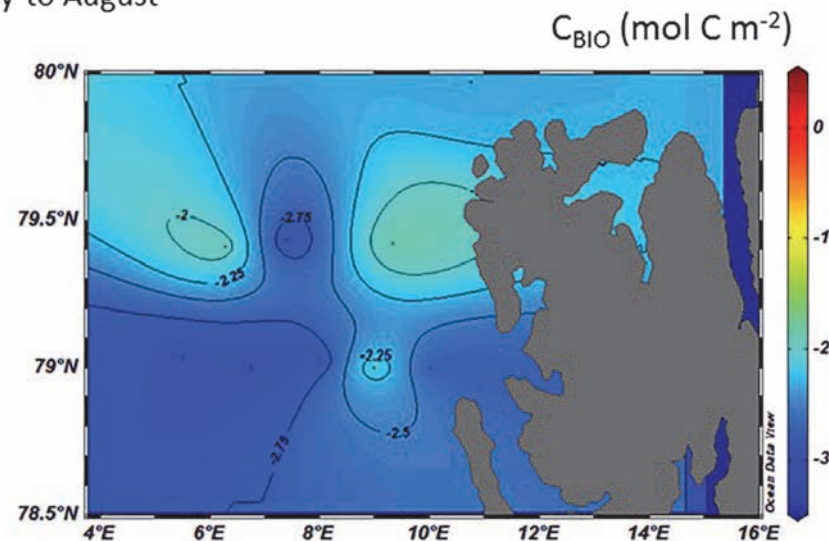


FIGURE 8 | Interpolated and integrated C_{BIO} in the top 50 m (mol C m^{-2}) calculated from the difference between January and: **(A)** May and, **(B)** August in 2014. Negative numbers denote a loss of carbon through carbon consumption during phytoplankton production and a positive denote a gain of carbon during respiration and remineralization of organic matter.

maximum 8-day mean values of chl_{sat} in the area $79.75\text{--}78.75^\circ\text{N}$ shown by longitude reached $>0.5 \text{ mg m}^{-3}$ (in the MWD) by 23rd April and reached the highest values of 6 mg m^{-3} in the beginning of July at 6°E (Figure 13A). After the peak, chl_{sat} rapidly decreased to reach values below 1 mg m^{-3} (Figure 13A). The succession of the bloom was also investigated in the three domains, where $\text{chl}_{\text{sat}} > 0.5 \text{ mg m}^{-3}$ was observed one week later in the AWD and SD domains than in MWD, on the 1st

May (Figures 13B,C). In the AWD, the chl_{sat} varied between 3 and 1.5 mg m^{-3} throughout the season and showed less seasonal variability than the other domains (Figure 13B). In the shelf domain at 9°E , generally higher chl_{sat} of about 3 mg m^{-3} was observed than on the shallow shelf at 10°E , where chl_{sat} values steadily increased and reached the highest values of 1.7 mg m^{-3} by the 23rd August. One week later, chl_{sat} values rapidly declined to undetectable values (Figure 13C). The chl_{sat} in the MWD

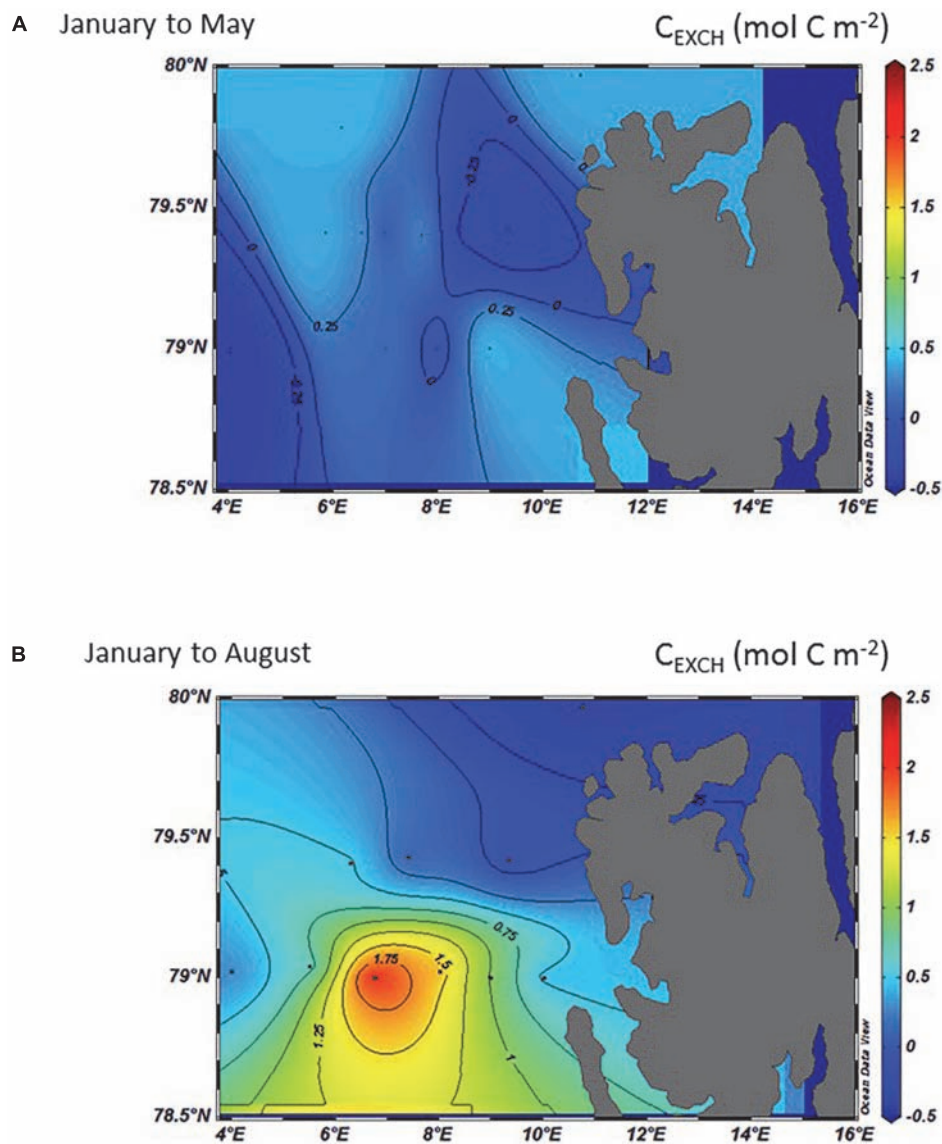


FIGURE 9 | The interpolated and integrated C_{EXCH} in the top 50 meters (mol C m⁻²) in 2014 calculated from the difference between January and: **(A)** May and, **(B)** August 2014. Negative numbers denote an ocean CO₂ sink from the environment, such as uptake from the atmosphere, and positive numbers denote an ocean CO₂ outgassing and source to the environment.

clearly showed a spring bloom between end of April to end of May, followed by a secondary bloom from mid-June to end of July (Figure 3A).

DISCUSSION

Succession of the Bloom and Variability in Primary Productivity Estimates

Our study agrees with several studies that show evidence of extensive spring blooms near the ice edge in the Arctic Ocean and its shelf seas. These blooms are mainly caused by relatively high-light conditions, meltwater-induced stratification and high

nutrient availability, controlled by the nitrate concentration (i.e., Sakshaug, 2004; Wassmann and Reigstad, 2011; Assmy et al., 2017). Randelhoff et al. (2018) found an overall increase in ammonium values from May to August, explained by the remineralization after the spring bloom when the plankton community shifted toward a nutrient-recycling state during summer. Later in summer these authors suggested that thermal convection added nutrients and likely CO₂-rich sub-surface water to the surface ocean. Increased remineralization (where C_{BIO} results in increased DIC) and mixing at the end of the summer would explain the rapidly changing conditions from a net biological DIC consumption and ocean CO₂ sink in August to a net biological DIC source in late August (Figure 11C).

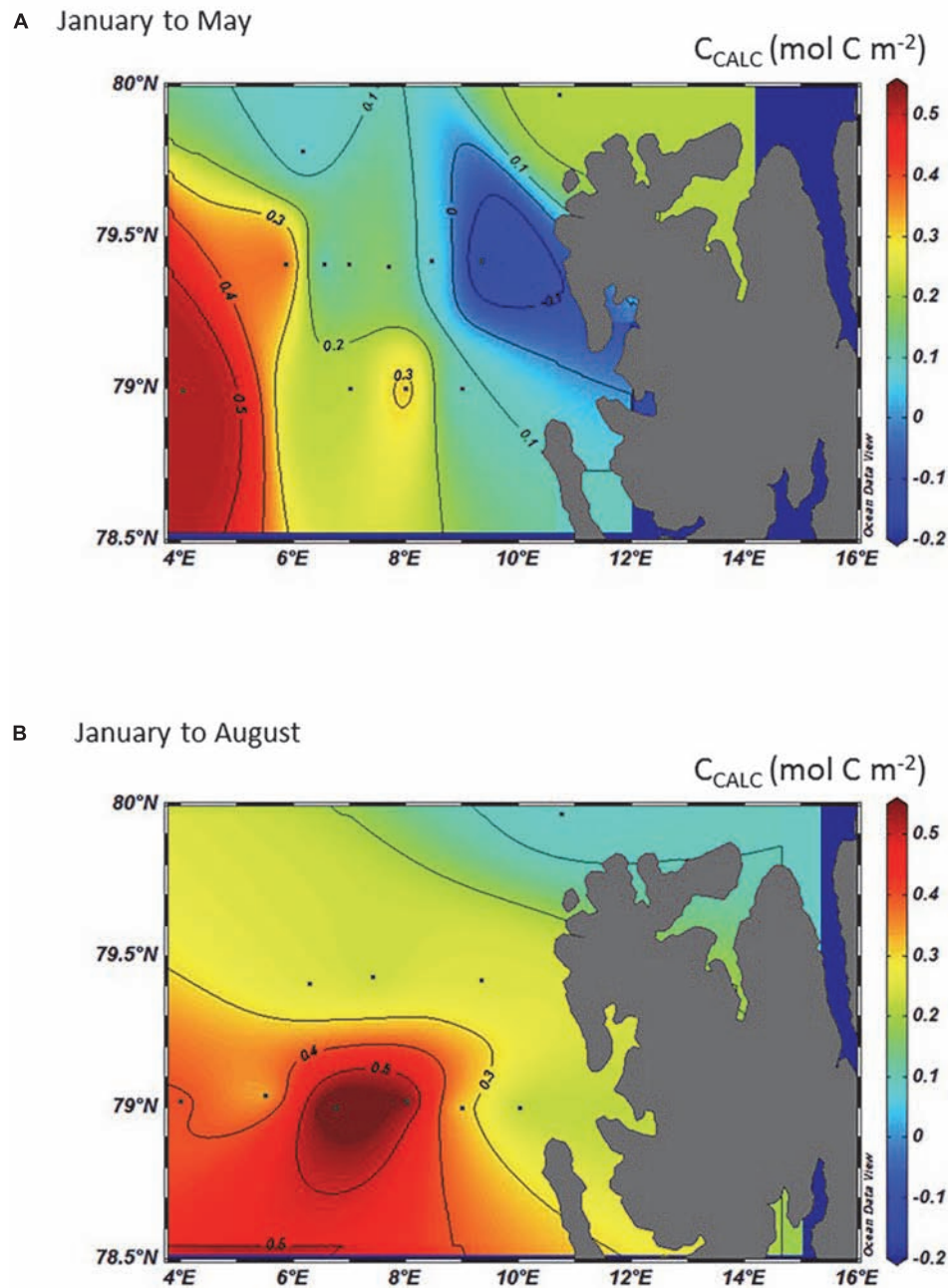


FIGURE 10 | The interpolated and integrated C_{CALC} in the top 50 meters (mol C m^{-2}) in 2014 calculated from the difference between January and: **(A)** May and, **(B)** August 2014. Positive values denote a gain in DIC through CaCO_3 dissolution and negative values a loss through formation of CaCO_3 .

Increased mixing of CO_2 -rich sub-surface water would also explain the change in C_{EXCH} from an ocean CO_2 sink area in August to atmospheric CO_2 release by the end of August. Our study supports these findings: the spring bloom started near the ice edge in the west and moved eastward as the season progressed with most of the biological DIC consumption estimated in the AW domain and on the shelf (SD; **Figure 11**).

Based on the difference between January and May (2.2 mol C m^{-2} and 26 g C m^{-2}) and between January and August

(3.0 mol C m^{-2} and 36 g C m^{-2}) estimates (**Figure 8** and **Table 1**), about 75% of the C_{BIO} occurred in spring, whereas the remaining 25% (0.8 mol C m^{-2} and $\sim 9 \text{ g C m}^{-2}$) occurred in summer (between May and August). This spring value is similar to the annual export production estimates of $28\text{--}32 \text{ g C m}^{-2}$ in the Barents Sea presented by Fransson et al. (2001) using a similar approach as in our study. Our C_{BIO} estimates are based on the loss of NO_3^- , sometimes referred to as new production, and do not consider production based on recycled nitrogen, other

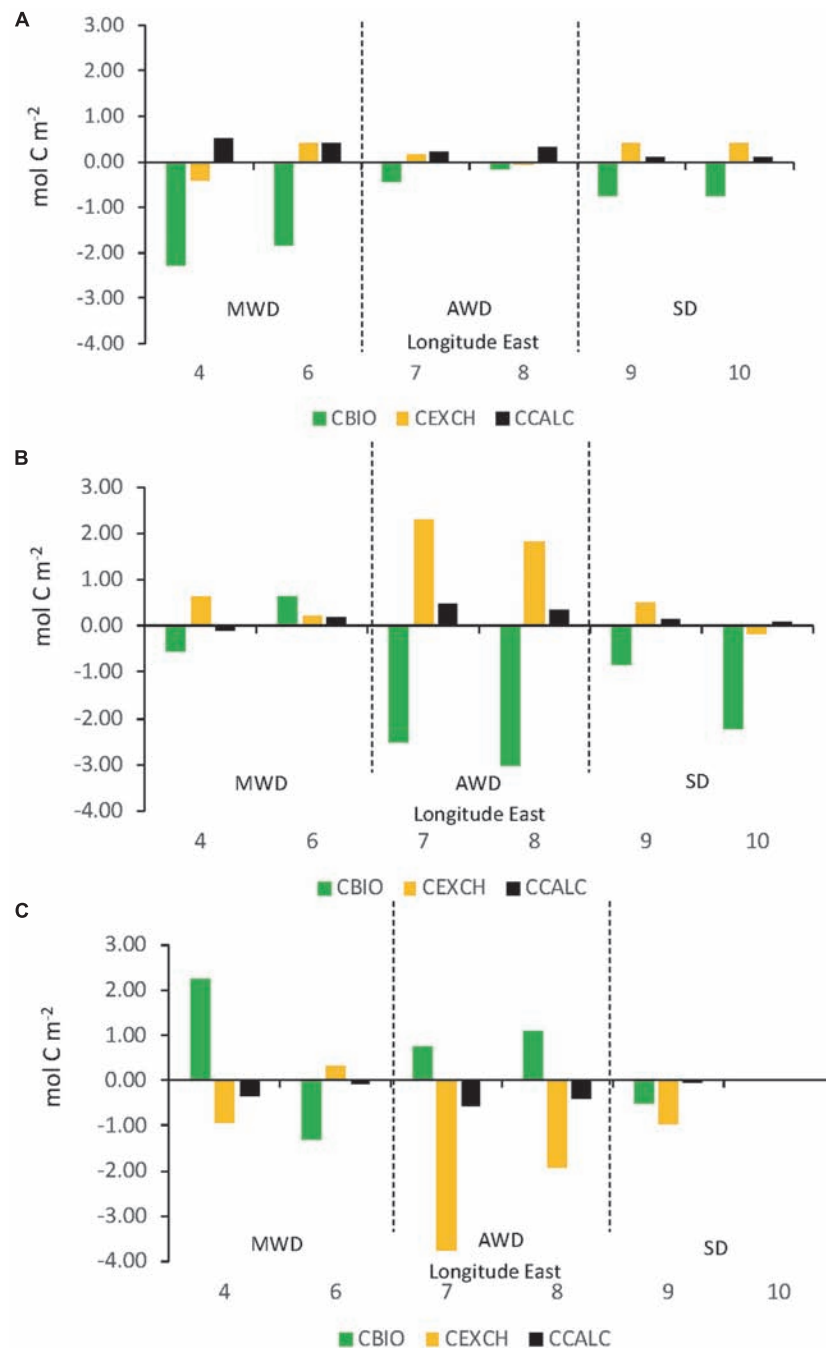


FIGURE 11 | The integrated change of C_{BIO} (green columns), C_{EXCH} (orange columns), and C_{CALC} (black columns) in top 50 meters (y-axis, mol C m^{-2}) between: **(A)** January and May, **(B)** May to August, and **(C)** August to end of August along the 79°N section in eastern Fram Strait (x-axis Longitude°E). The dashed vertical lines divide the section in the three domains; meltwater domain (MWD), the Atlantic water domain (AWD), and the shelf domain (SD). Positive numbers denote a gain of carbon, and negative denote a loss of carbon.

than nitrate (Muggli and Smith, 1993). In the Labrador Sea, primary production showed a similar bloom succession as in our area, with high nitrate-based spring bloom in May and recycled production in August (Tremblay et al., 2006). They estimated the ratio between the relative contribution of NO_3^- to total nitrogen uptake ratio, the f -ratio, to be 0.8 in May and 0.2 in August

(Tremblay et al., 2006). The f -ratios from their study was used to convert our C_{BIO} estimates to total production based on all nitrogen sources (C_{BIOTOT}). This resulted in a C_{BIOTOT} of up to 2.6 mol C m^{-2} for the spring bloom (between January and May), 1.4 mol C m^{-2} in summer (between May and August), and a total annual C_{BIOTOT} of 4.0 mol C m^{-2} .

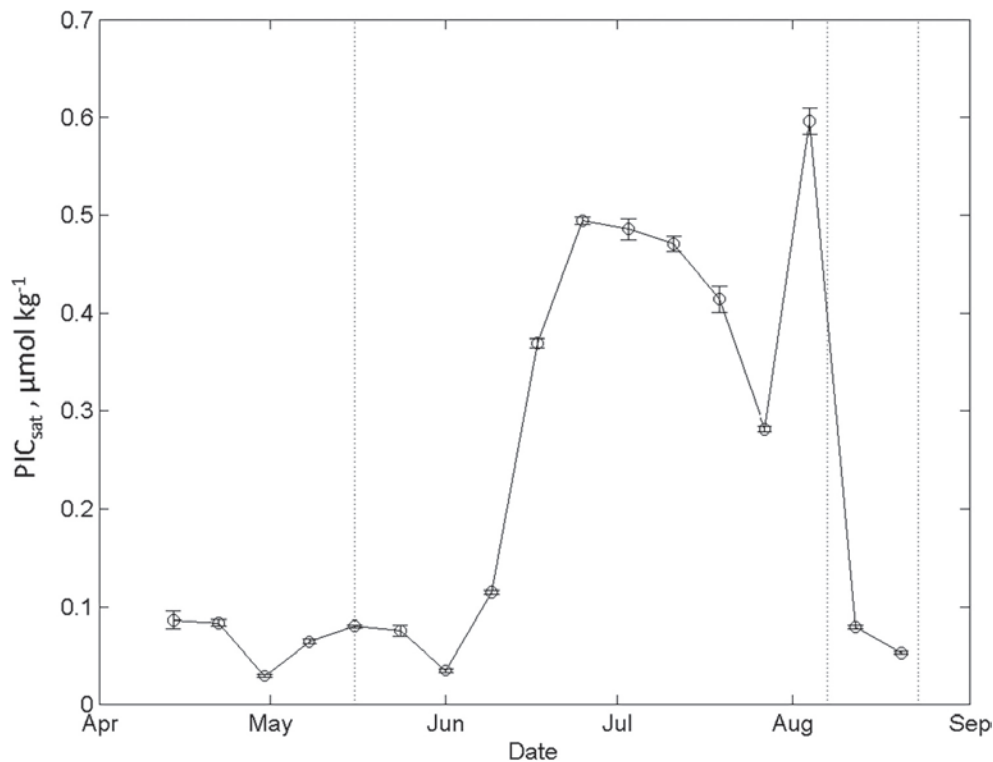


FIGURE 12 | The seasonal evolution of the remotely sensed particulate inorganic carbon (PIC_{sat}, μmol kg⁻¹) from mid-April to end of August 2014, in the area between longitude 4 and 10°E, and latitude between 78.5 and 79.5°N.

Based on chl_{sat} data, the onset of the bloom occurred close to the 1st of May, resulting in a daily C_{BIO} estimate of 0.10 and 0.14 mol C m⁻² d⁻¹, or 1.2 to 1.7 g C m⁻² d⁻¹ using data collected between 16th and 23th of May (equivalent to 16 to 23 “bloom days,” **Figure 13**). The daily total production estimate (C_{BIO}TOT) for May range between 0.11 and 0.16 mol C m⁻² d⁻¹ (1.4–2.0 g C m⁻² d⁻¹). Sanz-Martín et al. (2018) estimated total production (Gross Primary Production, GPP) west and north of Svalbard in May 2014. They used oxygen (O₂) production in incubations with water collected from the spring-bloom conditions. Their study estimated a daily GPP of about 6.2 μmol O₂ l⁻¹ d⁻¹ (converted to 4.8 μmol C l⁻¹ d⁻¹ by C:O ratio of 106:138) from northwest Svalbard shelf stations (P1 and P5, **Supplementary Table S1**). Converting their value to the same bloom period as ours, integrated to 50 m results in a daily estimate of 0.24 mol C m⁻² (2.9 g C m⁻² d⁻¹) which is larger than our daily C_{BIO}TOT estimates from 0.11 to 0.16 mol C m⁻² d⁻¹ (2.6 mol C m⁻² for 16–23 days). This is likely due to the integration of their value to 50 m, which probably overestimates the Sanz-Martín et al. (2018) GPP value. Wassmann et al. (2010) presented model estimates of GPP in the area west of Svalbard between 74 and 80°N, where they found a maximum annual GPP of 120 g C m⁻² (10 mol C m⁻²), with an annual mean of 75 g C m⁻² (6.3 mol C m⁻²).

In the open ocean north of Svalbard, Assmy et al. (2017) estimated a biological carbon consumption based on ¹⁴C uptake during the spring bloom of 1.3 mol C m⁻², integrated in the top

50 m for 27 days, between 25th of May and 22nd of June. In the same area and time, Fransson et al. (2017) used a similar method as in our study (nitrate-deficit method) and estimated a biological DIC consumption integrated in the top 50 m during the spring bloom of 1.6 mol C m⁻² in May–June. Both the estimates of Assmy et al. (2017) and Fransson et al. (2017) are lower than our C_{BIO} estimates of 2.2 mol C m⁻² in May, suggesting that the eastern Fram Strait region has larger net community production than the basin north of Svalbard, in spring.

Estimated remotely-sensed biological carbon consumption NCP_{sat} in our study area showed an annual net production up to 1.3 mol C m⁻² (**Figure 14**). Part of the difference between the NCP_{sat} and the C_{BIO} estimates of 3.0 mol C m⁻² (36 g C m⁻²) for the full period between January and August was likely caused by methodological considerations. A difference in the integration depth can be expected, NCP_{sat} was based on a surface chlorophyll a and PAR values, and variable euphotic zone depth, likely shallower than the 50-meter C_{BIO} estimate. For example, Randelhoff et al. (2018) measured a mixed layer depth of 10–15 m at the ice edge.

Dissolved inorganic carbon uptake by Arctic productivity is similar to Antarctic estimates. In the Atlantic sector of the Southern Ocean in the Weddell Sea, Hoppema et al. (2007) estimated the NCP using integrated nutrient-deficiency methods such as in our study, and estimated NCP (same as our C_{BIO}) to be 1.5 mol C m⁻² for a 4-month period between November and March 2005 (Hoppema et al., 2002). Extrapolated values to

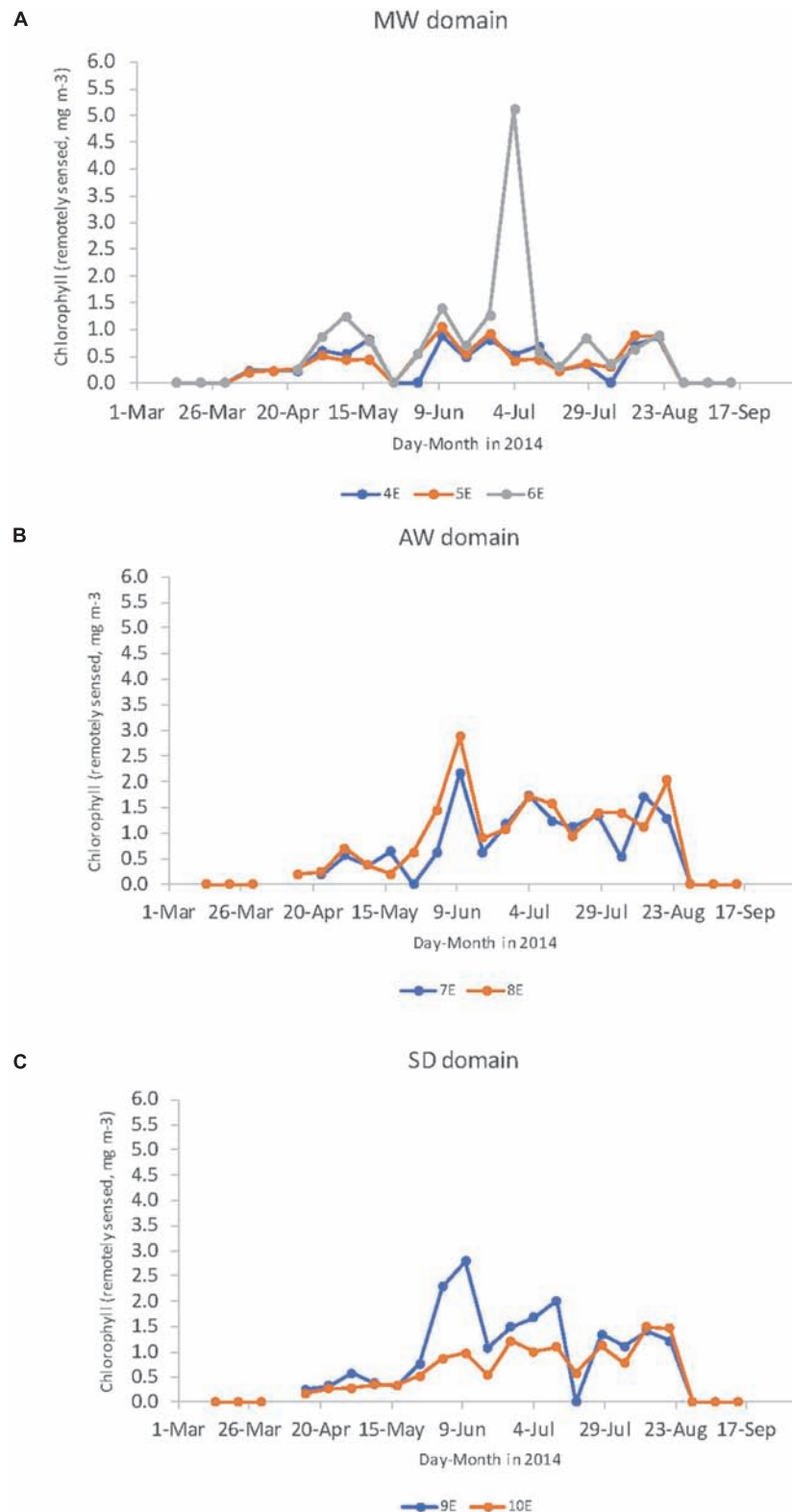
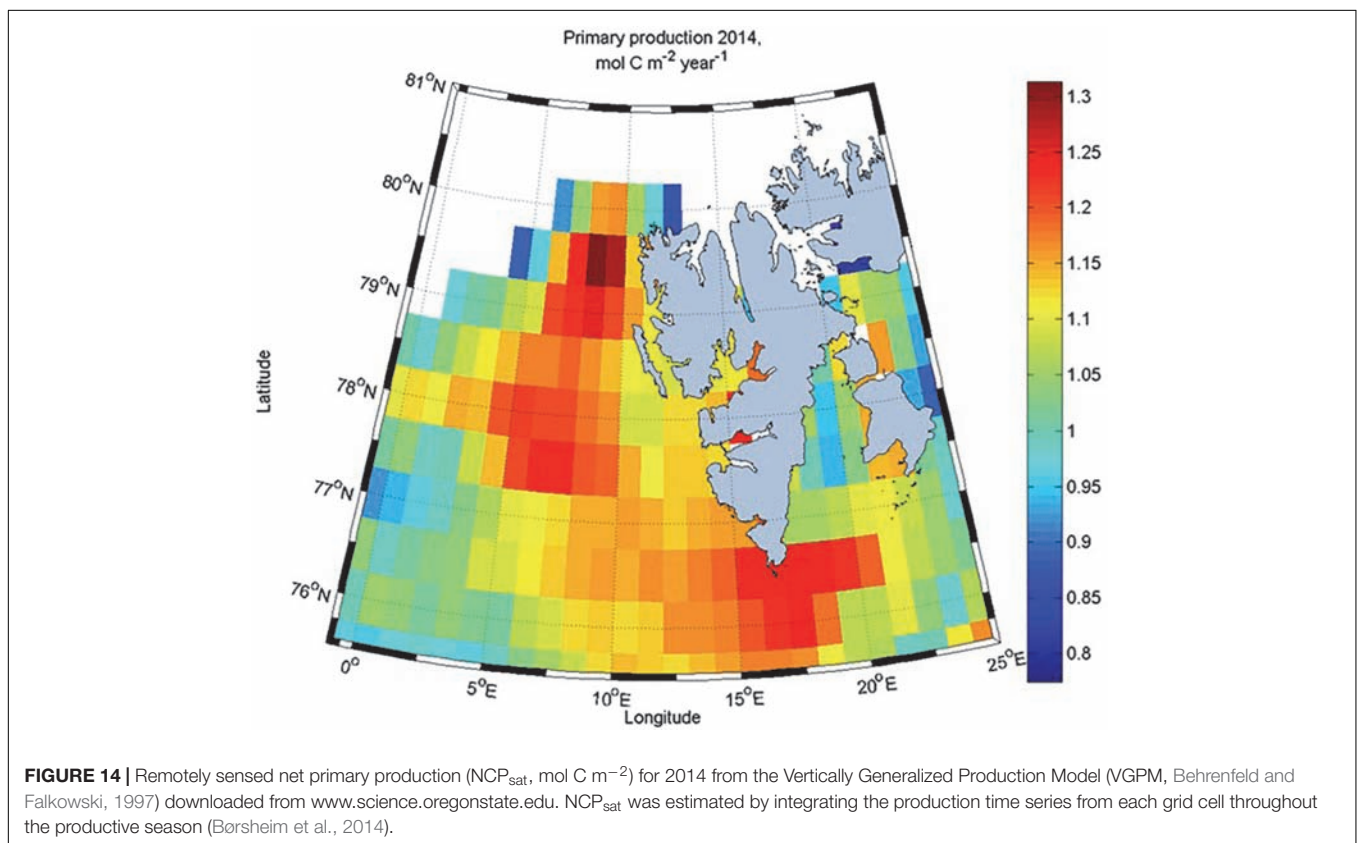


FIGURE 13 | The seasonal variability of the maximum value of remotely sensed chlorophyll a (mg m⁻³) in the area between 79.75 and 78.75°N from 4 to 10°E divided in the: **(A)** meltwater influenced domain (MWD), **(B)** the Atlantic water domain (AWD), and **(C)** in the shelf domain (SD) from 4th of February to 12th of October in 2014. Values are Level 3, 8-day binned, 9 × 9 km resolution arrays from the Moderate Resolution Imaging Spectroradiometer (MODIS) onboard Aqua spacecraft downloaded from NASA Goddard Space Flight Center, Ocean Ecology Laboratory, Ocean Biology Processing Group.

TABLE 1 | Summary and direction of the estimated drivers of the mean and standard deviation for the seasonal DIC change (C_{DIC} , mol C m⁻²) integrated in the top 50 meters in the three study domains: meltwater influenced domain, MWD, Atlantic water domain, AWD, and the shelf domain, SD, in May, August, and end of August 2014.

Month	Domain	C_{BIO} mol C m ⁻²	C_{EXCH} mol C m ⁻²	C_{CALC} mol C m ⁻²	C_{BIO} % of abs.tot	C_{EXCH} % of abs.tot	C_{CALC} % of abs.tot
May	MWD	-2.2 ± 0.3	0.1 ± 0.4	0.3 ± 0.5	83	5	12
	AWD	-0.3 ± 0.2	0.1 ± 0.2	0.3 ± 0.1	48	8	44
	SD	-0.8 ± 0.0	0.2 ± 0.4	0.2 ± 0.4	70	15	15
Average		-1.1 ± 1.0	0.1 ± 0.1	0.3 ± 0.2	67	9	24
August	MWD	-2.3 ± 0.9	0.4 ± 0.1	0.2 ± 0.2	80	12	8
	AWD	-3.0 ± 0.2	2.1 ± 0.1	0.7 ± 0.5	53	36	11
	SD	-2.1 ± 0.8	0.4 ± 0.5	0.2 ± 0.1	78	13	9
Average		-2.5 ± 0.6	1.0 ± 0.2	0.3 ± 0.3	70	20	9
Aug end	MWD	-1.7 ± 1.7	0.1 ± 1.1	0.1 ± 0.1	89	5	6
	AWD	-2.2 ± 0.1	-0.7 ± 0.8	0.2 ± 0.2	70	24	6
	SD	nd	nd	nd	nd	nd	nd
Average		na	na	na	na	na	na

Negative values denotes a loss of DIC and positive values denotes a gain in DIC caused by the following processes: nitrate based biological carbon uptake (C_{BIO} , carbon lost from the water), air-sea CO₂ exchange, C_{EXCH} , where positive values denotes an ocean CO₂ sink and negative an ocean CO₂ source, and the net effect of calcium carbonate dissolution (gain, positive) or formation (loss, negative), C_{CALC} . All values in mol C m⁻² total over the specified period. The role of each driver relative to the total absolute change is indicated in as percentage (%) in the three right columns. nd indicates no data and na not applicable.



include the entire marginal ice zone, resulted in much larger NCP estimates of up to 4.1 mol C m⁻² in the same area (Smith and Nelson, 1990).

In summary, there is a large variability in primary productivity estimates for polar regions, including our area of study, based on environmental and methodological considerations at different

time and spatial scales. The $C_{BIO_{TOT}}$ estimates are about half the maximum values from O₂ incubations and a third of the model estimates (both GPP), but twice as large as the primary production estimates based on ¹⁴C by Assmy et al. (2017), the nitrate-deficit values of Fransson et al. (2017) and the NCP_{sat} from this study. Seasonally, up to 75% of the net community

productivity is constrained to the spring bloom. Areas west of Svalbard present twice as much annual production than in the Arctic, north of Svalbard. Finally, the depth of integration and the length of the sampling period can bias estimates in regions with shallow, and variable, mixed layer depth. Our analysis, encompassing from winter to autumn, highlights the importance of the seasonal signal in this high-latitude region.

The Oceanic Sink of Atmospheric CO₂ in Fram Strait Area and Its Variability

Several studies estimating the air-sea CO₂ fluxes and the annual net CO₂ sink show that the Arctic Ocean, the Fram Strait and waters around Svalbard act as atmospheric CO₂ sinks (e.g., Tynan et al., 2016; Yasunaka et al., 2016, 2018; Fransson et al., 2017). The 18-year annual average of observed seawater $f\text{CO}_2$ and a self-organizing mapping technique showed that the Arctic Ocean acted as an ocean CO₂ sink between 8 and 12 mmol m⁻² d⁻¹ and a daily mean in a full annual cycle of 5 mmol m⁻² d⁻¹ (Yasunaka et al., 2018). In our estimates, the study area showed a small oceanic CO₂ sink until May at an average of 0.12 ± 0.06 mol C m⁻² for the period January to May. By August, the ocean CO₂ uptake increased to a large net ocean CO₂ sink of an average of 1.1 ± 1.0 mol C m⁻² and a maximum CO₂ sink of 2.1 mol C m⁻² (25 g C m⁻²) in the AWD for the January to August period (Table 1). This suggests a mean daily ocean CO₂ uptake of 10 mmol m⁻² d⁻¹ and a maximum of 21 mmol m⁻² d⁻¹ in August (100 days). By the end of August, the AWD shifted to a significant CO₂ source of about 0.7 mol C m⁻² (Table 1). Accounting for the study period between January and August, this results in an ocean net annual CO₂ sink between 4 and 8 mmol m⁻² d⁻¹, which are similar to the results by Yasunaka et al. (2018). The winter-to-summer ocean CO₂ uptake estimates of 3.7 mol C m⁻² (44 g C m⁻²) by Fransson et al. (2001) in the Barents Sea in the upper 50 m, are nearly twice as large as our maximum estimate of 2.1 mol C m⁻² (25 g C m⁻²). Their relatively large CO₂ uptake were mainly driven by biological DIC uptake in the biologically productive waters of the Barents Sea. Model estimates for the Barents Sea showed an annual oceanic CO₂ uptake between 10 and 40 g C m⁻², related to warm and cold years (Slagstad and Wassmann, 1996), which were similar to our estimates of the annual net oceanic CO₂ uptake between 10 and 25 g C m⁻² for the whole period from January to May and August. In the Greenland Sea, the ocean acted as a CO₂ sink throughout the year of about 53 g C m⁻² (Anderson et al., 2000). On the other hand, our estimate is much larger than the Atlantic water influenced Kara-Laptev Sea of 1 g C m⁻² (Fransson et al., 2001). In the southern Beaufort Sea, surface waters were undersaturated with respect to atmospheric CO₂ throughout the year and constituted a net sink of 14 g C m⁻² (1.2 mol C m⁻² yr⁻¹), with ice coverage and ice formation limiting the CO₂ uptake during winter (Shadwick et al., 2011a). They explained that the CO₂ uptake was largely driven by under-ice and open-water biological activity, with high subsequent export of organic matter to the deeper water column. These results emphasize the large regional variability of the annual net oceanic

sink of atmospheric CO₂ and the importance to consider the local processes driving the exchange.

In the high-latitude Southern Ocean, Fransson et al. (2004) used a similar method as in our study, i.e., winter-to-summer deficits of nitrate in several regions, such as the polar front (APF), winter ice edge (WIE), and the seasonal ice edge (SIE). In the SIE and the APF, a net ocean release of CO₂ to the atmosphere of 0.1–0.5 mol m⁻², respectively, was calculated over a time scale of several months (from austral winter to January). In the WIE, the ocean acted as a net atmospheric CO₂ sink of about 0.1 mol m⁻², which is similar to our values for the MWD for the period January to May (Table 1).

Dissolution and Sources of CaCO₃

Increased C_{CALC} suggests dissolution of CaCO₃, which may be caused by breakdown of CaCO₃ shells and skeleton from calcifying organisms or dissolution of ikaite minerals from sea ice melt water (Rysgaard et al., 2012, 2013; Fransson et al., 2013). Our estimate of C_{CALC} showed that the corresponding DIC change due to calcification or dissolution, was less significant than the C_{BIO} but at times similar to the values of C_{EXCH} (Figure 11 and Table 1). We found that the large C_{CALC} values in May were either found in the area influenced by sea ice formation and melt such as in MWD, or in the AWD domain in August.

The shells (coccoliths) affects the reflectance of the surface water and results in a turquoise milky surface which is clearly observed using remotely sensed sensors (Tyrrell et al., 1999). In our study area and time of year, the remotely sensed data on particulate inorganic carbon (PIC_{sat}) showed a clear seasonal trend from values less than 0.1 μmol kg⁻¹ in May to maximum PIC values of up to 0.6 μmol kg⁻¹ in August (Figure 12). The seasonal PIC_{sat} trend agrees with our C_{CALC} estimates for the AWD but as previously stated, the values are too low to explain the DIC gain through CaCO₃ dissolution estimated from C_{CALC} of maximum of 0.3 and 0.7 mol C m⁻² in May and August, respectively (Table 1). Calcifying phytoplankton blooms are known to occur after the spring bloom and may sustain growth in relatively nutrient depleted waters during summer. This is observed on the Arctic inflow shelves such as the Bering Sea and Barents Sea and very common in the North Atlantic (e.g., Robertson et al., 1994), but not common in the Arctic Ocean (i.e., Tyrrell and Merico, 2004 and references therein). The low PIC_{sat} during our study agreed with observations of very low cell numbers of calcifying phytoplankton observed during the CarbonBridge study (Egge et al., 2018). Perhaps these shells were not locally formed and dissolved but transported from the south with the Atlantic water inflow or from the West Spitsbergen fjords (e.g., Lalande et al., 2016). This was the explanation for the *E. huxleyi* blooms, the most common and opportunistic calcifying phytoplankton, that was observed in the upper 50 m of the marginal ice zone in the Barents Sea in August 2003 (Hegseth and Sundfjord, 2008). These blooms were attributed to intrusions of Atlantic water bringing cells of oceanic phytoplankton species via the subsurface circumpolar boundary current west of Svalbard and then eastward along the Eurasian Shelf break.

Another possible source for DIC gain through CaCO₃ dissolution is the dissolution of ikaite particles (which is a form

of CaCO₃ formed in sea ice) that has been recently released from melting sea ice and dissolved in the upper water column. Sea-ice cover will obstruct remotely sensed observations of ikaite and is most likely not included in the PIC_{sat} values (Figure 12). Consequently, sea-ice derived ikaite could explain the relatively high DIC gain from C_{CALC} of about 0.3 mol C m⁻² estimated between January and May. This implies that most of the C_{CALC} increase of about 0.4 mol C m⁻² (from 0.3 to 0.7 mol C m⁻²; Table 1) in the AWD between May and August is attributed to dissolution of advected CaCO₃ shells (Table 1). By the end of August, the C_{CALC} values are the lowest throughout the study area (Table 1), agreeing well with the drastic decrease in PIC_{sat} values (Figure 12).

The Role of Nitrogen Fixation and Denitrification Based on N*

N* values from our study varied with season and ranged between -3 and +2.5 μmol kg⁻¹, which is the same range as reported from other ocean basins (Gruber and Sarmiento, 1997). The high values (>1 μmol kg⁻¹) in the AWD is generally found in well-oxygenated waters, such as in the North Atlantic >35°N (Gruber and Sarmiento, 1997). Consequently, the high N* in the eastern Fram Strait may be enriched by the inflowing Atlantic waters and does not necessarily imply a local source due to on-site N₂ fixation. To estimate the different nitrogen sources and sinks requires information on the isotopic nitrogen ratios (Granger et al., 2011). Sipler et al. (2017) estimated the depth-integrated N₂ fixation in the ice-free season (June to September) west of Svalbard and the Barents Sea to about 1.5 g N m⁻² in the upper 50 m. In the Nansen Basin, north of Svalbard, integrated N₂-fixation was significantly lower and between 0 and 0.5 g N m⁻² (Sipler et al., 2017).

The negative N* values observed on the shelf slope and in shelf bottom water, especially evident in August, may indicate a nitrogen loss due to benthic denitrification (Figure 6L). This was observed to be the case in the Pacific Arctic inflow region, in the eastern Bering Sea shelf where benthic denitrification caused a nitrogen loss of between 2 and 13 μmol L⁻¹ in April 2007 and 2008 (Granger et al., 2011). This implies that modifications such as increased nitrogen loss on the Bering Sea shelf may decrease the nitrogen concentrations in the Pacific water inflow waters and the surface water column in the Arctic Ocean (e.g., Jones et al., 2003). The Arctic outflow water exits through the Fram Strait, mainly in the East Greenland Current along the Greenland shelf (e.g., de Steur et al., 2014). It is unlikely that the negative N* values observed in the water column in January and May in the MWD was caused by Pacific water outflow. Denitrification has also been found in melting Arctic sea ice before the under-ice spring bloom oxygenates the surface water (Rysgaard et al., 2008). This could explain the nitrogen loss in the upper water column in January as well as the increasing N* values in the surface water as the bloom progressed and oxygenated the water from May to August (Figures 4L, 5L, 6L). However, sea-ice processes cannot explain the negative N* values before May in the deeper parts of the water column (>200 m). The decreased N* from January to May below 200 m depth for whole area, may be

caused by contribution of another water mass. About half of the AW transported by the WSC, recirculated between 76 and 81°N, exits the Fram Strait from the north, and has modified the chemical and physical properties of AW (MAW; Rudels et al., 2000; Marnela et al., 2013). According to Sipler et al. (2017), N₂ fixation was much lower in the Arctic Ocean than in the AW inflow area. Consequently, one explanation for the decreased N* between January and May could be that the AW loses nitrogen as it resides in the low N₂ fixation area further north and during its return to the Fram Strait contains less nitrogen as well as less heat. By August, the nitrogen increased by 2 μmol L⁻¹, showing a nitrogen gain, which implies a larger contribution of original AW. The strength and magnitude of the recirculation of MAW in the Fram Strait show large interannual variability (Rudels et al., 2000; de Steur et al., 2014). Moreover, observations and models show that eddy activity results in substantial seasonal and spatial variability in the recirculation and facilitates subduction of AW (Hattermann et al., 2016).

CONCLUSION AND FUTURE OUTLOOK

Phytoplankton DIC uptake (C_{BIO}) played by far the most important role for the observed DIC change throughout the study area and explained up to 89% of the total DIC change. The C_{EXCH} played a minor to moderate role and was most significant in August in the Atlantic water domain, explaining about 36% of the relative importance of the DIC drivers. In May, dissolution of sea-ice derived CaCO₃ (ikaite) played a moderate but important role to explain the net effect of the DIC gain in all domains. By August, the biological DIC uptake (C_{BIO}) had increased in all domains, and at this time we observed the largest C_{EXCH} gain, and continuing gain from CaCO₃ dissolution, most likely from an advected source. Of the total DIC gain between January and August (sum of C_{EXCH} and C_{CALC} ~2.8 mol C m⁻², Table 1), 25% was explained by CaCO₃ dissolution and the remaining 75% of C_{EXCH} was due to ocean CO₂ uptake from the atmosphere as a result of the high biological CO₂ demand during photosynthesis between May and August.

In a future scenario, decreased sea ice and more open water exposed to atmosphere will facilitate direct ocean CO₂ uptake through increased air-sea CO₂ flux as long as the surface water is undersaturated in CO₂ relative to the atmospheric CO₂ level. In contrast, less sea-ice associated CaCO₃ dissolution (ikaite) will decrease the addition of total alkalinity, thus the buffering capacity against acidic input (e.g., CO₂), decreasing the CO₂ uptake potential in spring. However, with the influence of advected CaCO₃ shells later in summer, the buffering potential could be fully or partly restored but at a later stage. Moreover, less influence of melting sea ice may potentially decrease nitrate removal caused by denitrification. A larger inflow of well-oxygenated Atlantic water will also result in lower potential for denitrification to take place. Several studies show that increased CO₂ concentrations enhance primary production in spring in this area (Holding et al., 2015; Sanz-Martín et al., 2018), which would allow larger DIC uptake through biological CO₂ consumption. In that case, progressing ocean acidification in the

surface water would be mitigated fully or partly by biological CO₂ consumption. In a scenario of increased advection of Atlantic water, this buffer may become more important for the CO₂ uptake capacity and on-going ocean acidification. However, the net effect of the studied processes on the DIC change and ocean CO₂ uptake in the Arctic inflow region will ultimately depend on a combination of several processes such as changes in primary production, stratification, nutrient availability, the net carbon export out of the mixed layer, as well as changes in the advection of warm Atlantic water. Warming of the surface ocean will decrease the ocean CO₂ uptake solubility due to decreased CO₂ dissolution in warmer compared to colder water. With less meltwater in spring, the sea-ice ikaite contribution to the surface water would decrease, hence having consequences for the ocean to act as a net CO₂ sink in future. Furthermore, the increase in wind-induced vertical mixing due to increased open water in winter could contribute to increased DIC in the surface water, perhaps resulting in a CO₂ source.

DATA AVAILABILITY

The datasets generated for this study are available on request to the corresponding author.

AUTHOR CONTRIBUTIONS

MC, AF, and MV involved in the sampling and study design. MC performed the data analyses, and created the tables and

figures. MC completed the writing of the manuscript with contributions from MV and AF. MV contributed with the calculations. KB contributed with the calculations based on the remotely sensed data. MC and AF collected and analyzed the carbonate chemistry.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: <https://www.frontiersin.org/articles/10.3389/fmars.2019.00528/full#supplementary-material>

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Inter-Annual Variability of Organic Carbon Concentration in the Eastern Fram Strait During Summer (2009–2017)

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The Arctic Ocean plays a key role in regulating the global climate, while being highly sensitive to climate change. Temperature in the Arctic increases faster than the global average, causing a loss of multiyear sea-ice and affecting marine ecosystem structure and functioning. As a result, Arctic primary production and biogeochemical cycling are changing. Here, we investigated inter-annual changes in the concentrations of particulate and dissolved organic carbon (POC, DOC) together with biological drivers, such as phyto- and bacterioplankton abundance in the Fram Strait, the Atlantic gateway to the Central Arctic Ocean. Data have been collected in summer at the Long-Term Ecological Research observatory HAUSGARTEN during eight cruises from 2009 to 2017. Our results suggest that the dynamic physical system of the Fram Strait induces strong heterogeneity of the ecosystem that displays considerable intra-seasonal as well as inter-annual variability. Over the observational period, DOC concentrations were significantly negatively related to temperature and salinity, suggesting that outflow of Central Arctic waters carrying a high DOC load is the main control of DOC concentration in this region. POC concentration was not linked to temperature or salinity but tightly related to phytoplankton biomass as estimated from chlorophyll-a concentrations (Chl-a). For the years 2009–2017, no temporal trends in the depth-integrated (0–100 m) amounts of DOC and Chl-a were observed. In contrast, depth-integrated (0–100 m) amounts of POC, as well as the ratio [POC]:[TOC], decreased significantly over time. This suggests a higher partitioning of organic carbon into the dissolved phase. Potential causes and consequences of the observed changes in organic carbon stocks for food-web structure and CO₂ sequestration are discussed.

Keywords: dissolved organic carbon, particulate organic carbon, phytoplankton, bacteria, time series

INTRODUCTION

The Arctic Ocean undergoes fast environmental transformation due to climate change including a strongly declined summer sea ice extent that coincides with an intense loss of multi-year sea ice (Polyakov et al., 2010; Wassmann, 2011; Stroeve et al., 2012). The rate of warming in the Arctic exceeds two times the global average and may result in a temperature increase of up to 6°C by the 21st century (ACIA, 2014), assigning the Arctic as the most rapidly changing region of our planet (Solomon et al., 2013). In recent years, the loss of sea ice cover has increased, with a minimum of 3.41 million square kilometers in the summer of 2012 (National Snow and Ice Data Center, Colorado, United States). Many factors are responsible for Arctic change: the increased atmospheric concentration of greenhouse gases, as well as changes in aerosol abundance and land use, alter the radiative budget of the Earth leading to a net global warming of the atmosphere (Solomon et al., 2013). Besides rising atmospheric temperatures, there is also an increased advection of warm waters into the Arctic region due to changes in global oceanic currents (Comiso et al., 2008; Chylek et al., 2009; Spielhagen et al., 2011). Sea ice loss reduces the surface albedo, and amplifies warming and further sea ice melting processes in spring and summer (Serreze et al., 2007; Screen and Simmonds, 2010). In addition, the sea ice is drifting faster (Kwok et al., 2013) and is more prone to the deformation by storms (Itkin et al., 2017), leaving a changed icescape.

As a consequence of these processes, the marine ecosystem is expected to undergo changes because primary productivity and carbon cycling, including the production, degradation and respiration of organic carbon, are directly responding to altered temperatures and light conditions. Sea-ice melting starting before solar radiation allows for algal productivity and growth, thus the sea ice as algal habitat vanishes. The loss of sea ice will not only affect the timing of ice algal and phytoplankton blooms in the Arctic (Ji et al., 2013), but may lead to a trophic mismatch between primary producers and their grazers, e.g., zooplankton (Søreide et al., 2010). Additionally, this may lead to differences in carbon supply to the deep sea and sequestering of carbon in Arctic sediments (Lalande et al., 2009; Boetius et al., 2013; Harada, 2016). Warming and increased melt water input may also affect water column stratification and vertical supply of nutrients to the euphotic zone. Nutrient limitation of autotrophic growth not only reduces biomass production but also leads to an increasing fraction of organic carbon being partitioned into dissolved organic carbon (DOC) (Mykkestad et al., 1972; Biddanda and Benner, 1997; Engel et al., 2002). Warming may amplify this process since increasing temperatures have been shown to favor the partitioning of carbon into the dissolved organic matter (DOM) pool (Wohlers et al., 2009; Engel et al., 2011; Kim et al., 2011). Temperature is a key control of microbial activity. However, in Polar Seas (<4°C) temperature sensitivities of marine bacteria are strongly co-determined by bioavailable DOC (Kirchman et al., 2009b). Because DOC is the main substrate for microbial uptake (Azam and Hodson, 1977), a higher DOC production in the Arctic, due to warming or seawater acidification (Engel et al., 2013), may stimulate the

microbial food web, and also therefore the turn-over of organic carbon components (Azam et al., 1983; Thingstad et al., 2008; Kirchman et al., 2009a). Following these arguments, the influence of global change on the microbial utilization of organic carbon, and hence on the Arctic as a net sink for CO₂ (Bates and Mathis, 2009), may be coupled to the availability of labile DOC.

On a global scale, DOC comprises more than 90% of total organic carbon (TOC), equivalent to 662 Pg C (Hansell et al., 2009). Thereby, marine DOC represents the largest dynamic organic carbon reservoirs on Earth. Changes in the marine DOC pool may significantly affect atmospheric CO₂ concentrations on timescales of 1000–10,000 years (Hedges, 1992). In Arctic seawater, the concentration of DOC is often increased compared to other open ocean sites due to a high input of riverine DOC and slow degradation rates (Anderson et al., 1994; Bussmann and Kattner, 2000; Amon and Benner, 2003; Amon et al., 2003). Amon et al. (2003) reported DOC concentrations in the Nordic Sea basins (>1000 m) of ~50 μmol L⁻¹ DOC, clearly above deep values of other ocean basins 35–45 μmol L⁻¹ C (Benner, 2002). Terrestrial DOC introduced to the central Arctic through large river systems, such as the Siberian rivers, is mainly of high age, substantially modified and presumably less bio-available (Meon and Amon, 2004). In contrast, DOC released by melting of glaciers in Alaska and Greenland has been shown to contain labile components, readily bioavailable to microbiota (Hood et al., 2009; Paulsen et al., 2017). Yet, the contribution of glacier-derived DOC to seawater DOC is largely unknown.

In contrast to DOC, the concentration of particulate organic carbon (POC) in the ocean is often low and can reach values of <1 μmol L⁻¹. POC concentration varies pronouncedly with biological production and drives food web interactions at the higher trophic levels as well as carbon export fluxes. For the Arctic Ocean, it has been suggested that a longer ice-free period and thinner sea-ice, as well as the changing ice cover and the increase in melt ponds, will influence the light field for phytoplankton and may therefore lead to higher annual phytoplankton production (Arrigo et al., 2014; Arrigo and Van Dijken, 2015). This may also be stimulated by increasing amounts of anthropogenic CO₂ (Engel et al., 2013). The overall impact of sea-ice retreat on primary production, carbon cycling and partitioning between dissolved and particulate organic matter in the Arctic Ocean is still largely unknown. POC flux to depths in the ice-covered Arctic Ocean is usually extremely low (Cai et al., 2010; Harada, 2016) and is considered to be amongst the lowest in the global ocean (Honjo et al., 2008). However, with the transformation to a thinner cover, recent observations have detected phytoplankton blooms even beneath heavy snow-covered sea ice very early in the season (Assmy et al., 2017). In addition, ballasting of gypsum has recently been reported to increase the POC export flux (Wollenburg et al., 2018). Whether and how further seasonal and spatial shifts in primary production, as well as shifts in phytoplankton compositions, will influence POC standing stocks, transformation of organic matter and export is still an open question (Meier et al., 2014).

The Fram Strait, located in the transition zone between the northern North Atlantic and the central Arctic Ocean, is the only deep gateway to the Arctic Ocean. In the eastern Fram Strait,

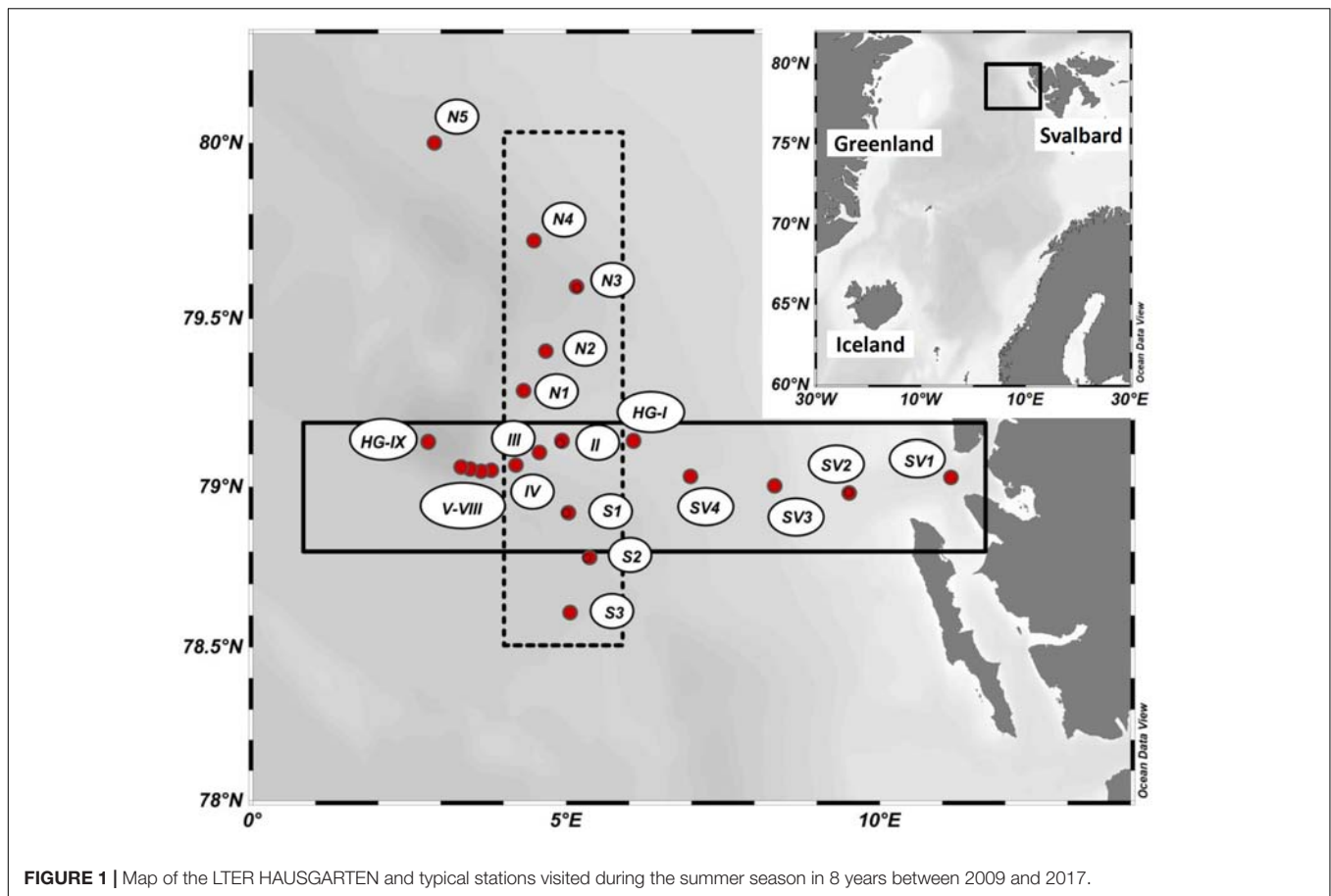


FIGURE 1 | Map of the LTER HAUSGARTEN and typical stations visited during the summer season in 8 years between 2009 and 2017.

the West Spitsbergen Current (WSC) carries warm (2.7°C – 8°C) Atlantic water into the Arctic Ocean, while the East Greenland Current (EGC) transports cold ($\sim -1.7^{\circ}\text{C}$ – 0°C) polar water in the upper 150 m toward the south in the western part of the Fram Strait. During the past decades, several studies on plankton dynamics have been carried out, which suggested shifts in phytoplankton community composition and size structure, changing from larger diatoms to smaller flagellates during the summer period in this area. This is co-occurring with higher advection of warmer North Atlantic water and less sea ice (Nöthig et al., 2015). Recent model results predicted a substantial difference in the pathways of carbon flow after warming and a shift in plankton community composition (Vernet et al., 2017), but overall small differences in the carbon export. Long-term monitoring from 1991 to 2012 revealed that chlorophyll-*a* (Chl-*a*) concentrations remain relatively constant in the colder western Fram Strait, while they continue to increase in the warmer eastern Fram Strait (Cherkasheva et al., 2014; Nöthig et al., 2015). The Long Term Research (LTER) observatory HAUSGARTEN (more details in Soltwedel et al., 2016) is situated in the eastern Fram Strait (Figure 1) and particles and biomass dynamics, including POC concentration, have been monitored since 1999 and DOC concentration has been monitored since 2009. Here, we analyze variations of surface water (0–100 m) concentrations of DOC and POC during summer for the HAUSGARTEN over

the period 2009 to 2017, and investigate how physical controls, such as the origin of water masses, and biological controls, in particular phytoplankton and bacteria, may explain the observed data variability. We also discuss how intra-seasonal variations in bloom dynamics and differences in the time of sampling may affect trends that we see in this long-term time series.

MATERIALS AND METHODS

Field Sampling

Up to 21 monitoring stations were visited every year between 2009 and 2017 (except for 2013) in the area at and around the LTER observatory HAUSGARTEN, i.e., between 78.0°N and 79.9°N , and 2.8°E and 11.1°E , with the research vessel *POLARSTERN* during eight cruises (Figure 1 and Supplementary Table S1). Field samples were always collected in summer (June–August) between the surface and 100 m depth. At selected stations, deep profiles were recorded and samples collected down to 2500 m depth. A rosette sampler, equipped with a SEA-BIRD CTD system and 24 Niskin bottle (12 L), was used to determine depth profiles of temperature and salinity, and to collect seawater from defined depths. Subsamples were taken in PE bottles and processed on board immediately after sampling as described below. Hydrographic data for this period, including

seawater temperature and salinity, were retrieved at PANGAEA. Since not all stations were visited each year, the numbers of samples varied between the years (**Supplementary Tables S1**).

Chlorophyll *a*

For Chlorophyll *a* (Chl-*a*), 0.5 – 2 L seawater were filtered onto glass fiber filters (Whatman GF/F) under low vacuum (<200 mbar). The filters were stored frozen at -20°C until analysis. Pigments on the filters were extracted with 5–10 ml of 90% acetone. Therefore, filters were sonicated in an ice bath for <1 min, and further extracted for 2 h in the refrigerator. Prior to measurement, they were centrifuged for 10 min at 5000 rpm at 0°C . Chl-*a* concentration was determined fluorometrically (Turner Designs), together with total phaeophytin concentration after acidification (HCl, 1.0 N) slightly modified to the methods described in Edler (1979) and Evans and O'Reily (1980), respectively. The standard deviation of replicate test samples was <10%.

Satellite-Derived Chlorophyll-*a* Concentrations

Satellite Chl-*a* concentrations, for the months April to August 2009 to 2017, were taken from the CMEMS Arctic product version 3¹. The data product is provided at 0.01×0.01 deg (ca. 1×1 km) pixel resolution and is based on the ESA Ocean Color Climate Change Initiative Remote Sensing Reflectance [merged, bias-corrected Remote Sensing Reflectance (Rrs); details see Sathyendranath et al., 2012] data, which are used to compute surface Chl-*a* (mg m^{-3}). The Rrs data are generated by merging the data from SeaWiFS (Sea-viewing Wide Field-of-view Sensor on Orb-View-2), MODIS (Moderate resolution Imaging Spectrometer on Aqua) and MERIS (Medium Resolution Imaging Spectrometer on ENVISAT) sensors and realigning the spectra to that of the SeaWiFS sensor. Chl-*a* concentration is estimated from the OC5ci algorithm, a combination of OCI (Hu et al., 2012) and OC5 (Gohin et al., 2008), developed at Plymouth Marine Laboratory (PML). Detailed description of the product and its calibration and validation given in the associated validation reports and quality documentation (see text footnote 1). The 8-days average products within 78.42°N – 79.5°N and 2.27°E – 6.2°E were analyzed for the mean, median, and standard deviation within the entire region. Following the method described in Nöthig et al. (2015), we determined the start and the end of a bloom for the chl-*a* satellite data set using a threshold value of 0.85 mg/m^3 chl-*a*.

Particulate Organic Carbon

For particulate organic carbon (POC), aliquots of 1 to 6 L of seawater were filtered at low vacuum (<200 mbar) onto combusted (4 h at 500°C) GF/F filters (pore size: $0.7 \mu\text{m}$). Filters were stored frozen (-20°C) until analysis. Prior analysis, filters were soaked in 0.1 N HCl for removal of inorganic carbon and dried at 60°C . POC concentrations were determined with a Carlo Erba CHN elemental analyzer.

¹<http://marine.copernicus.eu>

Dissolved Organic Carbon

For dissolved organic carbon (DOC) duplicate samples of 20 mL seawater were filtered through combusted GF/F filters and collected in combusted glass ampoules. Samples were acidified with 80 μL of 85% phosphoric acid, flame sealed and stored at 4°C in the dark until analysis. In 2017, samples were filtered through $0.45 \mu\text{m}$ GMF filters and acidified with 20 μL of 30% hydrochloric acid, flame sealed and stored at 4°C in the dark until analysis. DOC samples were analyzed by high-temperature catalytic oxidation (TOC-VCSH, Shimadzu) (Sugimura and Suzuki, 1988) using the modified protocol of Engel and Galgani (2016). The DOC concentration was determined in each sample out of 5 to 8 replicate injections. Replicate measurements varied with 2% standard deviation.

Bacterial Cell Abundance

Bacteria were counted by flow cytometry (FACS Calibur, Becton Dickinson) according to Gasol and del Giorgio (2000). Briefly, 4.5 mL were fixed with 25% glutaraldehyde (1% final concentration), and stored at -20°C until analysis. Immediately before analysis, samples were sonicated for 5 s, and filtered through a $50 \mu\text{m}$ mesh. Cells in 400 μL of sample were stained with the DNA-binding dye SybrGreen I (Invitrogen). The flow of the cytometer was calibrated with solutions of fluorescent latex beads [TruCount Beads™ (BD) and the Fluoresbrite® fluorescent beads (Polyscience, Inc., Warrington, PA, United States)]. Fluorescent beads were also added to each sample as an internal standard. The detection limit was 34 cells per 1 mL of sample and measurement error associated to this method was 2%.

Data Analysis

Average values are given by their median value and standard deviation unless otherwise stated. Depth integrated values for the water column (0–100 m) were calculated by linear interpolation of values obtained at 4–6 sampling depths in the range 5–100 m. Concentrations in the water column above the first value and below the last were assumed to be equal to the first and last value, respectively. Kruskal-Wallis One Way Analysis of Variance on Ranks and non-parametric *post hoc* pairwise multiple comparison (Dunn's Test) were applied for analysis of inter-annual variability. Statistical tests in data analysis have been accepted as significant for $p < 0.05$. Calculations, statistical tests and illustration were performed with Microsoft Office Excel 2010, Sigma Plot 12.0 (Systat), Ocean Data View (Schlitzer, 2015).

RESULTS

Physical Conditions at the Study Site

Considering the full period (2009–2017), seawater temperature in the upper 100 m of the water column ranged between -1.726 and 8.622°C , and salinity between 30.149 and 35.533 (data not shown). Adopting water mass classification for the region (Amon

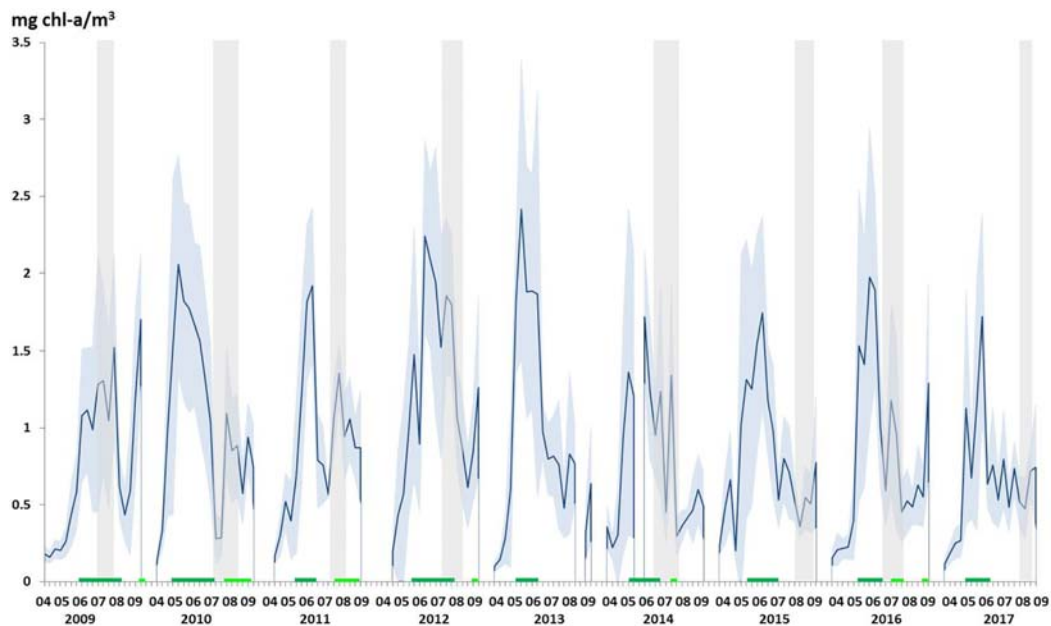


FIGURE 2 | Average (mean) chlorophyll *a* (Chl-*a*) concentrations during the period April–August from 2009 to 2017 as derived from satellite data (the standard deviation is indicated by the shaded area). Periods of the 1st bloom and the 2nd blooming time within a year (mean value above 0.85 mg/m³ chl-*a* concentration) are indicated by dark and light green lines, respectively. Periods of campaigns are indicated by gray bars. Chl-*a* concentration averages are based on 8-days average products within the HAUSGARTEN area (78.42°N–79.5°N and 2.27°E–6.2°E).

et al., 2003), both temperature and salinity in our data set were apparently influenced by the West Spitsbergen Current (WSC), carrying warmer ($>3^{\circ}\text{C}$) and more saline (>34.90 ppt) North-Atlantic waters poleward, and by the East Greenland Current (EGC), transporting cooler and fresher Polar Waters to the South. Polar Waters is a practical definition and includes all waters with salinity <34.7 and temperature $<0^{\circ}\text{C}$. Since organic carbon production in the ocean is closely connected to primary production, we analyzed phytoplankton biomass as indicated by Chl-*a* concentration from April to August, using remote sensing data obtained from SeaWiFS, MODIS, and MERIS (Figure 2). At the beginning of our time series (2009–2011), two blooms per year were regularly appearing, while the second blooms were absent or only there for a week in the more recent years. The duration of the first bloom was between three (minimum: 2011) and eleven (maximum: 2012) weeks with an average of seven weeks. The 2nd bloom's duration, if appearing, was one (in 2012, 2014, 2016), two (2009), six (2010), and seven (2011) weeks.

In general, from 2010 to 2017, seawater sampling during the cruises was conducted after occurrence of the phytoplankton biomass peak, as suggested from Chl-*a* concentration averaged over the HAUSGARTEN sampling-area (Figure 2). In those years, phytoplankton blooms, i.e., $>1\ \mu\text{g Chl-}a\ \text{L}^{-1}$, typically peaked in early June. Only in 2009, the time of sampling coincided with highest area-averaged Chl-*a* concentration during that year, albeit concentrations in 2009 were lower than maximum concentrations in other years. In general, the spatial coverage of phytoplankton blooms was also

larger during the month of June (sometimes also in July; Figure 3), while in 2009 high Chl-*a* concentrations in the HAUSGARTEN area were observed later in summer (July and August).

Variability of Organic Carbon Concentration

Dissolved Organic Carbon (DOC)

Overall, DOC concentration in the upper 100 m of the water column ranged between ~ 40 and $170\ \mu\text{mol L}^{-1}$ ($n = 643$) (Figure 4A and Table 1). Highest concentrations were observed within the upper 20 m, declining slightly to 30 m. Considerable variability was still observed at 100 m ranging between 40 and $95\ \mu\text{mol L}^{-1}$. In general, observed values lie within the range of previously determined DOC concentrations for the Fram Strait (Amon et al., 2003). Variability of DOC concentration clearly decreased below 250 m depth. Two deep profiles recorded in 2016 showed relatively stable DOC concentration between 250 and 2500 m of $52 \pm 2\ \mu\text{mol L}^{-1}$ ($n = 10$) (Figure 5A). This value is higher than the lowest values recorded for the upper 100 m of the water column in other years (Figure 4A) and may indicate deep export of water with higher DOC concentration, e.g., waters of polar origin, and/or processes leading to lowered DOC concentration in the surface ocean, such as DOC adsorption onto particles. DOC concentrations at the two deep stations in 2016 strongly increased toward the surface with highest values of $82\text{--}88\ \mu\text{mol L}^{-1}$ determined at 5 m depth. This indicates that DOC concentration at the immediate sea surface may clearly

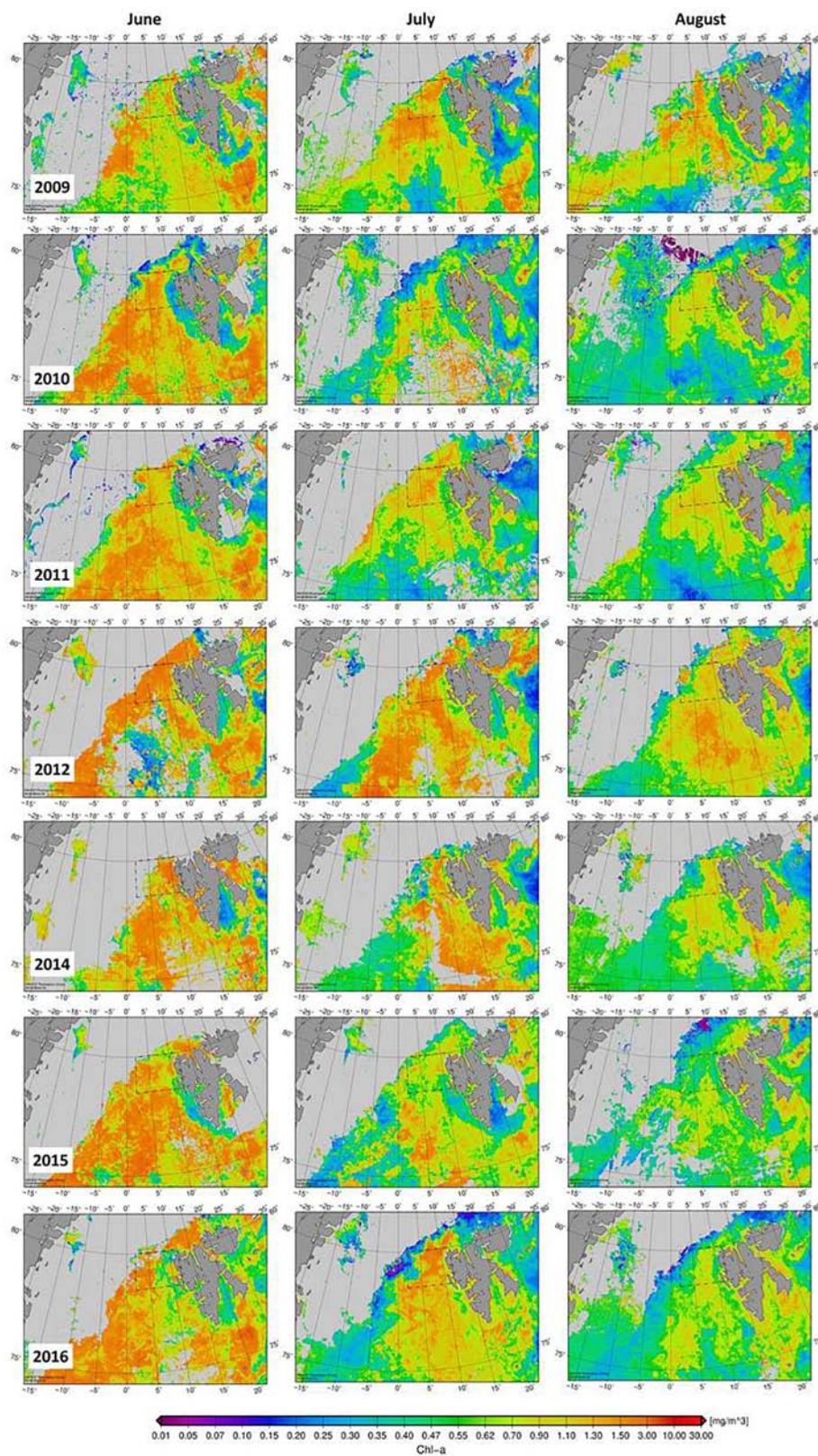
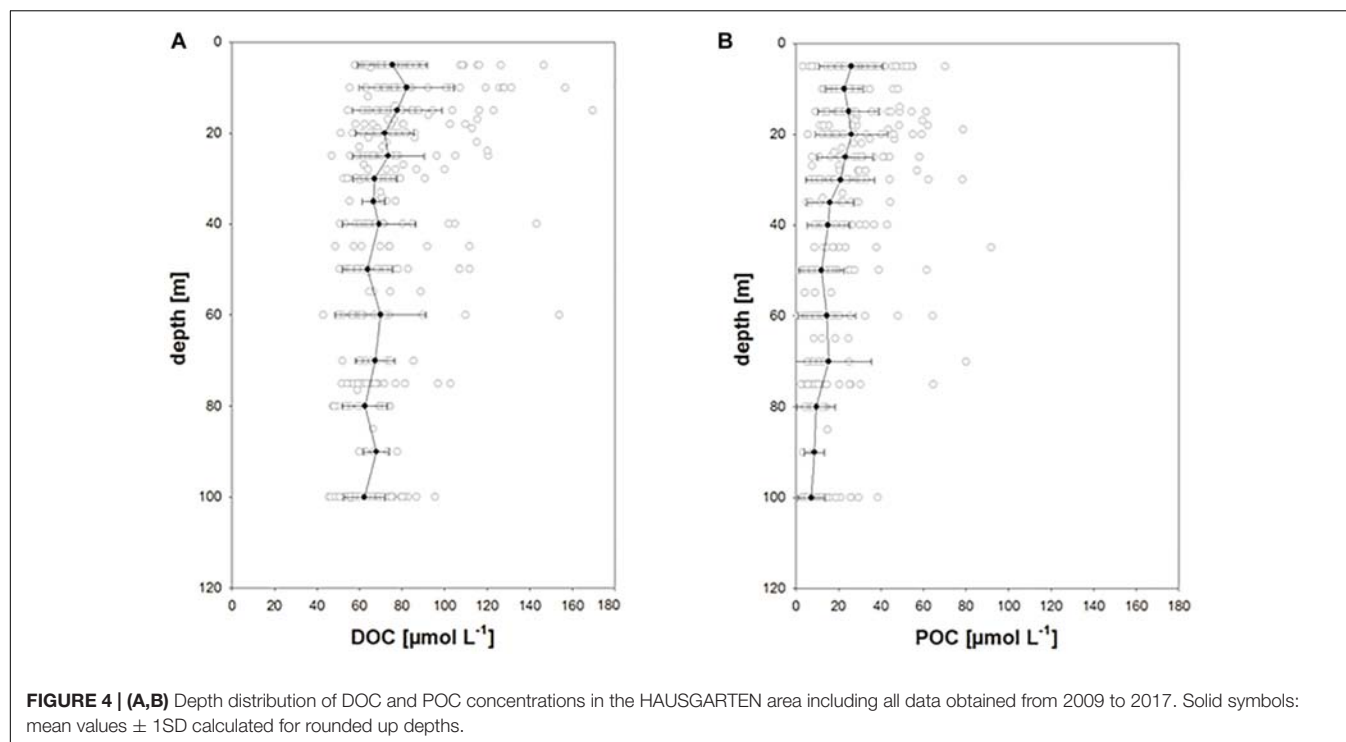


FIGURE 3 | Spatial variability of satellite derived Chl-a concentration (mg m^{-3}) in the Fram Strait during summer months (June–August) when sampling has been conducted. No cruise was conducted in 2013; data not available for 2017. Land area is indicated by dark gray shade, cloud coverage by lighter gray.



exceed DOC values typically recorded at 10 or 20 m depth by CTD sampling.

There was a pronounced inter-annual variability of DOC concentration with annual average values ranging from $59 \pm 8 \mu\text{mol L}^{-1}$ in 2015 to $73 \pm 24 \mu\text{mol L}^{-1}$ in 2016 (**Figure 6A**). No clear trend in DOC concentration was observed over the study period. However, differences in DOC concentration between years were statistically significant ($p < 0.001$), indicating a major control of DOC concentration by biological and/or physical factors in the surface ocean. The year 2016 stood out as the year of highest median DOC concentration of $73 \mu\text{mol L}^{-1}$ and highest data variability ($n = 86$) with $\sim 25\%$ of all data $> 100 \mu\text{mol L}^{-1}$. In contrast, only little variability was observed in 2014 with DOC concentrations ranging from 56 to $73 \mu\text{mol L}^{-1}$. However, the number of observations in 2014 of $n = 27$ was also lowest. Some years were not significantly different from each other, as revealed by multiple pairwise comparison of individual years. Specifically, the 2 years with highest DOC concentrations (2010, 2016) were not significantly different from each other as were the years with lowest DOC concentrations (2012, 2014, 2015, 2017). Annual minimum DOC concentration ranged between $40 \mu\text{mol L}^{-1}$ in 2017 and $59 \mu\text{mol L}^{-1}$ in 2016, not higher than deep DOC concentrations at 2500 m. This indicates a minimum DOC background concentration in order of $40 \mu\text{mol L}^{-1}$.

Particulate Organic Carbon (POC)

POC concentration in the upper 100 m ranged between 1 and $92 \mu\text{mol L}^{-1}$ (average: $13 \pm 14 \mu\text{mol L}^{-1}$, $n = 585$) (**Figure 4B** and **Table 1**) and was on average equivalent to $18 \pm 23\%$ of DOC concentration (range 1–190%). Like for

DOC, concentration of POC decreased with depth, but showed a more pronounced decrease below 30 m, where average POC concentration decreased from $\sim 20 \mu\text{mol L}^{-1}$ to values $< 10 \mu\text{mol L}^{-1}$. Deep profiles recorded in 2016 also showed little variation for POC concentration below 250 m with an average concentration of $2.59 \pm 0.86 \mu\text{mol L}^{-1}$ (**Figure 5B**). POC concentrations were highest in surface waters yielding $20\text{--}30 \mu\text{mol L}^{-1}$ at 10–20 m depth. Overall, when compared to the Redfield C:N ratio of 6.6, organic particles were only slightly enriched in carbon yielding a mean of 7.94 ± 4.18 ($n = 546$). This indicates that particles contained relatively fresh organic matter.

Substantial inter-annual variability was observed for POC concentration also, with median values ranging from $9 \pm 8 \mu\text{mol L}^{-1}$ in 2017 to $20 \pm 10 \mu\text{mol L}^{-1}$ in 2010 (**Figure 6B** and **Table 1**). Thus, highest average concentrations for POC did not coincide with those of DOC, although similar patterns were observed, like higher concentrations in 2016 compared to the previous and following year. Minimum concentration of POC during each sampling campaign ranged between 1 and $3 \mu\text{mol L}^{-1}$, indicating a very small pool of refractory POC, if any.

POC includes algal biomass that is often quantified by the concentration of Chl-*a*. Chl-*a* concentration in the HAUSGARTEN area ranged between the detection limit and $7.40 \mu\text{g L}^{-1}$, with an overall average of $0.51 \pm 0.97 \mu\text{g L}^{-1}$ (**Table 1**). High average Chl-*a* concentration was observed in 2009 and 2012. Absolute highest Chl-*a* concentrations were recorded at discrete stations in 2016, although average Chl-*a* concentration in that year was only $0.39 \mu\text{g L}^{-1}$, and therefore, below average of the observational period. In general, 2016 was

TABLE 1 | Range of variables determined in the upper 100 m of the LTR HAUSGARTEN in summer (June–August) from 2009–2017. Average values are given as median values, numbers of observations = *n*.

Year	2009	2010	2011	2012	2014	2015	2016	2017								
Cruise	PS74	n	PS76	n	PS78	n	PS80	n	PS85	n	PS93	n	PS99	n	PS107	n
T	10.07–17.07	59	02.07–23.07	156	14.07–29.07	100	10.07–26.07	118	28.06–14.07	26	24.07–12.08	102	28.06–09.07	86	26.07–14.08	100
°C	–1 to 7		–2 to 7		–2 to 8		–2 to 6		–1 to 6		–2 to 9		–1 to 7		–2 to 8	
PSU	33–35	59	32–35	156	30–36	100	33–35	118	32–35	26	32–35	102	32–35	86	32–35	100
μmol L ^{–1}	73	59	73	84	74	91	59	112	62	23	59	96	73	78	64	100
DOC avg.	43–103	59	47–121	84	55–170	91	48–154	112	56–73	23	47–88	96	59–157	78	40–92	100
DOC range	738	11	733	21	739	17	601	19	620	4	590	16	847	16	637	21
DOC avg.	13	52	20	121	18	65	18	89	19	5	9	90	13	85	9	79
POC avg.	3–33	52	3–80	121	3–57	65	2–92	89	3–23	5	2–25	90	3–79	85	1–35	79
POC range	131	11	236	15	178	8	196	14	98	1	86	15	171	16	79	16
mmol m ^{–2}	8.5	40	7.5	116	6.6	64	7.4	89	6.2	5	6.1	87	7.1	85	7.2	79
Mol:Mol	0.79	59	0.45	155	0.39	100	0.70	118	0.60	22	0.52	96	0.39	86	0.65	80
μg L ^{–1}	0.01–2.59	59	0.01–4.17	155	0.01–3.37	100	0.02–3.69	118	0.01–1.24	22	0.01–1.72	96	0.01–7.40	86	0.01–3.79	80
Chl-a range	10.7	59	11.3	92	3.29	98	9.25	84	6.27	23	9.35	96	5.73	75	5.33	80
bacteria avg.	2.33–21.0	59	2.59–35.1	92	0.16–18.8	98	1.47–29.6	84	2.39–23.0	23	3.20–21.0	96	2.21–75.0	75	2.31–12.5	80
bacteria range																

the year of highest variability of Chl-*a* concentration as also observed for DOC concentration.

Water-Column Integrated Pools of Organic Carbon

Integrated organic carbon concentrations in particulate and dissolved pools (0–100 m) accentuated the strong inter-annual variability of POC and DOC concentrations (**Figures 7A,C** and **Table 1**). Variability in water-column integrated data during the sampling campaigns, as indicated by total box height as well as by error bars, reflects the spatial heterogeneity of the systems. Accordingly, highest spatial heterogeneity was observed in the years 2010–2012 for both DOC and POC. In general, POC comprised between 6 and 49% of total organic carbon (TOC) (**Figure 7D**). While stocks of DOC and Chl-*a* showed no significant trend over time (**Figures 7A,B**), the amount of POC in the upper water column significantly decreased over the years ($r = -0.41$, $n = 105$, $p < 0.0001$) (**Figure 7C**), resulting in a significant decrease of [POC]:[Chl-*a*] ratios ($r = -0.30$, $n = 102$, $p < 0.001$; data not shown). In particular, depth-integrated POC values were highest during 2010–2012 and lowest in 2015 and in 2017. Along with the decrease in POC, a significant decrease of [POC]:[TOC] over time was observed ($r = -0.42$, $n = 98$, $p < 0.0001$) as well as a lower variability of [POC]:[TOC] in the years 2015–2017 (**Figure 7D**). This indicates a decreasing contribution of particulate carbon to total carbon over the observational period. Although depth-integrated values of Chl-*a* did not show a significant trend over time themselves, they were significantly related to POC ($r = 0.52$, $n = 125$, $p < 0.001$), indicating that changes in algal biomass were involved in the decline of POC over time.

Potential Controls of POC and DOC in the Fram Strait

Although all field campaigns in the eastern Fram Strait were carried out in summer, the timing of sampling varied slightly over the 8 years of observation, namely between the end of June and mid of August (**Figure 2**, **Supplementary Figure S1**, and **Supplementary Table S1**). As seen from satellite data, phytoplankton biomass clearly varies within summer, with phytoplankton blooms being more likely in June (**Figures 2, 3**). We therefore examined whether intra-seasonal variations in the time of sampling affected the amounts of DOC, POC and Chl-*a* in the upper water column (**Figures 8A–D**). Indeed, the day of sampling (Julian Day, JD) significantly correlated with the amount of DOC ($r = -0.44$, $p < 0.001$; $n = 126$) and became even more pronounced with the amount of POC ($r = -0.55$, $n = 105$, $p < 0.001$) in the water column, partly explaining the overall decline in [POC]:[TOC] ($r = -0.44$, $n = 98$, $p < 0.001$). High variability in DOC and POC concentrations, observed in 2010 and in 2012, could not be explained by day of sampling. In contrast to organic carbon, no significant correlation between time of sampling and Chl-*a* concentration was observed. However, variability in Chl-*a* concentration was highest between JD 180 and JD 210, reflecting higher spatial heterogeneity in

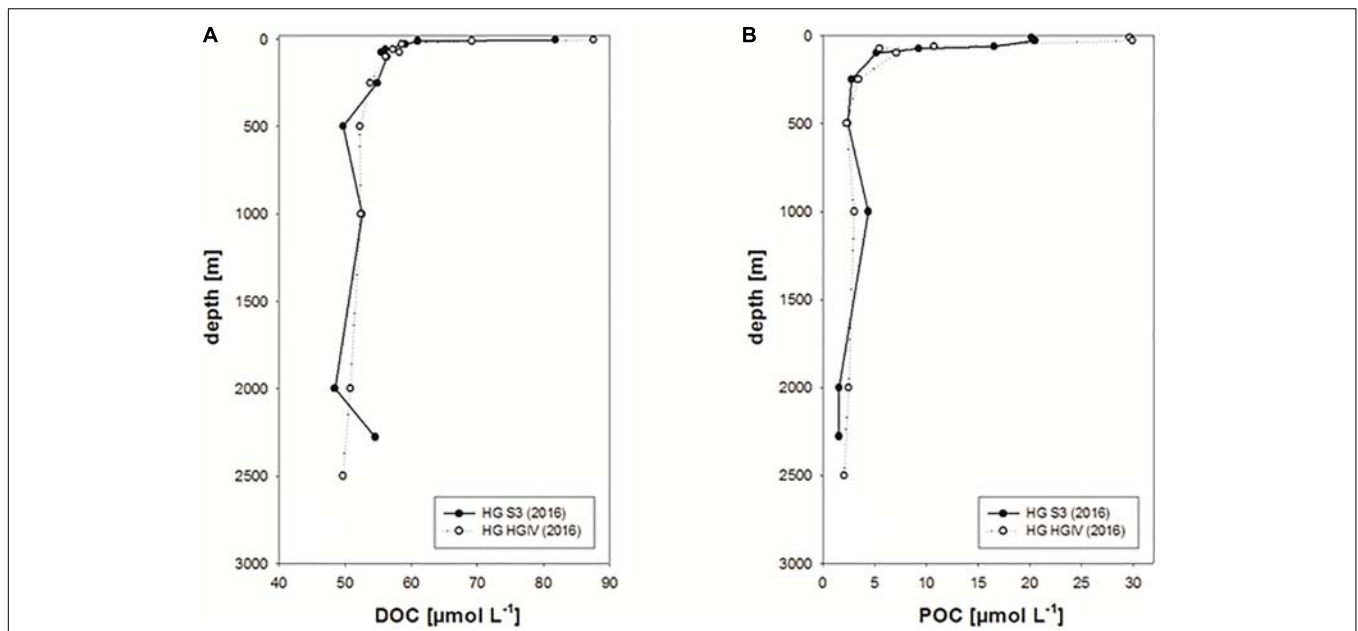


FIGURE 5 | (A,B) Deep profiles of DOC and POC concentrations observed in 2016 at the HAUSGARTEN stations S3 and HG/IV.

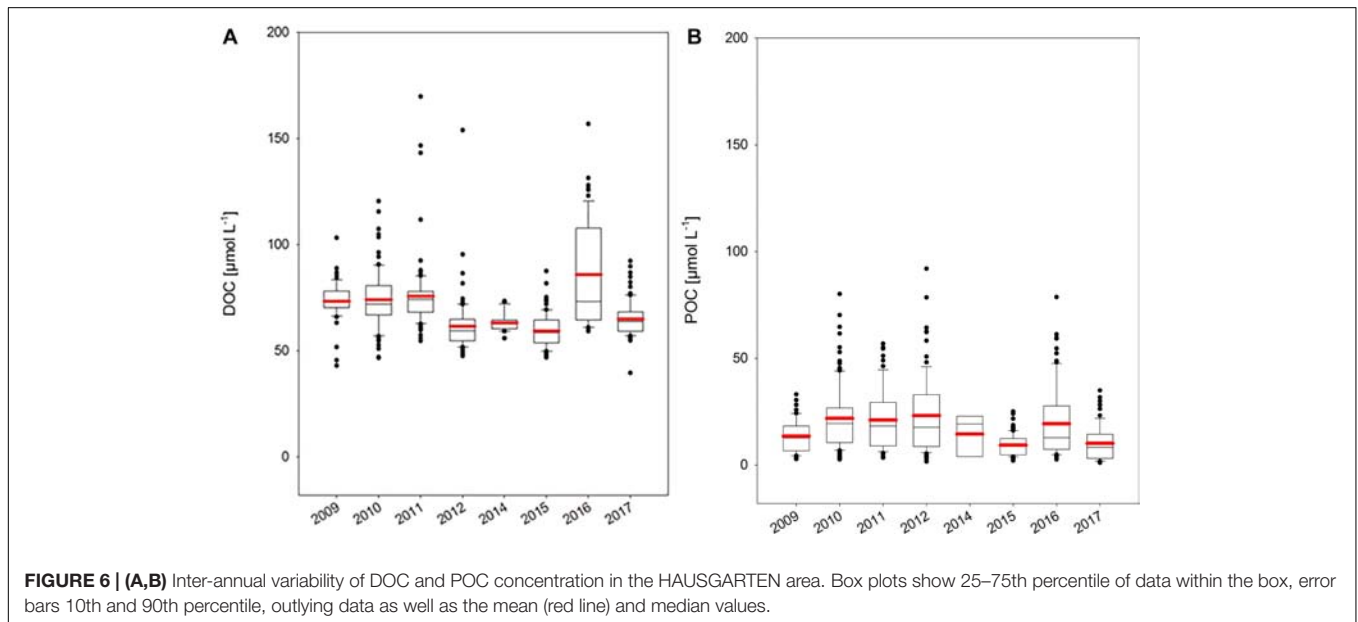


FIGURE 6 | (A,B) Inter-annual variability of DOC and POC concentration in the HAUSGARTEN area. Box plots show 25–75th percentile of data within the box, error bars 10th and 90th percentile, outlying data as well as the mean (red line) and median values.

phytoplankton distribution during June and July as also seen in the satellite data (Figure 3).

In addition to temporal variability, substantial spatial variability was observed for DOC and POC concentration and illustrated for one latitudinal and one longitudinal section located between 78.5–80°N and 4–6°E and between 78.8–79.2°N and 2–12°E (Figure 1), considering data from all years. In general, spatial patterns of low salinity and low temperature coincided with high DOC concentration, not only in the near surface waters (<20 m) but also at larger depth. Along the latitudinal

transect, lower salinity in the near surface waters coincided with colder temperature west of 5°E and with higher DOC concentrations at depth > 20 m (Figure 9). Along the longitudinal transect this co-occurrence of low temperature, low salinity and high DOC concentration was most pronounced between 79° and 79.5°N (Figure 10). Overall DOC concentration was significantly negatively related to temperature ($r = -0.21$, $n = 670$, $p < 0.001$) and to salinity ($r = -0.27$, $n = 474$, $p < 0.001$). No correlations with temperature or salinity were observed for POC concentration. In general, POC concentration

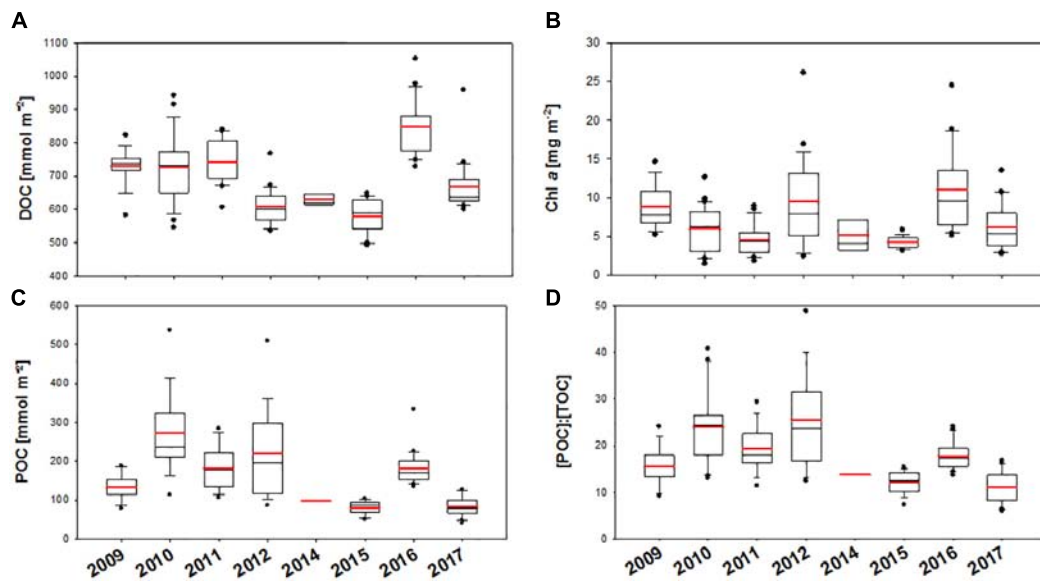


FIGURE 7 | (A–D) Inter-annual variability of integrated (0–100 m) DOC **(A)**, Chl a **(B)**, and POC **(C)** concentration as well as the percentage of POC in TOC **(D)** in the HAUSGARTEN area from 2009–2017. Box plots show 25–75th percentile of data within the box, error bars 10th and 90th percentile, outlying data as well as the mean (red line) and median values.

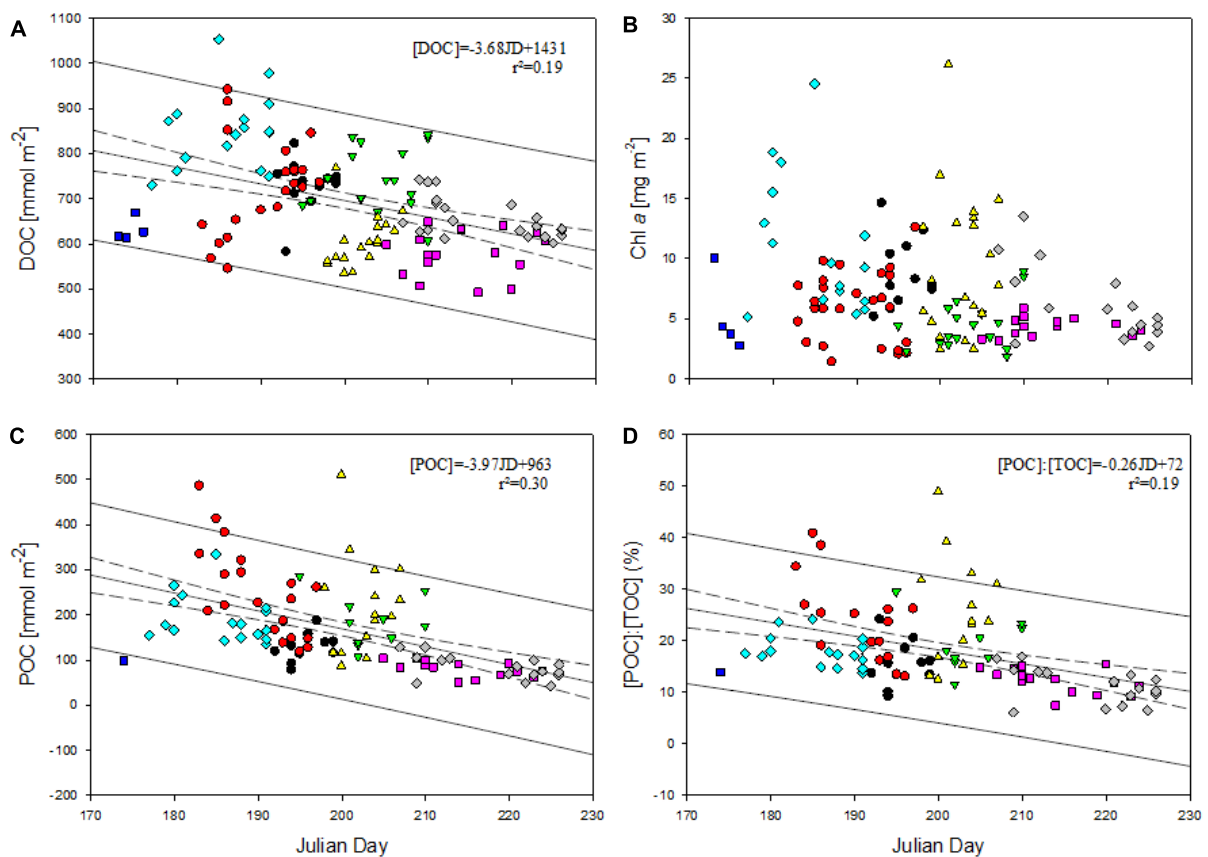


FIGURE 8 | (A–D) Relationship between integrated DOC **(A)**, Chl-a **(B)**, and POC **(C)** concentration and the Julian day (JD) of sampling as well as the ratio of POC to TOC **(D)**. Color code of years: black (2009), red (2010), green (2011), yellow (2012), blue (2014), pink (2015), turquoise (2016), gray (2017). Dashed lines represent the 95% confidence interval of the regression, solid lines the 95% confidence interval of the data population.

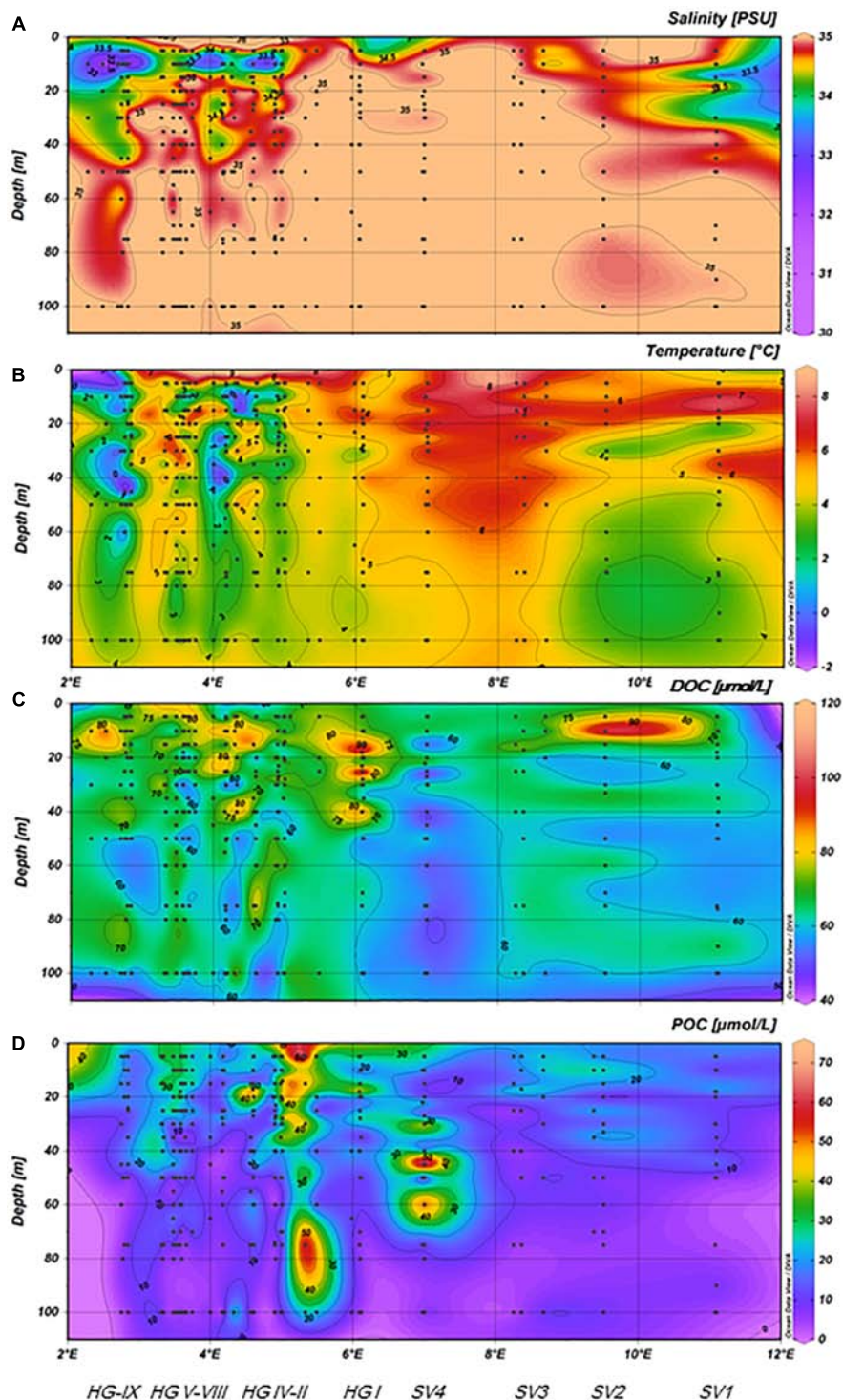


FIGURE 9 | (A–D) Spatial variability of salinity, temperature, DOC, and POC concentration along the ~79°N latitude during 2009–2017 (merged data).

was highly correlated with Chl-*a* concentration ($r = 0.70$, $n = 597$, $p < 0.0001$), while correlations between DOC and Chl-*a* concentrations were less pronounced, albeit still significant ($r = 0.23$, $n = 620$, $p < 0.001$).

Although DOC is the main substrate for heterotrophic bacteria, which overall varied between 3.3×10^5 cells mL^{-1} and 11.3×10^5 cells mL^{-1} (Table 1), no significant correlation was observed between bacterial abundance and

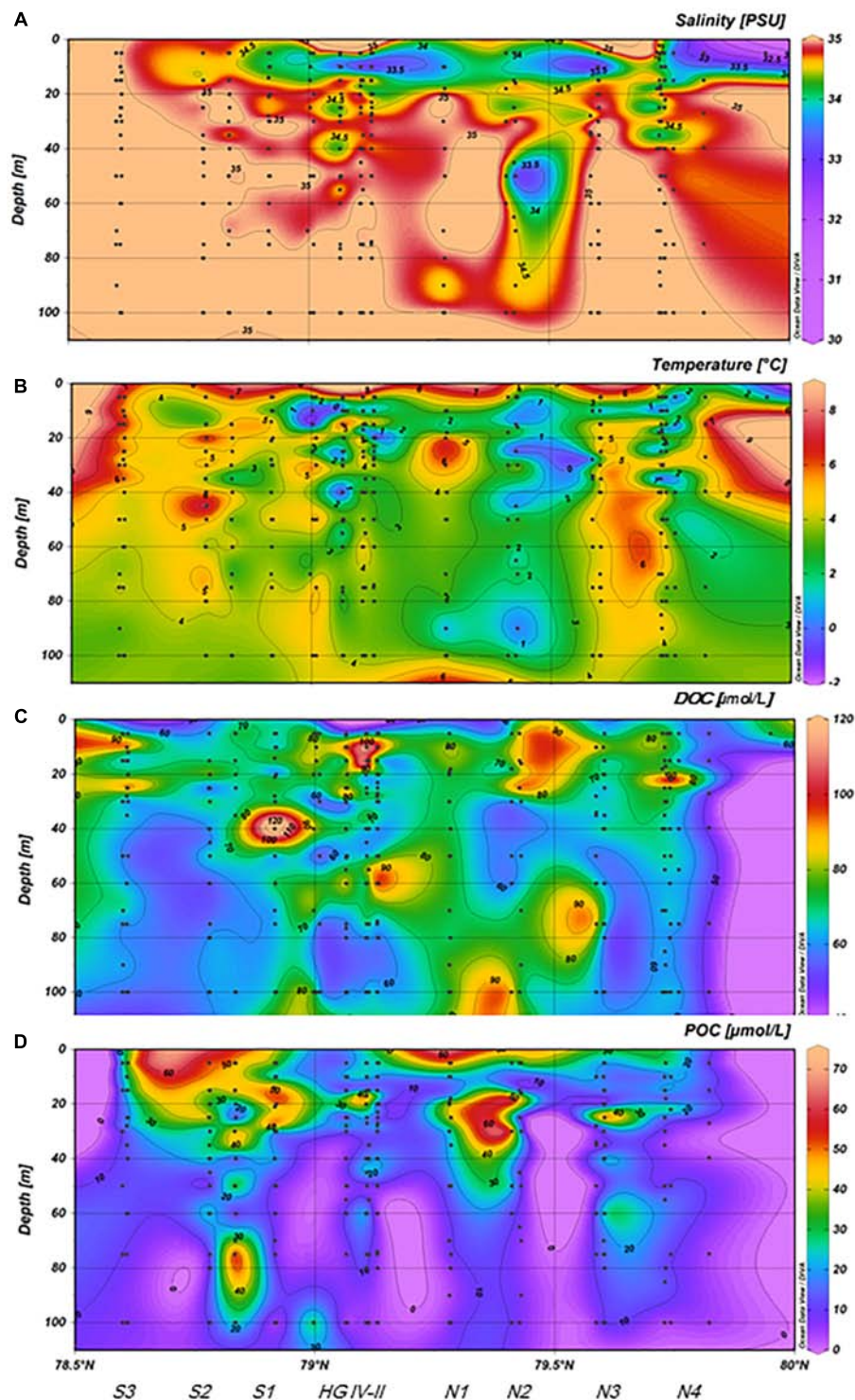
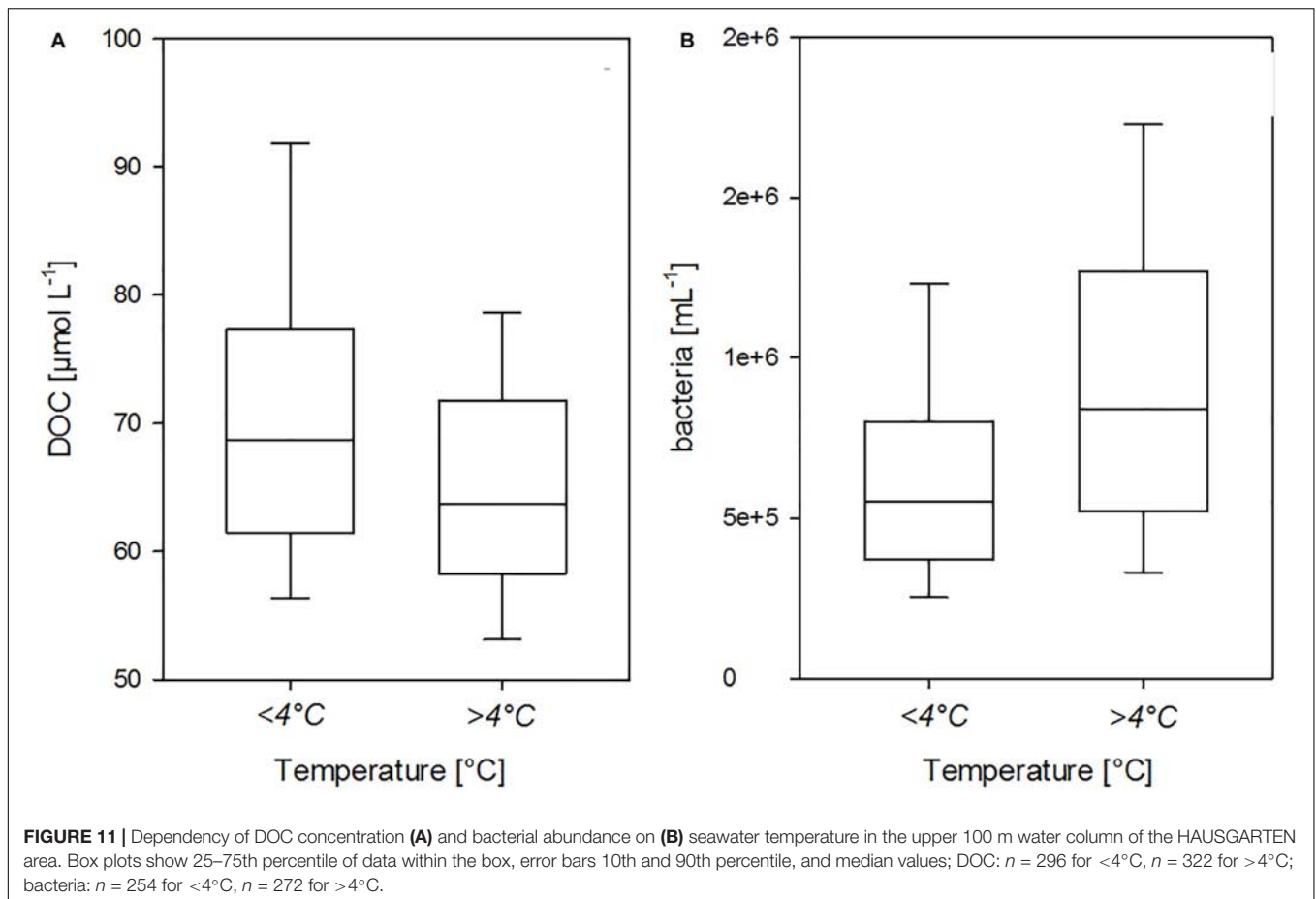


FIGURE 10 | (A–D) Spatial variability of salinity, temperature, DOC, and POC concentration along the ~5°E longitude during 2009–2017 (merged data).

DOC concentration over the total observational period. Instead, high DOC concentrations coincided with low bacterial abundance in waters $<4^{\circ}\text{C}$, whereas, higher bacterial abundance was observed mainly in seawater $>4^{\circ}\text{C}$ regardless

of DOC concentrations, indicating that water mass origin and temperature strongly impacted the coupling between DOC and bacteria in the Fram Strait (**Figure 11**). Thereby, DOC concentration and bacterial abundance at $<4^{\circ}\text{C}$ and



$>4^{\circ}\text{C}$ differed significantly (Mann-Whitney Rank Sum Test, $p_{\text{DOC}} < 0.001$, $p_{\text{bacteria}} < 0.0001$). No significant correlations between DOC and bacterial abundance were observed within water masses of temperatures $<4^{\circ}\text{C}$ or $>4^{\circ}\text{C}$ either. Instead, bacterial abundance was significantly correlated with Chl-*a* and POC concentration in waters $>4^{\circ}\text{C}$ ($r = 0.23$, $n = 302$, $p < 0.001$).

DISCUSSION

Biological formation of organic carbon is the initial step in a series of processes that controls CO_2 storage in the ocean, herewith the rate of exchange of CO_2 between the ocean and the atmosphere and may ultimately affect global climate. The Arctic Ocean has been assessed as a net sink of CO_2 at present day (Bates and Mathis, 2009), but predicting future carbon cycling requires a good understanding of the processes involved and their responses to environmental change, as well as profound knowledge of temporal variability in carbon pool size.

Our study focused on surface ocean organic carbon pools, i.e., DOC and POC, during the summer season in the Fram Strait and demonstrated a substantial spatial and temporal variability. Main factors identified to drive variability in the amount of DOC in this study were temperature and salinity, as colder and less saline Polar Waters entering the Fram Strait from

the North via the East Greenland Current, have higher DOC concentration than Atlantic water masses carried by the West Spitsbergen Current (Amon et al., 2003). Our findings are thus in good accordance with previous observations in the Fram Strait (Opsahl and Benner, 1999; Amon et al., 2003). Higher DOC concentrations in Polar Waters are due to an enhanced load of terrigenous compounds, mainly humic substances that enter the central Arctic Ocean through large river systems, e.g., Ob, Lena, Kolyma, Yukon, and Mackenzie (Kattner et al., 1999; Anderson and Amon, 2015). Humic substances are less bioavailable than autochthonous DOC mainly derived from primary production. The contribution of terrigenous substances in the DOC pool of the Fram Strait by Polar Waters may explain why we found no direct relationship between DOC concentration and bacterial abundance in our dataset. Nevertheless, the amount of DOC in the upper 100 m was significantly correlated to the day of sampling and presumably declines over the summer season, with a slope similar to that of POC. This and the observed correlation between DOC and Chl-*a* concentration indicate that, in addition to the terrigenous input, DOC concentration in the Fram Strait is controlled by the pelagic ecosystem. Experimental studies suggest that bacteria can utilize DOM of Polar Waters, particularly when temperature rises (Bussmann, 1999; Piontek et al., 2015). Thus, mixing of Polar Waters with warmer Atlantic waters in the Fram Strait may enhance bacterial

consumption of DOC, further stimulated by the production of fresh DOC over summer. However, a more targeted molecular analysis identifying the autochthonous and labile DOC fraction would be required, in order to understand microbial cycling of the DOC pool.

POC concentration in the upper water column of the Fram Strait was clearly related to plankton, primarily phytoplankton growth, partially explaining spatial and temporal variability. However, in contrast to Chl-*a*, our data revealed a decline in the amount of POC over the years 2009–2017. Since the amount of POC also declined with the JD of sampling, we cannot separate intra-seasonal from inter-annual variability. The observed decline of POC concentration over the years 2009–2017 may simply reflect changes in the ecosystem over summer, such as enhanced growth limitation of phytoplankton by inorganic nutrients, changes in phytoplankton community composition, or in heterotrophic feeding activity. In contrast to POC and DOC, no clear decline in depth-integrated Chl-*a* concentration was observed, neither for the summer season nor for the total period. One explanation may be a seasonal shift to species with a lower [POC]:[Chl-*a*] content, or a physiological acclimation, i.e., photoadaptation, of cells responding to decreasing light intensity, e.g., after solstice on June 21 or inter-annual variability in radiation during summer, with increasing Chl-*a* production (Morgan and Kalff, 1979). Yet, we cannot rule out that the observed POC decline occurred independently of intra-seasonal variation, and was induced by climate changes. Seasonal progression of the pelagic ecosystem over summer partly resembles effects expected for warming scenarios. A recent model study investigated a warming event in the Fram Strait, with a resulting shift from diatoms to flagellates, and indicated an ecosystem change toward an increase in the microzooplankton abundance, and thus a switching of other zooplankton feeding from herbivory to omnivory, detritivory and coprophagy (Vernet et al., 2017). Rising temperature has been suggested to shift carbon pathways and the partitioning from particulate to dissolved pools (Wohlers et al., 2009; Kim et al., 2011; Vernet et al., 2017). Also, a decrease in cell size of phytoplankton communities has been attributed to warming (Sommer and Lengfellner, 2008) and may affect POC concentration more than Chl-*a* concentration (Geider, 1987; Wohlers-Zöllner et al., 2012). In addition, an earlier on-set of phytoplankton growth due to the changing ice scape may result in a temporal shift of phytoplankton biomass peaks already under the ice and lead to earlier peaks of the associated POC concentration (Assmy et al., 2017). It is indeed likely that the observed changes in the POC pool reflect climate induced changes in the Fram Strait that have been reported for the phytoplankton community composition during ice-free summer months, i.e., the shift from diatoms to flagellates (Nöthig et al., 2015) and a stronger activation of the microbial loop, leading to higher heterotrophy but surprisingly not to a reduced carbon export flux (Vernet et al., 2017).

Clearly our study underlines the need for a better resolution of seasonal changes in Arctic ecosystems as scientific basis to identify inter-annual or even decadal variability. New

observational approaches and instruments are needed to cover the annual cycle with much higher temporal resolution, in order to capture the onset, peak and fate of biological production. A coupling of high frequency biological, chemical and physical observations will help to disentangle controls and consequences of environmental change, especially in remote and rapidly changing areas such as the Arctic, where data coverage has been impaired by accessibility. For organic matter, measurements of the optically absorbing and fluorescing fraction of DOM, i.e., colored and fluorescent dissolved organic matter (CDOM and FDOM), have demonstrated a strong correlation with DOC concentration for the Arctic Ocean (e.g., Stedmon et al., 2011; Gonçalves-Araujo et al., 2015), and to give proxies for water masses in the Greenland Sea (Stedmon et al., 2015; Gonçalves-Araujo et al., 2016). The further spectral resolution development of FDOM and also backscattering sensors to be mounted to autonomous platforms in the Arctic Ocean can help to resolve the variability of DOC and POC on larger temporal and spatial scale and may give insight into autochthonous sources of DOM (Romera-Castillo et al., 2011; Loginova et al., 2016). However, sensor measurements still need to be evaluated regularly and carefully, with discrete measurements of parameters directly assessing the different components of the carbon pool. This requires discrete ship-based observations, such as those currently undertaken by national and international efforts [e.g., FRAM (Soltwedel et al., 2016), Distributed Biological Observatory (DBO; Moore and Grebmeier, 2018), Changing Arctic Ocean (CAO)², and the MOSAiC campaign starting in fall 2019]³. In order to understand the impact of a changing physical environment on ecosystem dynamics and carbon cycling, we urgently need to close the knowledge and data gap on seasonal variability in the Arctic.

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All authors listed have made a substantial, direct and intellectual contribution to the work, and approved it for publication.

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²www.changing-arctic-ocean.ac.uk

³<https://www.awi.de/en/focus/mosaic-expedition.html>

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Asynchronous Accumulation of Organic Carbon and Nitrogen in the Atlantic Gateway to the Arctic Ocean

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Nitrogen (N) is the main limiting nutrient for biological production in the Arctic Ocean. While dissolved inorganic N (DIN) is well studied, the substantial pool of N bound in organic matter (OM) and its bioavailability in the system is rarely considered. Covering a full annual cycle, we here follow N and carbon (C) content in particulate (P) and dissolved (D) OM within the Atlantic water inflow to the Arctic Ocean. While particulate organic carbon (POC), particulate organic nitrogen (PON), and dissolved organic carbon (DOC) accumulated in the surface waters from January to May, the dissolved organic nitrogen (DON)-pool decreased substantially ($\Delta - 50 \mu\text{g N L}^{-1}$). The DON reduction was greater than the simultaneous reduction in DIN ($\Delta - 30 \mu\text{g N L}^{-1}$), demonstrating that DON is a valuable N-source supporting the growing biomass. While the accumulating POM had a C/N ratio close to Redfield, the asynchronous accumulation of C and N in the dissolved pool resulted in a drastic increase in the C/N ratio of dissolved organic molecules (DOM) during the spring bloom. This is likely due to a combination of the reduction in DON, and a high release of carbon-rich sugars from phytoplankton, as 32% of the spring primary production (PP) was dissolved. Our findings thus caution calculations of particulate PP from DIN drawdown. During post-bloom the DON pool increased threefold due to an enhanced microbial processing of OM and reduced phytoplankton production. The light absorption spectra of DOM revealed high absorption within the UV range during spring bloom indicating DOM with low molecular weight in this period. The absorption of DOM was generally lower in the winter months than in spring and summer. Our results demonstrate that the change in ecosystem function (i.e., phytoplankton species and activity, bacterial activity and grazing) in different seasons is associated with strong changes in the C/N ratios and optical character of DOM and underpin the essential role of DON for the production cycle in the Arctic.

Keywords: particulate and dissolved organic matter, nitrogen pools, dissolved primary production, high latitude ecosystems, marginal ice zone, Svalbard, West Spitsbergen Current, microorganisms

INTRODUCTION

In the Arctic Ocean, productive shelf seas surround parts of the deep and less productive central basins (Sakshaug, 2004). The primary production (PP) is subject to a strong seasonal cycle in irradiance, as well as to a varying degree of sea ice cover. Sea ice can restrict PP due to shading but can also lead to enhanced PP by stabilizing the water column as it melts. In spring when the ice starts melting, intense phytoplankton blooms can be encountered along the retreating ice edge (Sakshaug and Skjoldal, 1989). Although seldom lasting for longer than 20 days (Perrette et al., 2011), these blooms can generate over 50% of the annual PP in the Arctic Ocean (Sakshaug, 2004) and are hence crucial in fuelling the arctic marine food web. For the less productive central Arctic Ocean, import of organic matter (OM) from its more productive adjacent shelf seas is suggested as an important marine carbon source to sustain its heterotrophic metabolism (Walsh et al., 1989; Wheeler et al., 1997; Shen et al., 2012). Both, the Chukchi (Wheeler et al., 1997; Bates et al., 2005; Davis and Benner, 2005; Mathis et al., 2007) and the Barents Sea (Fransson et al., 2001; Kivimae et al., 2010), are net exporters of organic carbon to the central Arctic Ocean, but the largest transporter of volume, heat and biomass is the West Spitsbergen Current (WSC) (Fahrbach et al., 2001; Shen et al., 2012). In order to understand the ecosystem of the Arctic Ocean it is therefore essential to understand what governs the production, transformation and export of OM and nutrients at the productive rim of the Arctic Ocean, especially within the Atlantic water inflow to the Arctic Ocean.

Microorganisms play a fundamental role in the cycling of organic carbon and nutrients. Through photosynthesis, microscopic marine phytoplankton fix inorganic carbon into OM. The photosynthetically produced OM does not only occur as phytoplankton cells (i.e., particulate form), but is also released by phytoplankton as dissolved organic molecules (DOM) through passive diffusion of low molecular compounds over the cell membrane (Bjørnsen, 1988; Maranon et al., 2004) or by active excretion (Fogg, 1983; Mykkestad et al., 1989; Baines and Pace, 1991). The direct production of DOM by phytoplankton (PP_{diss}) can be a substantial fraction (up to 50%) of the gross PP and appears to be elevated especially in high latitude systems relative to temperate (Kirchman et al., 1991; Vernet et al., 1998). Further, the different species of phytoplankton produce photosynthate of different qualities. In the Arctic, for example, the bloom-forming prymnesiophyte *Phaeocystis pouchetii* produces copious amounts of neutral and acidic polysaccharides, which are released from exponentially growing cells, and can induce gel or transparent exopolymer particles (TEP) formation, in turn effectively promoting passive sinking (Le Moigne et al., 2015; Assmy et al., 2017; Engel et al., 2017).

The trophic fate of the photosynthetically fixed OM is different for particulate and dissolved forms. POM serves as food for phagotrophic (particle feeding) organisms of successively larger size and hence forms the basis for an effective energy transfer from the primary producers to higher trophic levels. During the transfer through the phagotrophic grazer food chain, parts of

POM are transferred to DOM, through sloppy feeding, excretion and defecation by phagotrophs (Jumars et al., 1989; Nagata and Kirchman, 1991; Strom et al., 1997). Viral lysis of bacteria (Middelboe et al., 1996) and phytoplankton (Bratbak et al., 1992; Agusti and Duarte, 2013) are additional DOM producing processes. The oceanic DOM pool thus originates from different autochthonous sources, both directly from the phytoplankton by PP_{diss}, and indirectly through the release of originally particulate matter through heterotrophic activities.

The process by which DOM is formed impacts its chemical composition and nutritional value for bacteria. DOM excreted by phytoplankton is often rich in carbohydrates (Ittekkot et al., 1981; Mykkestad, 1995), and can have high C/N ratio relative to the Redfield ratio (106:16 or 6.6) (Redfield, 1934, 1958), whereas DOM produced by trophic interactions is richer in nitrogen and consequently have C/N ratios closer to or below Redfield (Bronk et al., 1998; Saba et al., 2011). Generally, bacterial growth efficiency is higher when the C/N ratio of DOM is low, i.e., closer to their cellular C/N stoichiometry of 7.9 (Von Stockar and Liu, 1999), especially when inorganic N (DIN) sources are limiting (del Giorgio and Cole, 1998; Pradeep Ram et al., 2003). Labile DOM has a C/N stoichiometry of around 10, whereas the corresponding value for refractory DOM is 17.4 (Hopkinson and Vallino, 2005). Bacteria are likely to be net mineralizers of inorganic nutrients during degradation of labile DOM and net consumers of nutrients during degradation of substrates with a higher C/N stoichiometry (Goldman et al., 1987).

Primary productivity in the ocean is often limited by the availability of N. The productive surface layer of Arctic marine ecosystems is particularly low in DIN supply, as the concentrations of inorganic N in Arctic runoff are among the lowest worldwide (Dittmar and Kattner, 2003), there is little supply via N-fixating organisms (Sipler et al., 2017), and as strong stratification limits vertical mixing (Codispoti et al., 2013; Randelhoff et al., 2015). Therefore, Arctic Ocean phytoplankton blooms are mostly found to terminate with the depletion of nitrate (Popova et al., 2013; Tremblay et al., 2015). The current CO₂-enrichment of our atmosphere stimulates PP both on land (Reich et al., 2006) and in the ocean (Holding et al., 2015; Sanz-Martín et al., 2018). It is, therefore, speculated whether N-limitation could become more widespread in the future, especially in the Arctic where PP is also predicted to be stimulated by a longer ice-free season. This stresses the need to improve our understanding of how both phytoplankton and heterotrophic microorganisms affect the seasonal N-cycling in the region.

Here, we investigate (1) the link between biological processes and the partitioning of N-pools between DIN, dissolved organic nitrogen (DON), and PON during a full annual cycle and (2) the partitioning of particulate and dissolved PP during the spring bloom and post-bloom conditions, and how this influence the character and fate of the OM being produced. These observations are novel for the studied area and improve our knowledge on the interplay between biological processes and C/N stoichiometry of POM and DOM within the main Atlantic water inflow to the Arctic Ocean.

MATERIALS AND METHODS

General Sampling

The study was conducted on and off the shelf northwest of Svalbard (Figure 1) during cruises in January, March, May, August, and November 2014. The sampling concentrated on the core of the northwards drifting warm Atlantic water, which enters the Arctic Ocean north of Svalbard either south or north of the Yermak plateau. Heavy drift ice restricted the sampling to the shelf and shelf-break in May and August 2014. During January, March, and November, the area north of Svalbard was largely ice-free, which allowed sampling off the shelf-break into the Arctic Ocean during winter.

At all stations, depth profiles of temperature, salinity and fluorescence were taken with a CTD (Seabird SBE 911 plus). Water was sampled with Niskin bottles from discrete depths for analysis of inorganic nutrients, chlorophyll *a* (Chl *a*), microbial abundance, bacterial production (BP), as well as DOM and POM. In May and August, three stations were each sampled to investigate time-demanding processes, such as *in situ* PP and vertical export of POM. There are hereafter called “P-stations”: P1, P3, P4 in May (N.B. there is no P2 as moorings carrying PP incubations and sediment traps were lost), and P5, P6, P7 in August; see Figure 1 and Supplementary Table S1.

The sampling depths were 1, 5, 10, 20, 30, 50, 100, 200, 500, 750, and 1000 m. At stations on the shelf or shelf-edge with depths <1000 m, the deepest sample was taken close to the sea floor, and the sampling resolution close to the surface was increased by inserting additional sampling at 40 and 75 m, as well as at the depth of the Chl *a* maximum.

Chlorophyll *a* Concentration and Primary Production

Chl *a* ($\mu\text{g L}^{-1}$) was determined for two different size fractions by collecting suspended material onto Whatman GF/F, as well as membrane filters of 10 μm pore size (Whatman Nuclepore Track-Etch membrane). This allowed dividing the Chl *a* (determined from GF/F filters) into total and micro-size (>10 μm). Chl *a* was determined fluorometrically (10-AU, Turner Designs) from triplicates of each filter type after extraction in 5 mL methanol at room temperature in the dark for 12 h without grinding.

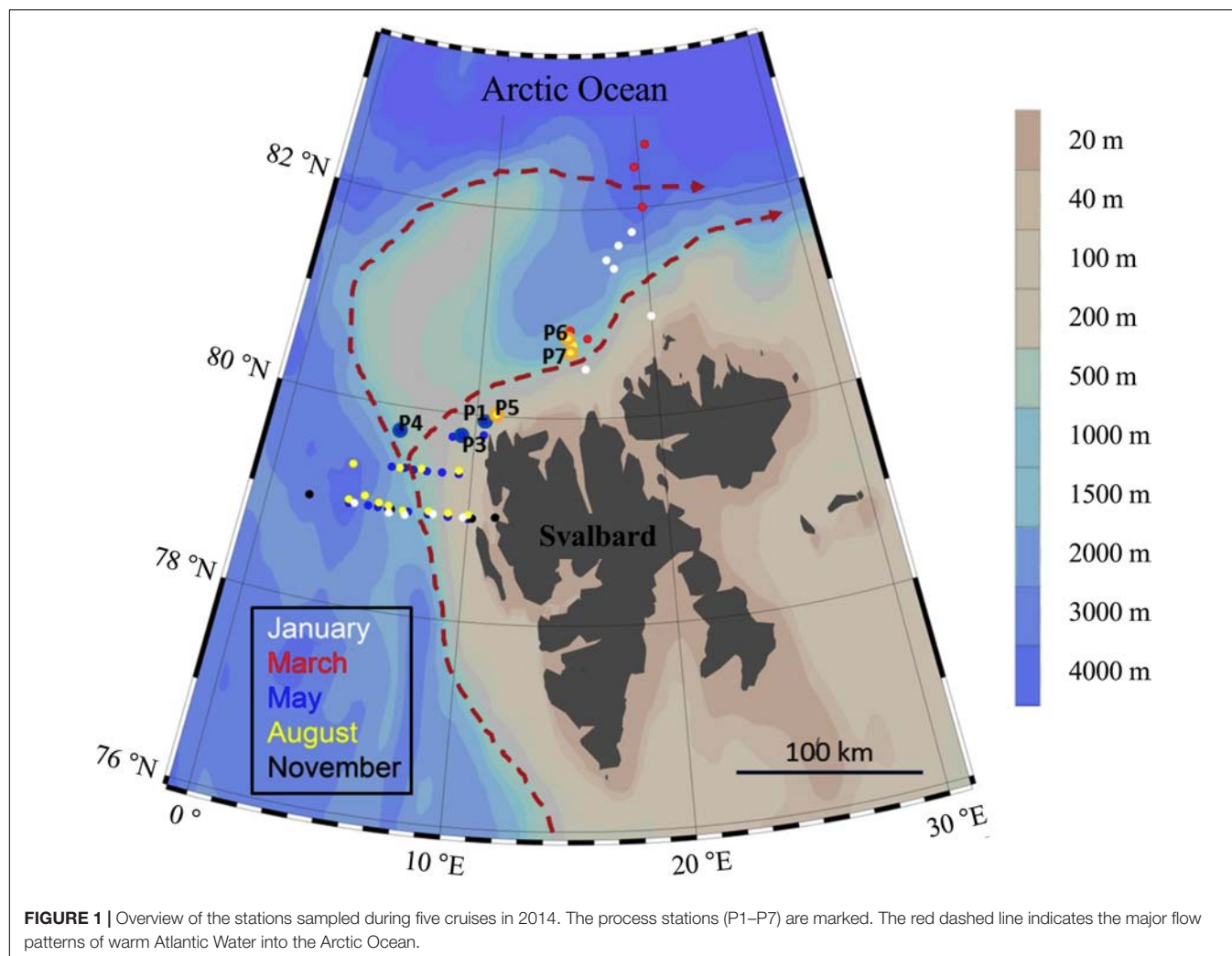
Water for PP measurements was collected from 0, 5, 10, 20, 30, 40, 50, and 75 m depth at all P-stations. The water from each depth was sampled and distributed in four 150 mL polycarbonate bottles; two light bottles and one dark bottle incubated *in situ* and one used as t_0 sample. 10 μCi of ^{14}C -labeled bicarbonate was dispensed into each bottle. The t_0 sample was immediately processed. For each depth, 100 mL were sampled onto a 6 mL scintillation vial containing 0.1 mL 6 N NaOH in order to estimate ^{14}C -bicarbonate concentration. The light and dark bottles were deployed at their respective sampling depths for approximately 22 h, using a mooring attached to an ice-float or drifting freely. At the end of the experiment, the bottles were recovered and sampled, keeping the bottles refrigerated. Light and dark bottles were treated equally: 0.2 mL of 20%

HCl was dispensed into each 6 mL scintillation vial containing either a Whatman GF/F filter (for PP_{part}) or 2 mL of seawater (for PP_{total}) in order to release any inorganic ^{14}C remaining in the sample. After 24 h, 5 mL of Ultima GoldTM XR LSC cocktail was added and the samples stored in the dark. On-shore, each vial was shaken and the ^{14}C activity measured in a Perkin Elmer scintillation counter (Tri-Carb 2900TR). PP was calculated by subtracting the activity in the dark bottle from the activity in the light bottles. Dissolved inorganic carbon (DIC) concentrations used for the calculation were measured by Melissa Cierici (pers. comm.) from total alkalinity and pH using the CO_2 -calculation program CO2SYS. For each depth, three PP estimates are provided, which are total primary production (PP_{total} , estimated from 2 mL water), particulate primary production (PP_{part} , estimated by filtering 98 mL water onto a Whatman GF/F filter), and dissolved primary production (PP_{diss} , which was calculated as $\text{PP}_{\text{total}} - \text{PP}_{\text{part}}$). The limit of detection is estimated at ca. 1 $\mu\text{g C L}^{-1} \text{d}^{-1}$. The percent dissolved PP ($\%\text{PP}_{\text{diss}}$) was calculated as $100 \times (\text{PP}_{\text{diss}}/\text{PP}_{\text{total}})$.

Bacterial Production, Carbon Demand, and Microbial Abundance

At the P-stations, BP was estimated from incorporation rates of ^3H -labeled leucine (specific activity: 5.957 TBq mmol^{-1}), measured by standard methods (Kirchman, 2001). Triplicate water samples of 1.9 mL volume were incubated with ^3H -leucine (final conc. 20 nM) from each profile depth in the dark at 1°C for 2 h. The incubation was terminated by adding trichloroacetic acid (TCA; final conc. 5%). To account for potential passive adsorption of radioactivity, a TCA-killed control sample was incubated with ^3H -leucine together with the live samples from each depth. All samples were microcentrifuged to collect the incorporated ^3H -leucine and rinsed with TCA and ethanol. The samples were dried before radio assaying with liquid scintillation liquid (Ultima GoldTM XR LSC cocktail) in a scintillation counter (Perkin Elmer Tri-Carb 2900TR). Leucine incorporation was converted into biomass production using a carbon fraction of proteins of 1.5 (Simon and Azam, 1989; Ducklow, 2003), assuming no isotope dilution. The bacterial carbon demand (BCD) was estimated as the sum of BP and bacterial respiration (BR). BR was estimated from BP as $\text{BR} = 3.69 \times \text{BP}^{0.58}$, according to Robinson (2008). Specific bacterial growth rates were calculated by dividing BP by the bacterial abundance.

Abundances of heterotrophic bacteria and nanoflagellates (HNF) were determined on an Attune[®] Focusing Flow Cytometer (Applied Biosystems by Life technologies) with a syringe-based fluidic system and a 20 mW 488 nm (blue) laser. Samples were fixed with glutaraldehyde (0.5% final conc.) at 4°C for minimum 2 h, shock-frozen in liquid nitrogen, and stored at -80°C until analysis. For enumeration of B and V, the samples were diluted 10-fold with 0.2 μm filtered TE buffer (Tris 10 mM, EDTA 1 mM, pH 8), stained with a green fluorescent nucleic-acid dye, SYBR Green I (Molecular Probes Inc., Eugene, Oregon) by incubation for 10 min at $+80^\circ\text{C}$. Prior to HNF-enumeration, the samples were stained with SYBR Green I (Molecular Probes, Eugene, OR, United States) for 2 h in the dark. A minimum of 1 mL was



measured at a flow rate of $500 \mu\text{L min}^{-1}$ and the population was discriminated from nano-sized phytoplankton and large bacteria on basis of green vs. red fluorescence following the protocol of Zubkov et al. (2007).

Total, Particulate and Dissolved Organic Matter

Total organic carbon (TOC) in unfiltered seawater was analyzed by high-temperature combustion using a Shimadzu TOC-V_{CSH}. All samples were acidified with HCl (to a pH of around 2) and bubbled with pure N_2 gas in order to remove any inorganic carbon. Calibration was performed using deep seawater and low carbon reference waters. A blank consisting of milliQ water was analyzed every eighth sample to assess any day-to-day instrument variability. The concentration of total nitrogen (TN) was determined simultaneously by high-temperature combustion using a CPH-TN nitrogen analyser. Total organic nitrogen (TON) was calculated by subtracting the inorganic nitrogen ($\text{DIN} = \text{NO}_3 + \text{NO}_2 + \text{NH}_4^+$) measured from parallel nutrient samples. The instrument was calibrated using a standard series of acetanilide and the accuracy of the

instrument was evaluated using seawater reference material provided by the Hansell CRM (consensus reference material) program.

For analysis of particulate organic carbon (POC) and particulate organic nitrogen (PON), triplicate subsamples (100–500 mL) were filtered onto pre-combusted Whatman GF/F glass-fiber filters (450°C for 5 h), dried at 60°C for 24 h and analyzed on-shore with a Leeman Lab CEC 440 CHN analyser. Prior to analysis, the dried samples were fumed by concentrated HCl for 24 h before re-drying at 60°C for 24 h to remove inorganic carbon.

The concentration of the DOM fractions was calculated as

$$\text{DOC} = \text{TOC} - \text{POC}$$

and

$$\text{DON} = \text{TN} - \text{DIN} - \text{PON}$$

Samples for NO_3^- and NO_2^- were stored frozen in acid-washed plastic bottles, and analyzed with standard seawater methods, applying Flow Solution IV analyser (OI Analytical) calibrated using reference seawater (Ocean Scientific

International). Samples for NH_4^+ were analyzed immediately upon sampling with the sensitive fluorometric method (Holmes et al., 1999). The sum of NO_3^- , NO_2^- , and NH_4^+ is called DIN hereafter.

Colored Dissolved Organic Matter (CDOM)

Samples for light absorption by colored DOM (CDOM) were taken directly from the Niskin bottles and filtered through $0.2\ \mu\text{m}$ pore size filters (PALL Life Sciences IC Acrodisc® with Supor® membrane) into pre-combusted 30 mL amber glass vials using non-pyrogenic syringes. The samples were stored in dark at $+4^\circ\text{C}$ until analysis. The absorbance of CDOM was measured in the spectral range between 240 and 700 nm with an increment of 0.5 nm using a Shimadzu UV-2450 spectrophotometer and 10 cm quartz cells with ultrapure Milli-Q as a reference, following a procedure described in Stedmon and Markager (2001). The following spectrophotometer settings were used: slit width of 5 nm and fast scan speed. Absorbance values were baseline corrected by MQ blanks and then converted to an absorption coefficient [$a_{\text{CDOM}}(\lambda)$ with m^{-1} as unit] following:

$$a_{\text{CDOM}}(\lambda) = 2.303 \cdot A(\lambda)/l + K,$$

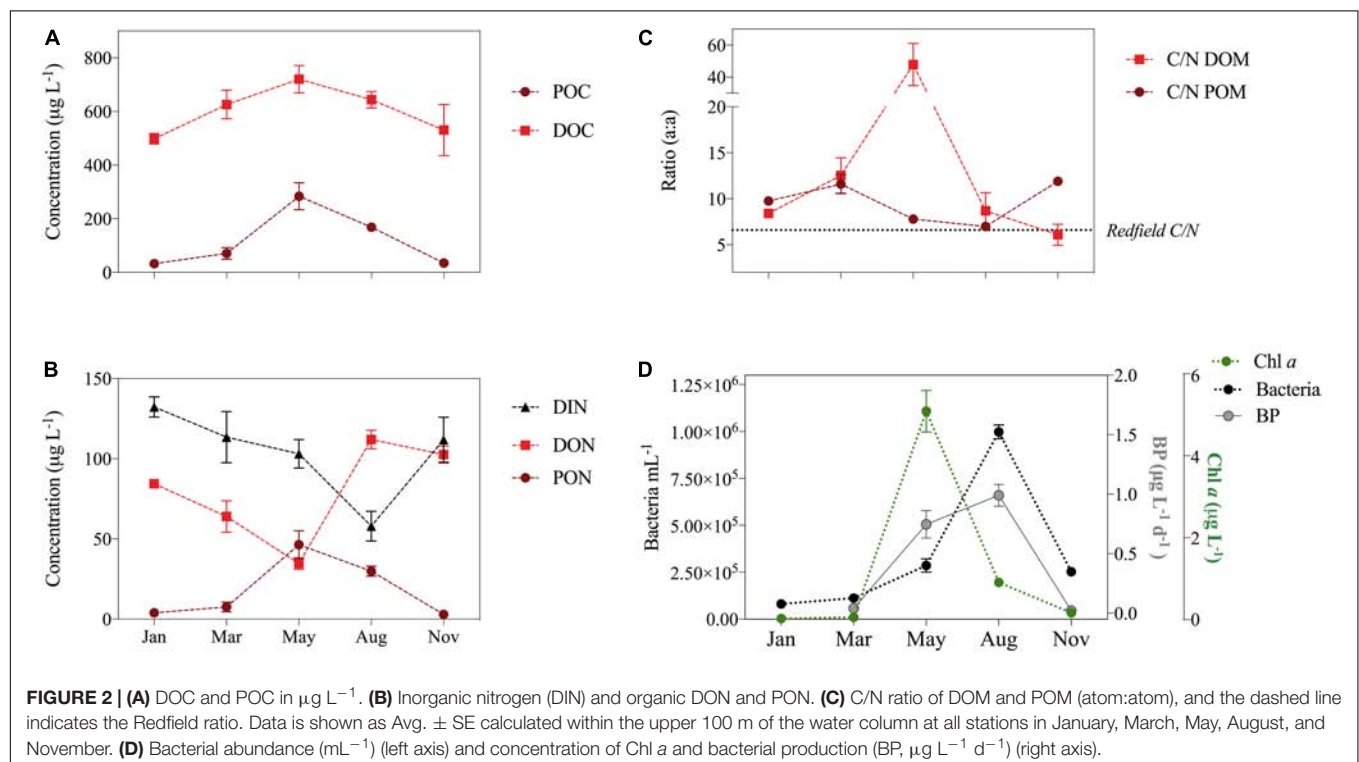
where $A(\lambda)$ is the absorbance at a given wavelength λ and l is the path length of a cuvette in meters (here 0.1 m). The spectral properties were modeled with an exponentially decreasing function and a constant using the software Prism 7.

$$a(\lambda) = a(\lambda_0)e^{-S(\lambda_0-\lambda)},$$

where S (nm^{-1}) is the spectral slope coefficient describing the relative steepness of the spectrum. The amplitude is a proxy for concentration, and the slope parameter is often used as a proxy for changes in the composition of CDOM (Stedmon and Markager, 2001; Twardowski et al., 2004). K is a background constant that allows for any baseline shifts or attenuation not caused by OM (Markager and Vincent, 2000). We here calculate the slope using most of the spectrum: $S[300\text{--}650\ \text{nm}]$ and within the UVB part of the spectrum only: $S[275\text{--}295\ \text{nm}]$.

Vertical Export of POM

Vertical export of POM within and out of the upper 200 m of the water column was measured by the deployment of a sediment trap array at all P-stations. The array was free drifting, either attached to an ice floe or hold by a buoy, and hence sampling was carried out in a semi-Lagrangian manner. The array had transparent plexiglass cylinders of 450 mm height and an inner diameter of 72 mm (aspect ratio 6.2) as traps, mounted to the array on a gimballed frame. No baffles were used in the cylinders opening, and no fixatives were added to the traps prior to deployment. Cylinders were deployed pairwise as traps at 20, 30, 40, 50, 60, 90, 120, and 200 m depth for 21 to 27 h. After recovery, the content in the traps was collected and subsamples processed for POC and PON, as described above. The traps used in this study (KC maskiner og laboratorieutstyr, Denmark) have been tested against ^{234}Th data from suspended and trapped material in the Barents Sea, demonstrating good catchment efficiency (Coppola et al., 2002).



Data Availability and Analyses

Data on microorganisms, Chl *a*, carbon and nitrogen measurements included in the paper are available from the data repository PANGAEA via Paulsen et al. (2017). Data were tested for normal distribution with a Shapiro–Wilk test in SPSS Statistics 23[®]. As normality was not given for all parameters, a non-parametric Spearman's correlation was applied to evaluate the covariation between different parameters.

RESULTS

To describe the production and fate of C and N pools the study included two different sampling strategies (1) measurements of C and N-pools along transects within the Atlantic inflow to the Arctic Ocean during five different seasons; winter (January), pre-bloom (March), spring bloom (May), post-bloom (August), early winter (November) (**Figure 1**) (2) dedicated process (P) stations focusing on the most productive season, May and August, to determine rates of PP and the sinking POM.

General Hydrography

All samples were collected within the Atlantic inflow to the Arctic Ocean and thus the dominating water masses were; the relatively warm and saline Atlantic Water (sal > 34.9, temp > 2°C) at the bottom and Arctic Surface Water at the surface, which is Atlantic water that has been influenced by sea ice melt and therefore is relatively colder and fresher (sal < 34.9). Sea ice samples from March indicate that sea ice meltwater is low in both DOC concentration ($480 \pm 80 \mu\text{g L}^{-1}$, $n = 4$) and CDOM absorption, e.g., $a_{\text{CDOM}}(290)$ ($0.28 \pm 0.04 \text{ m}^{-1}$, $n = 4$).

The Seasonal Cycle of Organic Matter

Throughout the year DOC dominated OM, with POC contributing successively more during the light season from March to May (**Figure 2A**). Both POC and PON displayed this seasonal pattern, with peak concentrations in May ($284 \pm 234 \mu\text{g POC L}^{-1}$, $46 \pm 41 \mu\text{g PON L}^{-1}$), causing a net accumulation of POM with a C/N ratio of 5.98 (calculated as $\Delta\text{POC}_{\text{January–May}}$ divided by $\Delta\text{PON}_{\text{January–May}}$) from January to May ($\Delta\text{POC}_{\text{January–May}}$ of $251 \mu\text{g POC L}^{-1}$ and $\Delta\text{PON}_{\text{January–May}}$ of $42 \mu\text{g N L}^{-1}$; **Table 1**). DOC concentrations also increased starting in January, peaking in May ($720 \pm 308 \mu\text{g DOC L}^{-1}$). The net accumulation of DOC from January to May ($\Delta\text{DOC}_{\text{January–May}} = 222 \mu\text{g C L}^{-1}$) was very similar to the net accumulation of POC during the same period.

Dissolved organic nitrogen concentrations, on the other hand, decreased from January to May, amounting to a net loss $\Delta\text{DON}_{\text{January–May}}$ of $49 \mu\text{g DON L}^{-1}$. DON concentrations then peaked in August ($109 \pm 36 \mu\text{g DON L}^{-1}$), corresponding to a $\Delta\text{DON}_{\text{May–August}}$ of $74 \mu\text{g DON L}^{-1}$ (**Table 1**). DIN decreased by $29 \mu\text{g DIN L}^{-1}$ from January to May meaning the DON-loss was 1.7 times larger than the DIN-loss. DIN continued to decrease until August (**Figure 2B** and **Table 1**), but not as much as DON. When summing the N-pools (PON, DON, and DIN) at the different seasons for the upper 100 m, the total nitrogen concentration (TN) remained stable throughout the period of

TABLE 1 | Average concentration ($\pm$ SD; $\mu\text{g L}^{-1}$) of total, dissolved, and particulate organic carbon (TOC, DOC, and POC), as well as of dissolved, particulate organic nitrogen (DON, PON), and inorganic N (DIN) within the upper 100 m of the water column at all stations in January, March, May, August, and November.

	January			March			May			August			November		
	Avg $\pm$ SD	$\Delta\text{November–January}$	Avg $\pm$ SD	$\Delta\text{January–March}$	Avg $\pm$ SD	$\Delta\text{January–May}$	$\Delta\text{March–May}$	Avg $\pm$ SD	$\Delta\text{January–May}$	Avg $\pm$ SD	$\Delta\text{May–August}$	Avg $\pm$ SD	$\Delta\text{August–November}$	Avg $\pm$ SD	
TOC	550 $\pm$ 94 (80)	–260	661 $\pm$ 129 (24)	111	964 $\pm$ 299 (141)	303	414	805 $\pm$ 180 (97)	–159	698 $\pm$ 96 (16)	–124	698 $\pm$ 96 (16)	–124	698 $\pm$ 96 (16)	
DOC	498 $\pm$ 90 (56)	–385	571 $\pm$ 137 (13)	73	720 $\pm$ 308 (86)	149	222	654 $\pm$ 215 (95)	–66	647 $\pm$ 99 (11)	–7	647 $\pm$ 99 (11)	–7	647 $\pm$ 99 (11)	
POC	33 $\pm$ 9 (56)	–2	71 $\pm$ 31 (13)	38	284 $\pm$ 234 (86)	213	251	168 $\pm$ 82 (103)	–116	35 $\pm$ 6 (12)	–133	35 $\pm$ 6 (12)	–133	35 $\pm$ 6 (12)	
DON	84 $\pm$ 9 (14)	3	51 $\pm$ 32 (12)	–33	35 $\pm$ 22 (64)	–16	–49	109 $\pm$ 36 (93)	74	81 $\pm$ 10 (10)	–26	81 $\pm$ 10 (10)	–26	81 $\pm$ 10 (10)	
PON	4 $\pm$ 1 (56)	1	8 $\pm$ 5 (12)	3	46 $\pm$ 41 (86)	38	42	30 $\pm$ 17 (103)	–16	3 $\pm$ 1 (11)	–27	3 $\pm$ 1 (11)	–27	3 $\pm$ 1 (11)	
DIN	132 $\pm$ 27 (56)	21	113 $\pm$ 34 (12)	–19	103 $\pm$ 54 (86)	–10	–29	58 $\pm$ 55 (103)	–45	111 $\pm$ 28 (11)	53	111 $\pm$ 28 (11)	53	111 $\pm$ 28 (11)	
ΔPOC : ΔPON				9.5		5.6	6		7.3		4.9				

observations (averaging $201 \pm 15 \mu\text{g TN L}^{-1}$), with a maximum in January ($220 \pm 37 \mu\text{g TN L}^{-1}$) and a minimum in May ($184 \pm 116 \mu\text{g TN L}^{-1}$).

The different seasonal dynamics of organic C and N pools led to opposing seasonal patterns in the C/N ratio of POM and DOM (**Figure 2C**). Particulate C/N ratios exceeded 10 during the winter months of January, March, and November, while during the productive season they dropped to an average of 7.8 ± 1.6 and 7.0 ± 1.1 in May and August, respectively. For DOM, highest C/N ratios (on average 48 ± 79) were observed during the spring bloom in May, and lowest in January (on average 8.4 ± 0.5) and August (on average 8.7 ± 11.4).

The pattern of seasonal Chl *a* concentration mirrored the pattern of POM, with highest average concentrations in May (**Figure 2A**). Consequently, Chl *a* and POC were strongly positively correlated in the annual dataset (**Table 2**). Annual concentration of DOC also co-varied with Chl *a*, albeit not as strongly as POC and PON. DON correlated negatively with Chl *a*. The concentrations of POC, PON, and DON were correlated negatively with DIN, while no such correlation was found for DOC. The highest abundances of bacteria (**Figure 2D**) and HNF were observed in August (**Supplementary Figures S2, S3**), as were highest median bacterial production rates (**Figure 2D**). However, the cell specific bacterial production was highest in May. Bacterial abundances correlated positively to the concentration of DON and weakly negatively to DOC, while BP correlated negatively to DOC and unrelated to DON (**Table 2**).

Seasonal Change in CDOM

The absorption spectrum provides both quantitative and qualitative information about CDOM. The intensity of absorption, $a(\lambda)$, at a specific wavelength (λ) is used as an expression of the CDOM concentration. The shape of the absorption spectrum, which can be described by the slope (S) indicates changes in CDOM composition. The absorption spectra of surface water (1–100 m) were averaged for each month and showed seasonal changes in the character of DOM (**Figure 3**) with the distinct absorption peak within the UV spectrum around 290 nm (range: 260–310 nm) in May being the most prominent change (**Figure 3A**). Vertically $a_{\text{CDOM}}(290)$ was elevated around 30–40 m at P1 and 2 but was not elevated at P3 (**Supplementary Figure S1**), and the absorption peak was further present below 100 m (data not shown) in May. In August, the spring-peak signal had disappeared (**Figure 3A** and **Supplementary Figure S1**) whereas a high absorption within the visible spectrum (400–600 nm) appeared. In the winter months, absorption in the visible spectrum was generally lower than in August and May (**Figures 3B,C**). The shape of the absorption spectrum was examined by fitting the exponential model. The slope estimated for the small UVB wavelength range S [275–295 nm] was by far lowest in May, and slightly lower in January and March (29.3 – $29.9 \mu\text{m}^{-1}$) than in August and November (30.7 – $31.8 \mu\text{m}^{-1}$). The slope of full spectrum S [300–650 nm] increased gradually from January ($16.1 \mu\text{m}^{-1}$) to March ($20.3 \mu\text{m}^{-1}$) to May ($25.7 \mu\text{m}^{-1}$), after which it decreased to $19.2 \mu\text{m}^{-1}$ in August and $18.9 \mu\text{m}^{-1}$ in November. It should be

noted that given the shape of the absorption spectra in May, the fit was poor for this month, i.e., low R^2 values (**Figures 3C,D**).

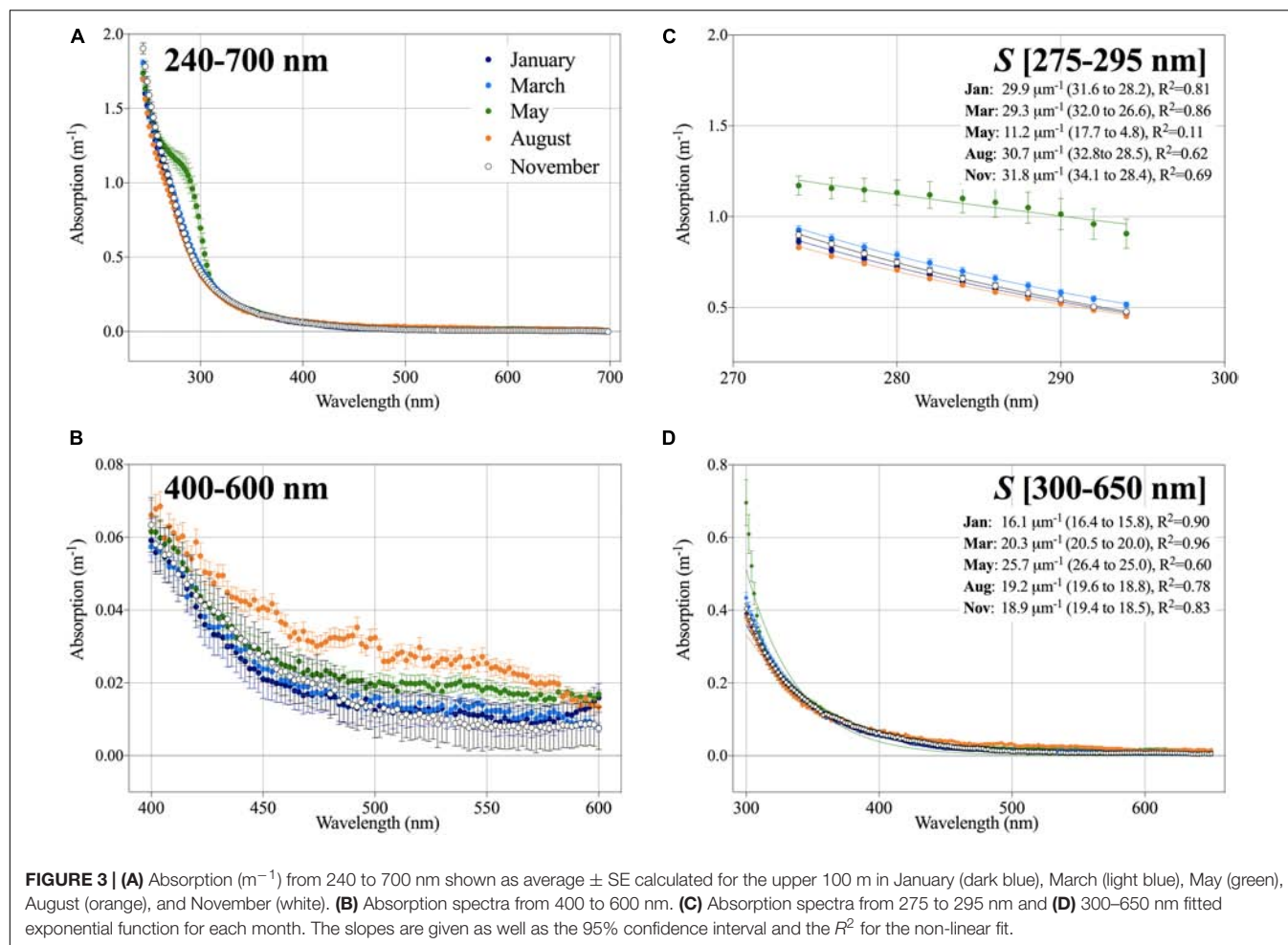
Physical Regime During Spring and Post-bloom

All process (P)-stations that were studied in more depth during the productive season were situated close to the ice edge Northwest-North of Svalbard (**Figure 1**). They shared similar hydrography, with Arctic Surface Water dominating the upper 40 m and Atlantic Water below. One exception was northernmost station P6, where Arctic Surface Water reached 150 m depth. The surface layer was fresher and warmer in August (**Figures 4A,B**) compared to May. The mixed layer depth was similar in May (10–11 m) and in August (9–15 m), while the photic zone deepened from approximately 20 m in May to 40 m in August (**Figures 4A,B**). For a more detailed description of the bloom stages and hydrography at the P-stations see **Supplementary Table S1** and [Reigstad and Wassmann, 2007; Randelhoff et al., 2018 (current special issue)]. In the following paragraphs, we present an average of the three P-stations profiles examined during spring bloom and post-bloom are plotted, in order to better visualize the differences between the two seasons. Every single P-station profile is included as **Supplementary Figures S1, S2**.

Primary and Secondary Production During Spring and Post-bloom

In May, an intensive ice-edge bloom was encountered at all three P-stations sampled and strong vertical gradients in PP were observed at all three P-stations (**Figures 4C–E**). For both PP_{part} and PP_{diss} , higher production rates were measured within the sea ice meltwater-influenced upper 10 m of the water column than below the pycnocline ($<1 \mu\text{g C L}^{-1} \text{d}^{-1}$). Maximum surface rates ($\text{PP}_{\text{part}} = 250$ and $\text{PP}_{\text{diss}} = 345 \mu\text{g C L}^{-1} \text{d}^{-1}$) were observed at station P1 (**Supplementary Figure S1**). PP rates in August were more than five times lower than in May and peaked in subsurface waters (**Figures 4C,D**). Highest PP_{part} ($45 \mu\text{g C L}^{-1} \text{d}^{-1}$) was measured at 10 m of station P7. PP_{part} rates dropped to $<1 \mu\text{g C L}^{-1} \text{d}^{-1}$ below 40 m depth at all stations in August, and hence elevated PP_{part} rates reached deeper in August than in May. The vertical profile of PP_{diss} did not mimic that of PP_{part} in August (**Figures 4C,D**). The highest rate of PP_{diss} ($21 \mu\text{g C L}^{-1} \text{d}^{-1}$) was measured at 10 m of station P5, while PP_{diss} rates at station P6 and P7 did not exceed $4 \mu\text{g C L}^{-1} \text{d}^{-1}$ at any depths. The relationship between PP_{diss} and PP_{part} differed between May and August. In May, PP_{diss} was strongly correlated to PP_{part} and moderately correlated to both total Chl *a* and Chl *a* $> 10 \mu\text{m}$ (**Table 3**), whereas similar relationships were not observed in August. Further, a moderate negative correlation of PP_{diss} with the concentration of DIN was found in May, but not in August (**Table 3**). On average, % PP_{diss} was lower within the upper 20 m in August (19%) than in May (32%). % PP_{diss} varied between 3 to 98% in May and 2 to 77% in August and showed a clear increase with depth (**Figure 4E**).

Chl *a* in the upper 20 m was 10-fold higher in May than in August (**Figure 4F**), resulting in higher productivity specific



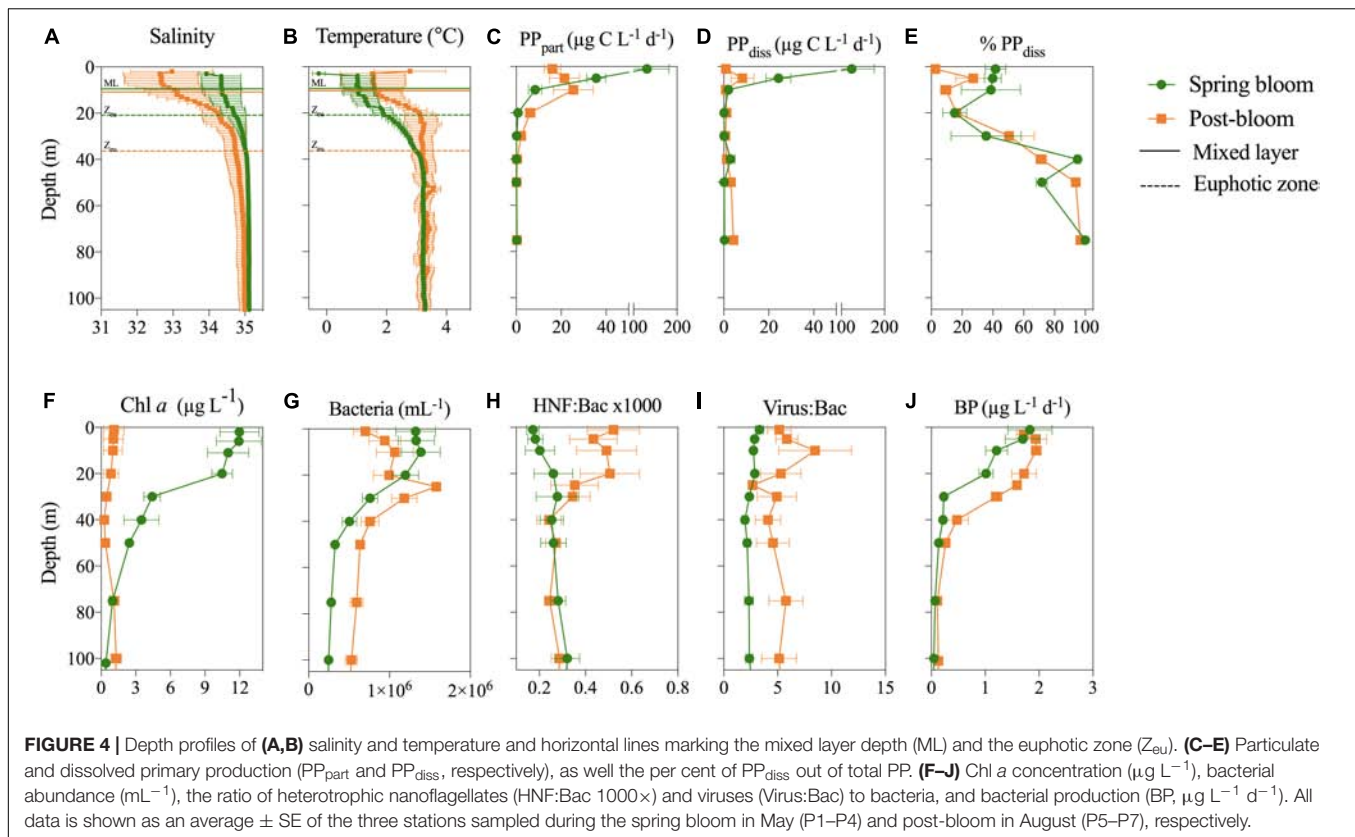
to phytoplankton biomass (based on Chl *a*) post-bloom. The abundance of bacteria, virus, and heterotrophic nanoflagellates (HNF) correlated positively with Chl *a* and PP_{part} in both

in May and August, but not to PP_{diss} (Table 3). The highest heterotrophic microbial abundances ($0.5\text{--}2 \times 10^6$ bacteria mL^{-1} and HNF 200–1000 HNF mL^{-1}) were found within the

TABLE 2 | Correlation matrix (non-parametric Spearman's rho, ρ) for particulate organic carbon (POC), particulate organic nitrogen (PON), dissolved organic carbon (DOC), dissolved organic nitrogen (DON), chlorophyll *a* (Chl *a*), concentration of nitrate, nitrite and ammonium (DIN), bacterial production (BP), and abundance (Bac), as well as abundance of heterotrophic nanoflagellates (HNF) and the abundance ratio of bacteria to virus (V:B) for the annual dataset.

		POC	PON	DOC	DON
Chl <i>a</i>	ρ	0.823**	0.819**	0.213**	−0.460**
	<i>n</i>	261	259	215	150
DIN	ρ	−0.702**	−0.694**	−0.052	−0.330**
	<i>n</i>	263	261	216	153
BP	ρ	0.813**	0.824**	−0.256**	−0.089
	<i>n</i>	105	104	86	71
Bac	ρ	0.302**	0.325**	−0.145*	0.402**
	<i>n</i>	240	238	192	152
HNF	ρ	0.581**	0.576**	−0.061	0.132
	<i>n</i>	240	238	192	152
V:B	ρ	−0.478**	−0.491**	−0.185**	0.265**
	<i>n</i>	240	238	192	152

**Correlation is significant at the 0.01 level *Correlation is significant at the 0.05 level.



productive upper 20 m of the water column at all P-stations. Bacterial abundance was slightly higher in the upper 20 m in May than August, while the subsurface abundances were highest in August (**Figure 4G**). Top-down control on bacteria is indicated by the ratio of HNF to bacteria (HNF:Bac $\times 1000$) and virus to bacteria (Virus:Bac), which are both elevated post-bloom relative to spring (**Figures 4H,I**). The ratio of HNF to bacteria averaged 0.3 ± 0.1 (3000 bacteria per HNF) below the pycnocline but increased to 0.5 ± 0.1 within the upper 20 m in August. Virus:Bac ratios averaged 1.9 ± 0.3 in the productive layer in May but increased to around 5 throughout the water column in August (**Figure 4I**).

Bacterial production (BP) rates were highest close to the surface ($3 \mu\text{g C L}^{-1} \text{d}^{-1}$) and dropped to $<1 \mu\text{g C L}^{-1} \text{d}^{-1}$ below 30 m (**Figure 4J**). BP rates were significantly higher during post-bloom than during spring bloom (**Figure 4J** and **Supplementary Figure S2**). Thus, both biomass specific PP and BP were higher during post-bloom, with higher rates sustained deeper in the water column (0–40 m) than in spring. BP and cell-specific bacterial production (BP/B), were moderately correlated to the concentration of Chl *a* and PP_{part} in both May and August (**Table 3**). Their relationship to PP_{diss} , however, changed with the season, being strongly positively correlated to PP_{diss} in May but not in August. In both May and August, calculated BCD largely exceeded PP_{diss} , except in the upper 5 m of three stations sampled in May, where BCD amounted to $<50\%$ of PP_{diss} , with lowest bacterial PP_{diss} consumption at station P1 (2–32%) and with $\sim 47\%$ highest at

station P4. The relationship between primary and secondary bacterial production (depth-integrated values 0–75 m) was heavily steered by the high production rates in the shallow upper mixed layer (**Figure 5**), indicating that depth-integrated PP_{diss} largely exceeded BCD at station P1 and P3, while BCD exceeded PP_{diss} at station P4 and all stations sampled in August.

Vertical Distribution of Organic Matter During Spring and Post-bloom

Dissolved organic carbon formed by far the largest carbon pool, with concentrations generally 10–30 times higher than POC, the only exception being within the shallow mixed surface layer in May, where DOC and POC were of the same order of magnitude. Maximum POC concentrations of 878 and $336 \mu\text{g L}^{-1}$ were found within the upper 20 m in May and August, respectively (**Figure 6B**). DOC concentrations did not display a pronounced vertical decrease similar to that of POC, with DOC concentration in the upper 100 m ($720 \pm 250 \mu\text{g L}^{-1}$) never significantly exceeding concentrations in the deep 750–1000 m samples ($695 \pm 76 \mu\text{g L}^{-1}$) even during the productive season. As a result, the DOC/POC ratio was <5 in the upper 30 m and 2–3 times higher at depth (**Figure 6C**). DOC concentrations did not vary significantly within the upper 100 m between May and August (**Figure 6A** and **Table 1**), in contrast to the clear shift observed in the organic N-pools; PON was the largest N-pool in the upper 20 m in spring, whereas DON increased threefold

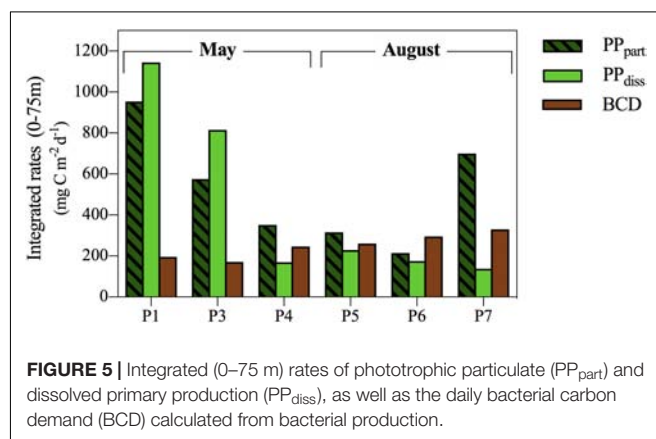
TABLE 3 | Correlation matrix (non-parametric Spearman's rho, ρ) of particulate primary production (PP_{part}), dissolved primary production (PP_{diss}), total chlorophyll *a* (Chl *a*), Chl *a* > 10 μm , concentration of nitrate, nitrite and ammonium (NO_x), bacterial abundance (Bac), bacterial production (BP) and cell-specific bacterial production (BP/B) in May and August.

			PP_{part}	PP_{diss}	Chl <i>a</i>	Chl <i>a</i> > 10 μm	NO_x
MAY	PP_{diss}	ρ	0.699**				
		<i>n</i>	19				
	Chl <i>a</i>	ρ	0.766**	0.495*			
		<i>n</i>	22	21			
	Chl > 10 μm	ρ	0.737**	0.465*	0.971**		
		<i>n</i>	22	21	24		
	NO_x	ρ	-0.799**	-0.593**	-0.705**	-0.703**	
		<i>n</i>	22	21	24	24	
	Bac	ρ	0.771**	0.431	0.723**	0.746**	-0.859**
		<i>n</i>	22	21	24	24	24
	BP	ρ	0.810**	0.619**	0.657**	0.681**	-0.848**
		<i>n</i>	22	21	24	24	24
	BP/Bac	ρ	0.666**	0.608**	0.458*	0.494*	-0.708**
		<i>n</i>	22	21	24	24	24
AUG.	PP_{diss}	ρ	0.108				
		<i>n</i>	17				
	Chl <i>a</i>	ρ	0.572**	0.164			
		<i>n</i>	23	17			
	Chl > 10 μm	ρ	0.495*	0.216	0.902**		
		<i>n</i>	23	17	26		
	NO_x	ρ	-0.694**	0.082	-0.434*	-0.253	
		<i>n</i>	21	15	22	22	
	Bac	ρ	0.678**	0.147	0.868**	0.933**	-0.378
		<i>n</i>	23	17	26	26	22
	BP	ρ	0.890**	0.015	0.736**	0.650**	-0.807**
		<i>n</i>	23	17	26	26	22
	BP/Bac	ρ	0.752**	-0.135	0.411*	0.249	-0.909**
		<i>n</i>	23	17	26	26	22

**Correlation is significant at the 0.01 level *Correlation is significant at the 0.05 level. Data from P-stations (0–75 m depth).

and was dominating the N-pool in August (Figures 6D,E and Table 1). The dissolved inorganic N (DIN) pool was equally low ($<2 \mu\text{g L}^{-1}$) in May and August in the upper 10 m but continued to decrease in subsurface waters (20–80 m) from May to August (Figure 6F). As a result, DON comprised the largest N pool within the productive surface layer during post-bloom. Both in May and August, POC was strongly positively correlated with Chl *a* and PP_{part} , and negatively correlated to DIN (Supplementary Table S2). For DOC, these correlations were weaker both on annual and monthly timescales. DOC and DON were weakly negatively correlated with Chl *a*, uncorrelated to both PP_{part} and PP_{diss} , and weakly positively correlated to DIN in May. In August, DOM was not significantly related to PP_{part} , PP_{diss} , Chl *a* nor DIN, except for a negative correlation between DON and DIN (Supplementary Table S2).

During the phytoplankton spring bloom in May, the C/N ratios of the DOM pool were high (avg. 43 ± 45 within the upper 100 m) with a maximum of 179 at 1 m at station P1 (Supplementary Figure S2). In August, the dissolved pool was characterized by low C/N ratios (average 10 ± 14 ; range: 4–99), when DON concentrations were high (Figure 6A). Suspended POM had C/N ratios close to Redfield in the upper 200 m



both May (7.7 ± 0.6) and slightly lower in August (6.9 ± 0.9), although elevated ratios ($\text{C/N} \geq 10$) were observed at station P4 (Supplementary Figure S2). We observed the lowest C/N of suspended POM at ca. 20 m and found an increase toward 100 m during both post- and spring bloom (Figure 6H). The C/N ratio of sinking POM reflected largely that of suspended POM

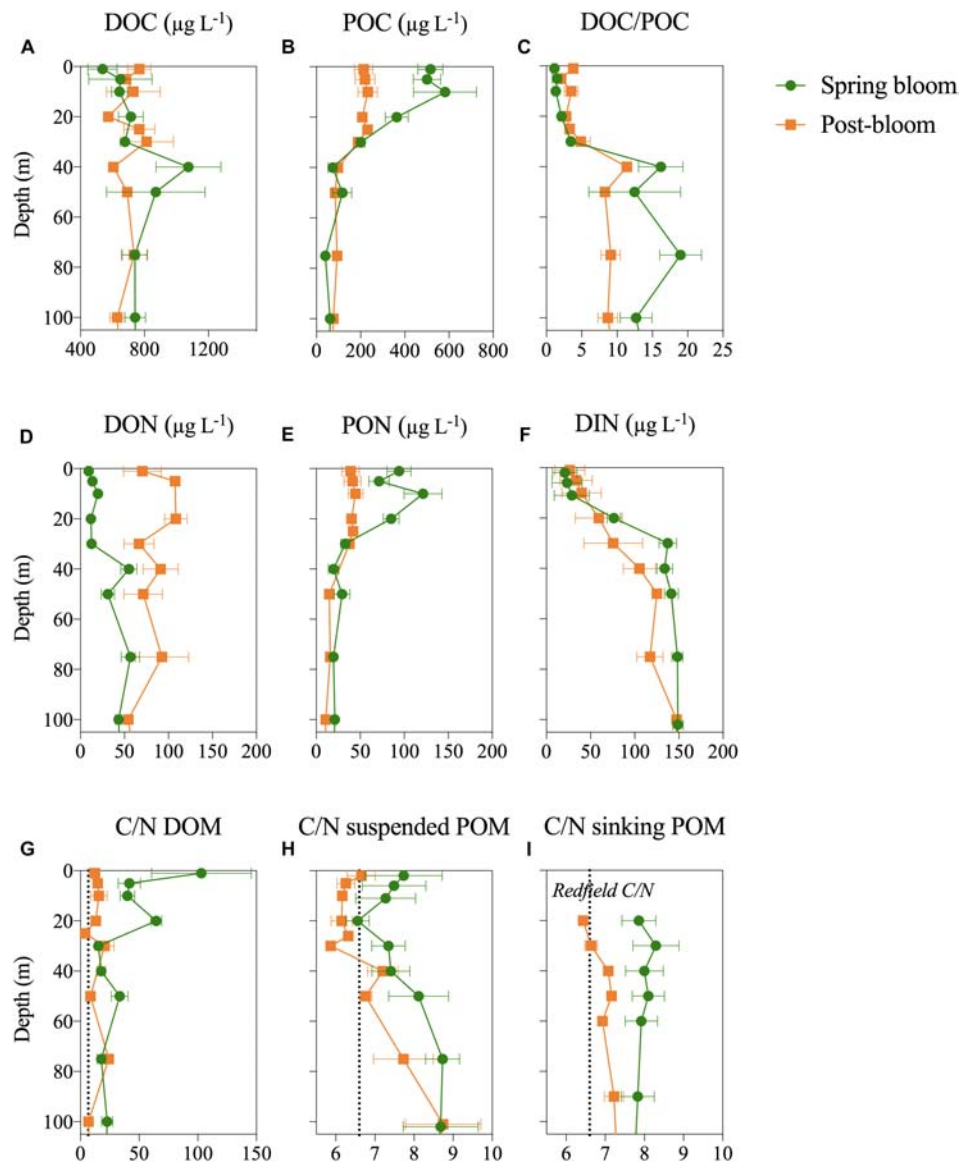


FIGURE 6 | Depth profiles of the C and N-pools. **(A)** Dissolved organic carbon (DOC), **(B)** particulate organic carbon (POC), **(C)** DOC/POC, **(D,E)** dissolved and particulate organic nitrogen (DON and PON, respectively) and **(F)** dissolved inorganic nitrogen (DIN). **(G–I)** The carbon to nitrogen ratios (atom:atom) of DOM, suspended POM and sinking POM retrieved from sediment traps. The Redfield C/N ratio is indicated by the vertical dotted line. All data is shown as an average $\pm$ SE of the three stations sampled during the spring bloom in May (P1–P4) and post-bloom in August (P5–P7), respectively.

at the same station but showed less vertical variability than the suspended POM (Figure 6I).

DISCUSSION

Dissolved Primary Production and Other Sources of DOM

The PP changed notably from spring to post-bloom conditions (Figures 4, 5). The significant contribution of PP_{diss} to total PP in May and August are both higher than corresponding values from the Nordic Seas during summer [Poulton et al. (2016); avg. 15%,

range 2–46%], but within the range of previous measurements from the central Arctic Ocean Gosselin et al. (1997) and the Barents Sea (Vernet et al., 1998). A positive relationship between PP_{part} and PP_{diss} is expected when physiologically-driven extracellular release from vital phytoplankton is the dominating mechanism of DOM production (Baines and Pace, 1991), while the absence of such a relationship may be interpreted as trophic interactions being the primary release mechanism of DOM (Teira et al., 2003). The significant relationship between PP_{part} and PP_{diss} as observed in May, but not in August, thus suggests that physiological processes dominated DOM production under the spring bloom, while trophic interactions

became more important under post-bloom conditions. PP_{diss} correlated significantly and positively to $Chl\ a > 10\ \mu m$ (Table 3), presumably because diatoms and colonies of *P. pouchetii*, which dominated the phytoplankton community during the spring bloom and are known to release DOM during growth, were important producers of PP_{diss} (Ittekkot et al., 1981; Mykkestad, 1995; Alderkamp et al., 2007). In August, the solar irradiance was lower and phytoplankton biomass and production were reduced, while heterotrophic processes had increased bacterial production and the ratio of virus and HNF to bacteria had increased (Figure 4). The system had entered a stage of regenerated production (Randelhoff et al., 2016), with small phytoplankton and heterotrophic microorganisms dominating the plankton (Paulsen et al., 2016). Size-fractionation experiments further suggested a high degree of bacterivory and predation on picophytoplankton by heterotrophic flagellates (Paulsen et al., 2016). These observations support the notion that trophic interactions were important for DOM production (Taylor et al., 1985; Nagata and Kirchman, 1991) and responsible for the decorrelation of PP_{part} and PP_{diss} in August.

Phytoplankton Impact on the C/N Ratio of Organic Matter

Active DOM release by phytoplankton (the suggested May situation), has been described as an overflow mechanism by which phytoplankton releases excess photosynthate, ensuring a balance between carbon demand for anabolism and photosynthetic assimilation (Berman-Frank and Dubinsky, 1999). Freshly produced phytoplankton DOM is rich in carbon (Sambrotto et al., 1993; Søndergaard et al., 2000) and may explain the high C/N ratio in May (Figures 2A, 6G). Moreover, large-celled phytoplankton normally releases relatively less DON than smaller phytoplankton (Hasegawa et al., 2000; Varela et al., 2006), and the shift in phytoplankton size from diatoms and *Phaeocystis* in May to pico- and nano-sized autotrophs in August likely increased the release of DON relative to DOC during summer. In addition, trophic interactions led to the release of DOM with a C/N ratio closer to the Redfield ratio. Both mechanisms work in the direction of N-enriched DOM production in August, resulting in the observed seasonal difference in DON release. Randelhoff et al. (2016) report low *in situ* concentrations of nitrate within the euphotic zone in August, despite relative high upward turbulent diffusive nitrate flux across the nitracline, and low assimilation of nitrate into phytoplankton cells, which support our interpretation.

Potential Fate of POC and PON

The seasonal dynamics in the POM pool suggested that nitrogen incorporated in POM was rapidly sinking out of the upper 100 m of the water column during the productive season. C/N of accumulated POM was lowest during the productive period in May (7.8) and August (6.9), close to both Redfield ratio and averaged C/N ratios reported from the Arctic Ocean and pan-Arctic shelves (7.4; Frigstad et al., 2014). Almost identical C/N ratio of suspended and sinking POM in May and August indicate that the flux was too high for the system to degrade sinking POM within the surface and thus N is not retained in the surface waters

opposed to what Tamelander et al. (2013) suggest. The sinking loss of PON helps to close the annual N-budget, as it explains the drop in total N (TN) during the productive season. Other factors may affect the C/N ratio of sinking POM. Colonization of sinking particles by bacteria and other heterotrophic microbes (that were all more abundant during post-bloom), for example, could have increased the nitrogen content of initially nitrate-deprived sinking POM (Kawakami et al., 2007). Further, phytoplankton composition affects the stoichiometry of sinking material (Olli et al., 2002). Diatoms, for example, export relatively more carbon than *P. pouchetii*, most likely due to their large lipid reserves (Reigstad and Wassmann, 2007; Le Moigne et al., 2015). Indeed, diatoms were more abundant than *P. pouchetii* in May, where export C/N ratios were slightly higher than in August (Figure 6I and Supplementary Figure S2). Whatever the exact mechanisms behind the relatively larger net loss of PON from May to August, the data are coherent with earlier observations that diatoms and other large-celled phytoplankton are crucial for effective export of POC to depth (Lalande et al., 2013).

Bacterial Turnover of DOM

The net accumulation of DOM in the surface waters during spring (Figure 2A) suggests a decoupling between the biological production and consumption of DOM. DOC accumulating in the water column over the spring as well as the observed increase in the $a_{CDOM}(260-310)$ signal in March relative to the other winter months (Figure 3C), indicate that DOC production exceeded DOC loss rates as early as March. In this context it is worth noting that PP_{diss} largely exceeded estimated BCD at the stations where the phytoplankton spring bloom was still growing (station P1) or just had reached stationary growth (station P3) (Figure 5), indicating that bacteria were not able to use all of the newly produced DOC. As soon as the bloom started to decay (i.e., station P4), the estimated BCD slightly exceeded PP_{diss} , and a tighter coupling between the two was observed as the bloom progressed.

Bacterial carbon demand depends heavily on the growth efficiency (BGE) of the respective community (del Giorgio and Cole, 1998). BGE, in turn, depends on the taxonomic composition of the bacterial community (Reinthal and Herndl, 2005), temperature (Kritzberg et al., 2010), as well as the quality of DOM (del Giorgio and Cole, 1998; Wear et al., 2015). Most often BGE increases with bloom progression (Carlson and Hansell, 2013; Wear et al., 2015) and assuming this was the case in our study, the calculated BCD was overestimated for the early bloom (P1), and underestimated for the decaying bloom (P4). This only strengthens our hypothesis of tighter coupling between PP_{diss} and BCD as the bloom progressed, which is furthermore supported by the significant positive correlation between PP_{diss} and BP in May. The question remains though why the bacterial community, although stimulated by PP_{diss} , were not able to consume DOM at the same rate as it was produced. Limitation of bacterial production by inorganic nutrients (Zweifel et al., 1993; Thingstad et al., 1997), low bioavailability of the DOC (Carlson et al., 1996), inhibition of bacterial growth by low temperatures (Pomeroy and Deibel, 1986), and high bacterial mortality due to high grazing pressure (Zweifel, 1999; Duarte

et al., 2005), are all mechanisms proposed to explain why DOC escapes bacterial degradation and accumulates above background levels in the ocean's surface. In our case, limitation by inorganic nutrients appears unlikely, as DOC started to accumulate early in the season when nutrients were still ample. The organisms dominating the spring bloom phytoplankton community, diatoms and *Phaeocystis*, are known to release complex DOM compounds, which might be less bio-available to bacteria (Aluwihare and Repeta, 1999; Alderkamp et al., 2007). However, bacterial groups known to be effective consumers of diatom exudates proliferated at the P-stations in May (Wilson et al., 2017) and should have been able to utilize freshly produced DOC. The high absorption signal within the UV region $a_{\text{CDOM}}(260\text{--}300)$ produced during spring bloom and possibly transformed to an absorption signal within the visible spectra by August indeed indicate that bacteria might have partly mediated the transformation of fresh and labile DOC into more degradation-resistant molecules, as suggested by Lechtenfeld et al. (2015).

Surprisingly, the release and uptake of DON were seasonally out of phase with that of DOC. While DOC was at its lowest during winter, DON decreased during spring and was at a minimum in May. A possible explanation is that when DIN becomes limiting, the demand for organically bound N increases. Extensive DON uptake and remineralization by heterotrophs during early bloom development has been suggested previously by experimental and modeling work (Van den Meersche et al., 2004). However, phytoplankton may also obtain a substantial part of their N via DON (Bronk et al., 2007). Further studies are needed to identify which organisms are responsible for the POM production by uptake of DON during late winter-early spring. Whatever the reasons underlying the mobilization of the DON pool in spring, our data suggest that the significant spring accumulation of POM was not only based on inorganic nitrogen sources, but also on organic ones.

Seasonal Changes in the Characteristics of CDOM

The CDOM absorption spectra agree with previous observations in the Fram Strait region (Pavlov et al., 2015). The relatively low values reflect that the study was conducted within Atlantic influenced water, as Atlantic water carries low amount of both CDOM and fluorescent DOM relative to the Arctic water (Jørgensen et al., 2014; Pavlov et al., 2015). Also, the $S[300\text{--}650\text{ nm}]$ estimated here (range: 16–26) are similar to those found within Atlantic water in Fram Strait region (Granskog et al., 2012) (range 14–32).

Colored dissolved organic matter absorption has never previously been measured during a full annual cycle in this region and the absorption peak within the UV spectrum $a_{\text{CDOM}}(260\text{--}310\text{ nm})$ in May (Figure 3A) not previously described. The $a_{\text{CDOM}}(260\text{--}310)$ does not correlate directly with Chl *a* or PP, and photosynthates are not expected to absorb light. Rather, this peak could be indirectly linked to the spring bloom production, similar to what was observed in a Svalbard mesocosm experiment, where high CDOM absorption within the UV band [$a_{\text{CDOM}}(310\text{--}360\text{ nm})$] was attributed to increased

bacterial activity following maximum PP (Pavlov et al., 2014). The signal could alternatively be related to mycosporine-like amino acids (MAAs), secondary phytoplankton metabolites that also produce an absorption maxima within the UV band (Vernet and Whitehead, 1996). These were previously reported at high concentrations in a *Phaeocystis* sp. dominated Svalbard fjord, even when Chl *a* concentrations were low (Ha et al., 2012).

There is generally a negative correlation between $S[500\text{--}700\text{ nm}]$ and molecular weight of DOM, while slope values for the UVB wavelength range $S[275\text{--}295\text{ nm}]$ are correlated with positively molecular weight (Stedmon and Nelson, 2015). As the slope value for May is low in the UVB range and high in the visible range, this suggest that DOM in May had lower molecular weight than DOM in the other months. This agrees with the observed high PP_{diss} in May and the accumulation of small carbon-rich molecules, with the 'early bloom-stage' P1 having both the highest PP_{diss} and the highest $a_{\text{CDOM}}(290)$ (Supplementary Figure S1). Our CDOM observations further indicate that the spring bloom OM is transformed as soon as August and thus that OM produced during summer at the ice edge is altered before reaching the central Arctic Ocean.

Arctic Perspective and Significance

The present study demonstrates that the strongly seasonal pulsed production in the marginal ice zone allows for a temporal decoupling of the production and the utilization of OM, and hence the accumulation of both POM and DOM above background concentrations in surface waters in spring and summer. The results caution against calculations of PP_{part} from winter nitrate drawdown (as is done in several studies i.e., Tremblay et al., 2006; Randelhoff et al., 2015). Almost half of the accumulated organic carbon from January to May was found as DOM, and hence POM production estimated from nitrate drawdown would lead to a severe overestimation of POM available for trophic transfer or potential export to depth. Our results are in agreement with earlier studies suggesting DON play an essential role in the N-cycle of sea ice influenced waters in Arctic systems (Skoog et al., 2001; Davis and Benner, 2005; Mei et al., 2005) and thus further cautions calculations of PP_{part} from winter nitrate drawdown, as DON apparently is an active N-source. The large DON pool that accumulated during post-bloom could serve as important nitrogen storage in stratified DIN-depleted waters and serve as a substrate for microbial production well beyond the productive season. We, therefore, recommend organic N-pools are investigated when studying biogeochemical cycling in the Arctic Ocean. Our findings also encourage future studies to identify which organisms are responsible for the uptake of DON in late winter-early spring and how this influence the entire POM production in relation to the DIN budget.

AUTHOR CONTRIBUTIONS

LS and MP equally lead the data analysis and the writing of the article. LS performed measurements of bacterial production and POM. MP was responsible for bacterial counts, DOM

and CDOM measurements. MV and MC were in charge of primary production measurements. All authors contributed to the interpretation of the data and commented on the text.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: <https://www.frontiersin.org/articles/10.3389/fmars.2018.00416/full#supplementary-material>

FIGURE S1 | Depth profiles of particulate and dissolved primary production (PP_{part} and PP_{diss} , respectively), and the percent of PP_{diss} , as well as the

absorption of CDOM at 290 nm, bacterial production and the bacterial carbon demand as percent of dissolved primary production (PP_{diss}) for the stations in May (**upper**; P1–P4) and August (**lower**; P5–P7). 100% is indicated by a dashed line.

FIGURE S2 | Depth profiles of carbon to nitrogen ratios (atom : atom) of dissolved organic matter (DOM), particulate organic matter (POM), and sinking POM retrieved from sediment traps (dashed line indicates the Redfield ratio), and the abundance of bacteria and heterotrophic nanoflagellates as well as the ratio of virus to bacteria at all stations in May (**upper**) and August (**lower**). The P-stations are emphasized with circles in May and diamonds in August, while the gray lines indicate other stations sampled during the same month (**Figure 1**).

FIGURE S3 | Median and percentiles (5 and 95%) of abundance of heterotrophic nanoflagellates (HNF), the ratio of virus to bacteria (Virus:Bac), as well as bacterial production (BP) and cell-specific bacterial production (BP/Bac), within the upper 100 m of the water column at all stations in January, March, May, August, and November. Note difference in scales. No data (n.d.).

TABLE S1 | Overview over the conditions at the process station in May and August as given in Randelhoff et al. (2018): sea ice concentrations, depths of the mixed layer (d_{ML}), photic zone (Z_{eu}) and the upper and lower end of the nitracline (d_N) at each station. The water layer from the surface to the lower end of d_N defines here the productive layer (0–30 m in May; 0–40 m in August). The average concentration of nitrate and nitrite (NO_x), phosphate (PO_4^{3-}), silicate (Si), and chlorophyll *a* (Chl *a*) within the productive layer are given (range of concentrations given in brackets). The phytoplankton bloom stage is classified as given in Reigstad et al. (unpublished).

TABLE S2 | Correlation matrix (non-parametric Spearman's rho, ρ) of particulate organic carbon (POC), particulate organic nitrogen (PON), dissolved organic carbon (DOC), dissolved organic nitrogen (DON), nitrate, nitrite and ammonium (DIN), and chlorophyll *a* (Chl *a*) concentration at all depth (0–1000 m) at all stations in May and August.

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Influence of Glacial Meltwater on Summer Biogeochemical Cycles in Scoresby Sund, East Greenland

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Greenland fjords receive considerable amounts of glacial meltwater discharge from the Greenland Ice Sheet due to present climate warming. This impacts the hydrography, via freshening of the fjord waters, and biological processes due to altered nutrient input and the addition of silts. We present the first comprehensive analysis of the summer carbon cycle in the world's largest fjord system situated in southeastern Greenland. During a cruise onboard *RV Maria S. Merian* in summer 2016, we visited Scoresby Sund and its northernmost branch, Nordvestfjord. In addition to direct measurements of hydrography, biogeochemical parameters and sediment trap fluxes, we derived net community production (NCP) and full water column particulate organic carbon (POC) fluxes, and estimated carbon remineralization from vertical flux attenuation. While the narrow Nordvestfjord is influenced by subglacial and surface meltwater discharge, these meltwater effects on the outer fjord part of Scoresby Sund are weakened due to its enormous width. We found that subglacial and surface meltwater discharge to Nordvestfjord significantly limited NCP to 32–36 mmol C m⁻² d⁻¹ compared to the outer fjord part of Scoresby Sund (58–82 mmol C m⁻² d⁻¹) by inhibiting the resupply of nutrients to the surface and by shadowing of silts contained in the meltwater. The POC flux close to the glacier fronts was elevated due to silt-ballasting of settling particles that increases the sinking velocity and thereby reduces the time for remineralization processes within the water column. By contrast, the outer fjord part of Scoresby Sund showed stronger attenuation of particles due to horizontal advection and, hence, more intense remineralization within the water column. Our results imply that glacially influenced parts of Greenland's fjords can be considered as hotspots of carbon export to depth. In a warming climate, this export is likely to be enhanced during glacial melting. Additionally, entrainment of increasingly warmer Atlantic Water might support a higher productivity in fjord systems. It therefore seems that future ice-free fjord systems with high input of glacial meltwater may become increasingly important for Arctic carbon sequestration.

Keywords: Arctic fjords, Greenland, carbon cycle, net community production, meltwater discharge, glaciers, Scoresby Sund, biogeochemical cycling

1. INTRODUCTION

Increasing atmospheric CO₂ concentrations and the resulting warming of atmosphere and ocean have led to a drastic decrease in the summer sea-ice cover and the widespread retreat of Arctic glaciers (e.g., Carr et al., 2017; Nienow et al., 2017). Since the last two decades, a substantial thinning of the Greenland Ice Sheet (GrIS), reflected in increasing surface and submarine melting and weakening of the ice mélange, has been caused by warming ocean waters, rising air temperatures, and an increase in the surface wind stress and surface ocean currents (Straneo et al., 2013; Khan et al., 2014). As a result, the GrIS is one of the most important contributors to the global mean sea level rise (van den Broeke et al., 2016).

Dynamics of sea ice and glacial ice have profound effects on biogeochemical cycles and primary production in the Arctic Ocean (e.g., Bhatia et al., 2013; Hawkings et al., 2015; Harada, 2016). Greenland's fjords constitute the primary pathway for the transport of meltwater and icebergs between the GrIS and the open ocean. Within the confined areas of the fjords, meltwater from marine and land-terminating glaciers are mixed with Arctic and Atlantic Water from the shelf regions off the coast of Greenland (Straneo and Cenedese, 2015). Surface meltwater runoff enhances the uptake of atmospheric CO₂ by fjord waters due to the inverse relationship between CO₂ solubility and salinity (Sejr et al., 2011; Rysgaard et al., 2012; Fransson et al., 2013; Meire et al., 2015), while both surface and subsurface meltwater discharge can influence the fjord's circulation pattern and therefore the distribution of organic and inorganic matter (Arendt et al., 2010; Cowton et al., 2016; Beaird et al., 2018). Enhanced surface layer stratification and light attenuation by terrestrial lithogenic material contained in the meltwater (such as silicates, carbonates, clay) may diminish productivity within the fjord waters (Murray et al., 2015; Holinde and Zielinski, 2016; Burgers et al., 2017). The majority of the carbon fixed by primary production, forming a pool of particulate organic carbon (POC), is retained and respired at the surface, but a fraction of the POC is exported below the euphotic layer. While limiting productivity as a result of increased turbidity, meltwater input can also facilitate POC export by the incorporation of so-called "ballast minerals" into settling organic aggregates (Armstrong et al., 2001; Hamm, 2002; Ploug et al., 2008; Iversen and Robert, 2015; van der Jagt et al., 2018). Ballast minerals, such as silt from melting glaciers, increase the density and size-specific settling velocity of organic aggregates and, thereby, increase POC export (Iversen and Ploug, 2010; Iversen and Robert, 2015; van der Jagt et al., 2018). Compared to other ocean areas, fjords are considered hotspots of organic carbon burial, as their burial rate per unit area might be a hundred times larger than the global ocean average (Smith et al., 2015). In light of the increasing amount of meltwater discharge to the fjord due to climate warming, a better understanding of its influence on the fjord's carbon cycle is urgently needed to make more precise projections on the future of Arctic glacial fjords.

Few studies have examined the carbon cycling in Arctic fjords while considering both physical and biological processes (e.g.,

Rysgaard et al., 2012; Meire et al., 2015, 2017; Sørensen et al., 2015). Studies on biogeochemical cycling in Scoresby Sund, which is the largest fjord system in the world and influenced by several marine and land-terminating glaciers, are presently lacking. Scoresby Sund differs from other east Greenland fjords due to its unique topographic and bathymetric structure, consisting of several narrow (~5 km) inner fjords with depths of more than 1,000 m, and a wider (~40 km) and shallower (~600 m) outer fjord. Both the inner fjord arms and the outer fjord significantly vary in the magnitude and mode of delivery of glacial meltwater exported from the GrIS, which allows for the examination of the particular influence of meltwater on the fjord's biogeochemical cycling.

We examine patterns of carbon cycling and export within Scoresby Sund in an effort to shed light on the influence of meltwater with regard to the functioning of this poorly studied coastal fjord system. The study presents a snapshot of the carbon dynamics in Scoresby Sund during the summer season, i.e., net community production (NCP) and POC flux estimates, supplemented with information on the hydrography of the fjord derived from a summer 2016 cruise along a transect from the shelf to the fjord head. Further data from a second cruise in summer 2018 were used to discuss circulation patterns within the fjord system. In addition to the whole fjord system, special attention was given to processes close to a prominent marine-terminating glacier at the head of a branch of Scoresby Sund. Our results show that productivity and POC fluxes were dependent on the degree of meltwater supply, with low productivity and high fluxes in the vicinity of glaciers. Our study provides for the first time a detailed description of Scoresby Sund's biogeochemical cycling, and gives a perspective on how this and similar glacial fjord systems may respond to increasing glacial melt from the GrIS in the future.

2. DATA AND METHODS

2.1. Study Area

Scoresby Sund covers an area of 13,700 km² with a total distance of 350 km between the head of the inner fjord and the mouth (Figure 1). The adjacent continental shelf has a width of 80–100 km until the shelf break. Lewis and Smith (2009) determined the average annual meltwater production in the climatic region of Scoresby Sund (which is about 5% of Greenland's surface area) to be 8 km³, plus an unknown volume from a number of potential meltwater outlets that could not be confirmed by satellite images. This corresponds to 2% of the average annual meltwater production of all climatic regions of Greenland. The fjord itself is divided into separate parts: the wide outer fjord (hereafter named Outer Scoresby Sund, OSS) with a maximum depth of 650 m and a rather uniform bottom topography, as well as several narrower inner fjords. The inner fjord arms are characterized by complex bottom topography and steep slopes, with water depths of up to 1,500 m (Funder, 1972; Dowdeswell et al., 1993; Ó Cofaigh et al., 2001). This study is focused on the northernmost fjord arm, Nordvestfjord. Nordvestfjord has a total length of 140 km and a width of about 5 km. Numerous smaller branches join this fjord (Dowdeswell et al.,

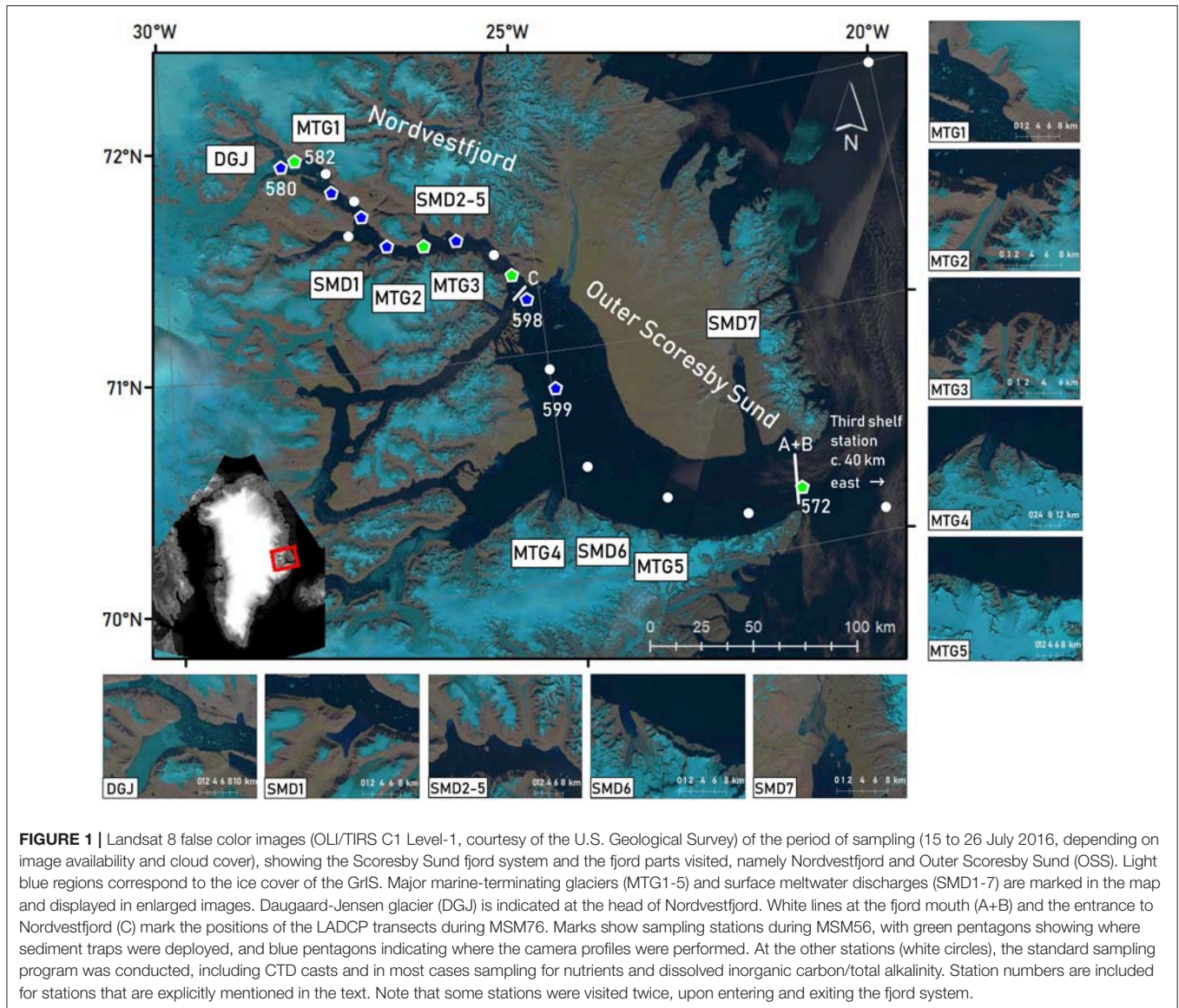


FIGURE 1 | Landsat 8 false color images (OLI/TIRS C1 Level-1, courtesy of the U.S. Geological Survey) of the period of sampling (15 to 26 July 2016, depending on image availability and cloud cover), showing the Scoresby Sund fjord system and the fjord parts visited, namely Nordvestfjord and Outer Scoresby Sund (OSS). Light blue regions correspond to the ice cover of the GrlS. Major marine-terminating glaciers (MTG1-5) and surface meltwater discharges (SMD1-7) are marked in the map and displayed in enlarged images. Dagaard-Jensen glacier (DGJ) is indicated at the head of Nordvestfjord. White lines at the fjord mouth (A+B) and the entrance to Nordvestfjord (C) mark the positions of the LADCP transects during MSM76. Marks show sampling stations during MSM56, with green pentagons showing where sediment traps were deployed, and blue pentagons indicating where the camera profiles were performed. At the other stations (white circles), the standard sampling program was conducted, including CTD casts and in most cases sampling for nutrients and dissolved inorganic carbon/total alkalinity. Station numbers are included for stations that are explicitly mentioned in the text. Note that some stations were visited twice, upon entering and exiting the fjord system.

2016) which is separated from the OSS by a sill having a depth of <350 m.

Dagaard-Jensen glacier at Nordvestfjord's head is a prominent marine-terminating glacier and the main generator of icebergs (Ó Cofaigh et al., 2001). The closest hydrographic station to the glacier terminus was situated 8–10 km away. Other large marine-terminating glaciers as well as major surface meltwater runoff pathways were identified by visual inspection of Landsat satellite images (USGS, EarthExplorer, Landsat 8 OLI/TIRS C1 Level-1, **Figure 1**) collected during our occupation of the fjord. In addition to Dagaard-Jensen glacier, three marine-terminating glaciers drain into Nordvestfjord and two into the OSS, with front widths of 1–11 km. Seven meltwater rivers flow into Nordvestfjord and two into the OSS.

2.2. Sample Collection and Analysis

Data were collected during a comprehensive sampling program with the German research vessel *RV Maria S. Merian* (cruise MSM56) (Koch, 2016). Twenty-two stations were sampled between 10 and 19 July 2016 along a transect from the inner Nordvestfjord to the fjord mouth, and additional three stations at the Greenland shelf (**Figure 1**).

At each station a CTD (Conductivity-Temperature-Depth) probe (SBE11plus Deck Unit with SBE9 sensors, Sea-Bird Scientific) equipped with additional sensors recorded vertical profiles of temperature, salinity, turbidity (ECO-NTU, WET Labs, Sea-Bird Scientific), chlorophyll *a* fluorescence (ECO-AFL/FL, WET Labs, Sea-Bird Scientific), and dissolved oxygen (SBE43, Sea-Bird Scientific) (Friedrichs et al., 2017). If not denoted differently, we report *in situ* temperatures in °C. Water

samples were drawn from a rosette sampler with 24 Niskin bottles from discrete depths during the up-cast. Dissolved oxygen samples were taken for sensor calibration at all stations, and measured onboard within 24 h using Winkler titration. Salinity samples were collected in glass bottles and measured in the home laboratory. Note that all salinities in this paper are given on practical salinity scale (determined by electrical conductivity of seawater). Samples for nutrients (phosphate, nitrate, silicate) were collected in 50 ml LDPE bottles and stored frozen until analysis in the home laboratory. Nutrient concentrations were determined by a spectrophotometric autoanalyzer (QuAatro39, SEAL Analytical) using slightly modified standard methods (Kattner and Becker, 1991). The measurement precision was 0.3% (coefficient of variation). Calibration of the nutrient analyses was performed using certified reference material (NMIJ CRM 7602-a, Seawater for Nutrients, National Metrology Institute of Japan, Ibaraki, Japan). Water samples for the determination of dissolved inorganic carbon (DIC) and total alkalinity (TA) were collected in 300 ml borosilicate bottles, poisoned with mercuric chloride, sealed, and stored in a cool place and in the dark. Measurements of DIC and TA were conducted with a VINDTA 3C (Versatile Instrument for the Determination of Total inorganic carbon and titration Alkalinity, Marianda, Kiel) including a CO₂ coulometer CM5015 (UIC Inc.) in the home laboratory. DIC was determined at 10°C by coulometry (Johnson et al., 1993; Dickson et al., 2007) with a precision of 1.4 $\mu\text{mol kg}^{-1}$. TA was measured at 25°C by applying a Gran potentiometric titration (Gran, 1952) with a precision of 1.8 $\mu\text{mol kg}^{-1}$. The methods were calibrated using certified reference material (batches #102 and #161) supplied by Scripps Institution of Oceanography, USA.

We used free-drifting surface tethered sediment traps to measure export flux at 100, 200, and 400 m depth for 5–10 h (Figure 1). The drifting traps consisted of a single drifting array with a surface buoy equipped with a GPS satellite transmitter, 12 small buoyancy balls serving as wave breakers to reduce the hydrodynamic effects on the sediment traps, and two 25 l glass buoyancy spheres. Each collection depth had four gimbal mounted collection cylinders, each 1 m tall and 10.4 cm in inner diameter. The collection cylinders were filled with filtered sea water with slightly increased salinity (4 permille increase) before deployment. The collected material was fixed with mercuric chloride and stored at 4°C until further analyses in the home laboratory. For the determination of the POC flux at the trap depths, samples were filtered on pre-combusted (450°C, 12 h) and pre-weighted Whatman GF/F filters (diameter: 25 mm) after removing swimmers, and dried for 48 h at 50°C. To remove particulate inorganic carbon, filters were fumed with 37% fuming hydrochloric acid for 24 h, dried for 24 h, and analyzed with a gas chromatograph (GC) elemental analyzer (EURO EA). In order to obtain discrete estimates of the POC flux in $\text{g C m}^{-2} \text{d}^{-1}$ at the depths of the trap deployments, the weight of POC in a sample was divided by the area of the trap opening and the deployment time of the traps. For the determination of continuous POC flux profiles based on the discrete POC flux estimates of the sediment traps, we conducted optical recordings of vertical profiles at 12 stations using an *in situ* camera system (Figure 1). The

custom camera system was self-constructed at AWI/MARUM and equipped with an infrared camera (acA2010-25gc GigE camera, Basler), an Edmund Optics compact fixed focal length lens 25 mm (#67-715) with aperture F#16, and an infrared light source. Every 500 ms (equivalent to a 15 cm depth interval), one picture was taken covering a volume of 20.46 cm³. The pictures were analyzed for particle size distribution and abundance by image processing using the image processing toolbox in Matlab R2015a (The MathWorks, Inc., Natick, MA, USA), following the method of Iversen et al. (2010) (see section 2.3). POC fluxes obtained from sediment trap deployments were used to fit the particle masses and sinking velocities (Iversen et al., 2010).

A HyperPro II profiling system (Satlantic, Canada) was used to acquire underwater light field information at selected stations depending on sea, weather, and daylight conditions, following procedures from Holinde and Zielinski (2016). Hyperspectral Ed(λ) data were then processed with ProSoft v.7.7.16 (Satlantic) and binned to 1 m depth intervals to calculate photosynthetically active radiation (PAR). Based on PAR(z), the 1% depth of PAR (a common indicator for the depth of the euphotic zone) was derived following Richlen et al. (2016), where PAR(0 m) data was extrapolated from the top 5 measurements.

In order to put the observed hydrographic and biogeochemical distributions into the context of ocean circulation, we analyzed direct velocity observations. Because they were not available from the cruise MSM56 in summer 2016, we use data that were obtained during the RV *Maria S. Merian* expedition MSM76 in summer 2018. This cruise was later in the year (11 August to 11 September 2018), but we believe that summer conditions, including the melting of marine- and land-terminating glaciers, led to similar circulation patterns as during the cruise MSM56 2 years earlier. Two meridional CTD and LADCP sections were carried out across the mouth of Scoresby Sound (sections A and B; see section Figure 1) from coast-to-coast, each comprising six stations. The work on section A started in the late afternoon, while section B was occupied 30 h later. Both sections were accomplished within roughly 7 h. In addition, one section consisting of four stations was carried out from coast-to-coast across the transition between the OSS and Nordvestfjord (section C; see Figure 1).

Regarding marine-terminating glaciers, the resolution of our dataset does not allow to distinguish between subglacial discharge (surface melt that is discharged through channels at the glacier base) and submarine melt (meltwater from below sea level) (Straneo and Cenedese, 2015). We therefore use both terms synonymously, even if we are aware that both meltwater types might enter the fjord waters in different ways.

2.3. Data Compilation

To assess the productivity of the fjord system, we calculated the net community production (NCP), which is defined as the gross primary production minus all losses in carbon due to respiration. It is used as a measure for the fraction of primary production that will be exported out of the surface layer, i.e., export production (Williams, 1993; Hansell and Carlson, 1998; Lee, 2001). NCP quantifies all biological activity that has occurred since ice break-up in spring until the time of sampling. While there are different

methods to determine NCP (e.g., Hansell and Carlson, 1998; Bates et al., 2005; Munro et al., 2015), we utilize the difference in nutrients (particularly nitrate+nitrite and phosphate) between the winter and the time of sampling (Hoppema et al., 2007; Ulfssbo et al., 2014). In the high-latitude oceans and thus also in fjords, a remnant layer from the previous winter occurs below the seasonally heated surface layer. In this layer, nutrient concentrations are found as in winter (though sampled in summer). The winter remnant layer is defined by a temperature minimum below the seasonal halocline, and therefore kept out of contact with the atmosphere (Rudels et al., 1996; Hoppema et al., 2000, 2007; Ulfssbo et al., 2014). Because local vertical mixing had modified the temperature minimum to some extent, resulting in variability of the nutrient concentrations, we used the mean nutrient concentration of the Polar Water on the shelf (see definition of this water mass in section 3); here we assume that this is the main subsurface water source to the fjord and its residence time is more than 1 year. The temperature and salinity sections (**Figures 4A,B**) appear to confirm the Polar Water to be this source. Mean concentrations in the Polar Water at three shelf stations were $6.3 \pm 1.3 \mu\text{mol l}^{-1}$ for nitrate+nitrite, and $0.6 \pm 0.09 \mu\text{mol l}^{-1}$ for phosphate. For the depth of the winter remnant layer we took the temperature minima at the individual stations (between 41 and 135 m depth).

The net nutrient drawdown was obtained at each station by integrating the difference between the concentration in the temperature minimum and that in the surface layer above it. To exclude dilution by ice melt, evaporation, and precipitation, nutrient concentrations were normalized to a constant salinity of 34.5, as described in Hoppema et al. (2007). We then applied the following equation (modified after Ulfssbo et al., 2014):

$$\text{NCP}_x [\text{mmol C m}^{-2} \text{ period}^{-1}] = \int_0^{T_{\min}} (X_{\text{initial}} - X_{\text{measured}}) dz \cdot R_{C/X}, \quad (1)$$

where X represents the nutrient concentration, either initial in the winter remnant layer, or measured at each sampling depth. $R_{C/X}$ is the stoichiometric nutrient ratio which is necessary to convert nutrient units to carbon units. In this study we use the canonical Redfield ratio of 106C:16N:1P (Redfield et al., 1963). The integration was performed by linear interpolations between nearest sampling depths. In Young Sound, primary production below sea-ice was negligible because of a thick snow cover and active sea-ice melt which limited sea-ice-related production rates to 1 month or less (Glud et al., 2007). Based on this, we assumed that biological production in Scoresby Sund started with ice break-up (which we identified using satellite images), and could then calculate the daily NCP. The dates of ice break-up, the number of open water days until sampling, and the NCP based on nitrate+nitrite and phosphate deficits at each station are listed in **Table 1**. Upwelling of nutrients from depth can result in an underestimation of the NCP. However, upwelling during summer in Scoresby Sund does not fuel the whole surface layer (see section 4.2.1). Hence, we believe that it does not severely affect primary production and, thus, the production

estimate based on nutrient deficits. NCP estimates can fluctuate depending on the assumptions made during the computation process. The main assumptions in the calculation of NCP are: (1) The source water is the Polar Water from the shelf near the mouth of Scoresby Sund; the source concentrations of nutrients may have been changed during transfer through the fjord system, both laterally and vertically. Since the Polar Water is vertically separated from its neighboring water masses by strong gradients, little exchange will likely occur with these during its transfer through the fjord. For the same reason, the vertical exchange at the stations is thought to be relatively small. (2) Homogeneity of the water column during winter and negligible winter draw-down of nutrients; in other fjords, winter draw-down has been observed, although not in all fjords (Glud et al., 2007); this may lead to a slight underestimation of the computed NCP. Accounting for variability in our definition of winter nutrient concentrations resulted in deviations in our estimates of NCP of $\pm 18\%$ (from nitrate+nitrite deficits) and $\pm 41\%$ (from phosphate deficits) from the ones presented here.

Figure 2 presents the total aggregate volume and the POC flux throughout the water column as estimated from camera images. In the following, we use the term “particles” to refer to aggregates of inorganic and dead organic material and fecal pellets, while the POC flux only comprises the mass flux of organic carbon that is incorporated in the particles. Particle abundance and size were recognized using an image analyzing tool (*medfilt2* function in Matlab R2015a) after converting the pictures into binary files and correcting them for background disturbance, such as shadows from illumination artifacts and spots on the camera lens. The pixel number of each projected particle area was determined and converted into equivalent spherical diameter (ESD) using the pixel to mm ratio. Detected particles were sorted into 20 logarithmically spaced size bins (d) based on their ESDs, ranging from 20 to 3415.03 μm . Each picture was concatenated to its respective *in situ* depth. Knowing the volume of the water cell pictured by the camera, the number of particles per liter and size class could be calculated (ΔC), and from it the total particle volume (**Figure 2A**). To account for statistical relevance, especially for the sparse large particles, we binned 10 consecutive pictures and only included size bins that contained five or more aggregates. In order to calculate the particle size distribution n , the number of particles per liter in a given size class was divided by the size difference between the concomitant size classes, as described by Iversen et al. (2010). As the POC flux within a certain time period was estimated from sediment traps that were deployed at three depths in the water column, a time dimension and POC estimate could be given to the particle volume (**Figure 2B**). For this, the total POC flux F was assumed to be an integration of the mass flux spectra of all particle sizes (modified after Iversen et al., 2010):

$$F = \int_{\text{size class 1}}^{\text{size class 20}} n(d) \cdot m(d) \cdot w(d) \cdot d(d), \quad (2)$$

where n ($\# \text{ m}^{-3} \text{ cm}^{-1}$) is the particle size distribution in a given small size range, $d(d)$, m is the particle mass (as POC), and w (m d^{-1}) is the average sinking velocity of the particles in a given

TABLE 1 | Time of ice breakup, NCP (based on nitrate+nitrite, and phosphate), and flux of particulate organic carbon measured in sediment trap samples per station (stations with only CTD and shelf stations casts are not included). At station 595, four sampling rounds were conducted within 24 h.

Station	Region	Ice breakup	Open water (days)	NCP _P ^a	NCP _N ^b	POC flux _{100m} ^c	POC flux _{200m} ^c	POC flux _{400m} ^c
577	Nordvestfjord	11.06.2016	32	30	62			
579	Nordvestfjord	11.06.2016	32	37	34			
580	Nordvestfjord	11.06.2016	32	41	33			
582	Nordvestfjord	11.06.2016	32	34	33	0.33	0.37	0.55
583	Nordvestfjord	11.06.2016	32	36	33			
584	Nordvestfjord	11.06.2016	34	36	35			
585	Nordvestfjord	11.06.2016	34	34	34			
586	Nordvestfjord	11.06.2016	34	33	34			
588	Nordvestfjord	11.06.2016	35	33	33			
590	Nordvestfjord	11.06.2016	35	24	32			
592	Nordvestfjord	11.06.2016	35	27	32	0.11	0.10	0.16
593	Nordvestfjord	11.06.2016	36	22	33			
594	Nordvestfjord	11.06.2016	36	42	43			
595-01	Nordvestfjord	11.06.2016	37	35	42	0.13	0.11	0.08
595-10	Nordvestfjord	11.06.2016	37	33	38			
595-20	Nordvestfjord	11.06.2016	37	31	40			
595-29	Nordvestfjord	11.06.2016	37	22	25			
572	OSS	07.06.2016	35	91	101	0.13	0.11	0.16
598	OSS	30.06.2016	19	64	79			
599	OSS	30.06.2016	27	53	68			
600	OSS	23.06.2016	27	25	42			
601	OSS	23.06.2016	27	43	70			
602	OSS	23.06.2016	27	69	72			

^acalculated based on phosphate deficits, in $\text{mmol C m}^{-2} \text{ d}^{-1}$.

^bcalculated based on nitrate+nitrite deficits, in $\text{mmol C m}^{-2} \text{ d}^{-1}$.

^cin $\text{g C m}^{-2} \text{ d}^{-1}$.

small size range, $d(d)$. While n and d are known, m and w have to be determined. Since both particle mass m and sinking velocity w scales as a power relationship when expressed as a function of particle diameter d , the product of m and w also scale as a power relationship as a function of d . We used a minimization procedure to find the factor and exponent providing the best-fit between the trap collected fluxes and F obtained from the *in-situ* images at the trap depths, using the Matlab R2015a function *fminsearch*.

As most of the camera profiles did not cover the water column down to the bottom, we fitted a Martin curve to the profiles for extrapolation (Martin et al., 1987; Belcher et al., 2016):

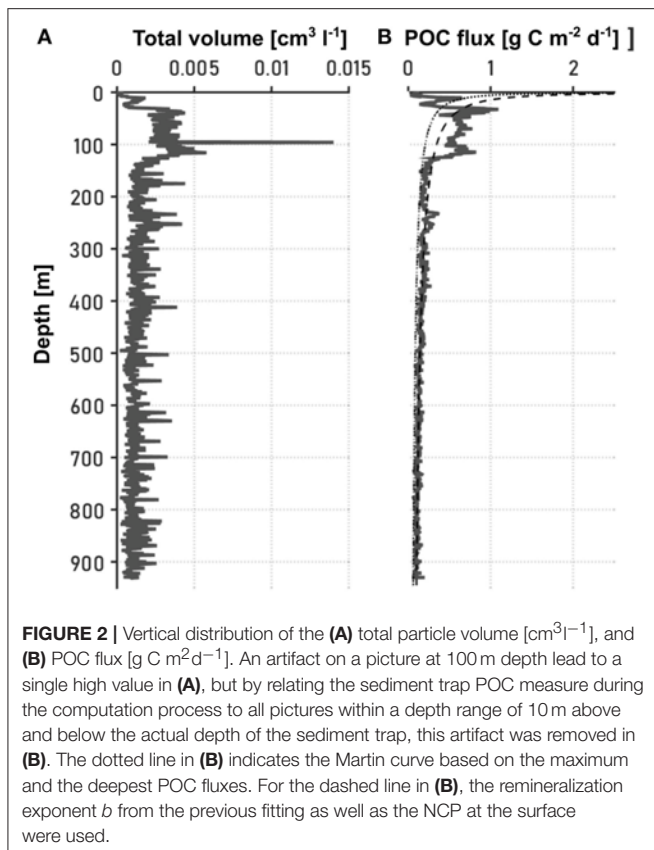
$$F(z) = F(z_0) \cdot (z/z_0)^{-b}, \quad (3)$$

where F is the POC flux at depths z_0 and z , and b is the remineralization exponent. This exponent can also be considered as efficiency with which carbon that is exported from the upper ocean, i.e., $F(z_0)$, decreases with depth (Guidi et al., 2015). High b values indicate high degradation of organic matter, while negative b values show initially increasing POC flux with depth. From the camera profiles we obtained a b value for each station. By replacing $F(z_0)$ by the NCP at each station and using the corresponding b value, the fraction of NCP potentially reaching the sea floor was determined (Figure 2B).

The Martin curves differ considerably from the POC flux profiles at the surface, which might be the result of small particles that could not be detected on the images. However, the general pattern of the decrease in POC flux is consistent: POC flux and total aggregate volume peak in the upper 100 m of the water column, and particles are attenuated to low and quasi constant fluxes at depths below 200 m. To test the robustness of the findings based on the b value with a more simple approximation of export and remineralization, we calculated the ratio between the discrete POC fluxes at 100 m depth and the NCP estimates at the camera stations (by relating sediment trap stations with the closest camera stations).

3. RESULTS

On the shelf of east Greenland, Polar Water (PW) with a salinity (S) below 34, and temperature (T) near the surface freezing point—exported from the Arctic Ocean—is advected toward the south near the sea surface. Below the PW, a warm and saline water mass ($T > 0^\circ\text{C}$) is found, referred to as Atlantic Water (AW). A warmer and more saline variety of AW originates from waters recirculating in Fram Strait, while a slightly colder and fresher AW type is exported from the Arctic Ocean (Rudels



et al., 2002). The characteristics of PW and AW are well-reflected by the water masses in OSS (**Figures 3A, 4A,B**), with PW found approximately above 200 m. Specifically, pronounced PW properties with temperatures below -1.4°C are observed at depths shallower than 150 m. Within the AW layer, found approximately below 200 m, salinity increases toward the bottom, while there is a temperature maximum near 1.2°C well-above the sea floor and a temperature minimum of $T < 0.7^\circ\text{C}$ at the bottom (**Figures 4A,B**). In addition, above the PW a ~ 10 m thick very fresh surface layer was recorded, with temperatures sometimes exceeding 3°C , most likely reflecting summertime surface discharge of meltwater from the GrIS combined with solar heating in the fjord. As a result, maximum mixed layer depths are limited to the upper 10 m of the water column. During the cruise we noticed the presence of icebergs from calving glaciers in the whole fjord with increasing density toward the fjord head.

Hydrographic properties change along the fjord axis from the mouth toward the inner part of Nordvestfjord. At depths below 400 m, the entire Nordvestfjord is filled by AW with temperatures exceeding 1.1°C (**Figure 4A**). This indicates that the sill separating the OSS and Nordvestfjord only allows for the warmer and less dense AW fraction to flow from the OSS into Nordvestfjord, while the colder AW bottom layer is held back. While the AW temperature maximum remains largely unchanged throughout the fjord system all the way into inner Nordvestfjord, the subsurface waters above the AW layer

experience substantial warming with increasing distance from the mouth. As can be seen from **Figures 3A, 5A,B** temperatures are higher than -1.0°C in this layer in Nordvestfjord, even up to 0.5°C . Consequently, the steep transition in T/S space from PW to the AW temperature maximum present at the mouth of Scoresby Sound is observed to level off toward the inner fjord with the sill toward Nordvestfjord marking at particularly pronounced transition in T/S space around the 27.5 kg m^{-3} isopycnal (**Figure 3B**). At the same time, the 27.9 kg m^{-3} isopycnal deepens from 300 m in the OSS to 500 m in Nordvestfjord, indicating higher densities (salinities) to be present in the OSS compared to Nordvestfjord in this depth range. This pattern is reminiscent of a deep overflow (spill) of AW across the sill that, however, does not extend all the way to the bottom in Nordvestfjord.

Dissolved oxygen concentrations were lowest in the deep basin (> 700 m), reaching $\sim 240 \mu\text{mol kg}^{-1}$. In Nordvestfjord between 10 and 30 m depth, the highest dissolved oxygen concentrations were found reaching $350 \mu\text{mol kg}^{-1}$ and in the OSS in the same depth range these values decreased to $320 \mu\text{mol kg}^{-1}$. In the upper 10 m of the water column of the OSS, dissolved oxygen concentrations were much lower reaching $280 \mu\text{mol kg}^{-1}$, but increased to $300 \mu\text{mol kg}^{-1}$ toward the fjord mouth (**Figures 4C, 5C**).

The surface water nutrients in the upper 25 to 50 m were largely depleted, with concentrations of about 0.1, 0.2, and $1.2 \mu\text{mol l}^{-1}$ for nitrate+nitrite, phosphate, and silicate, respectively (**Figure 6**). An exception was a region at 120–150 km section distance characterized by high surface meltwater discharge (**Figure 1**, SMD2-5) where silicate concentrations reached up to $6.0\text{--}6.1 \mu\text{mol l}^{-1}$, which is 2–3 times higher than in the surface layer at all other stations (**Figure 6C**). No other nutrient had such elevated concentrations here and also chlorophyll *a* fluorescence did not show a maximum. Between 20 and 30 m depth, chlorophyll *a* fluorescence was high with maximum values of up to $6.6 \mu\text{g l}^{-1}$ at the innermost stations (0–100 km section distance), but decreased considerably to about $1.4 \mu\text{g l}^{-1}$ at a section distance of 100 km and further toward the transition to the OSS (**Figures 4F and 5F**). Beneath 30 m depth, nutrient concentrations were significant but not homogeneously high within the water column of Nordvestfjord. The OSS was supplied by nutrients from the Greenland shelf that were transported within PW and AW at depths from 40 m to the bottom with concentrations of up to $12 \mu\text{mol l}^{-1}$ for nitrate+nitrite, $0.8 \mu\text{mol l}^{-1}$ for phosphate, and $6.0 \mu\text{mol l}^{-1}$ for silicate. These concentrations decreased toward the sill to Nordvestfjord (**Figures 4G–I**). Chlorophyll *a* fluorescence was high with maximum values of $9.8 \mu\text{g l}^{-1}$ within a layer at 25–50 m depth (**Figure 5F**).

Two patches of high chlorophyll *a* fluorescence in the OSS with 1.2 and $9.8 \mu\text{g l}^{-1}$ correlated with patches of high dissolved oxygen concentrations (301.5 and $302.4 \mu\text{mol kg}^{-1}$) and high turbidity (0.14 and 0.35 NTU) at 46 and 27 m depth and 260 and 300–340 km section distance, respectively (**Figures 5C,D,F**). Otherwise, turbidity was low in the OSS with about 0.09 NTU compared to Nordvestfjord with 0.3–0.5 NTU and a throughout turbid water column (**Figure 4D**). Highest turbidity in the

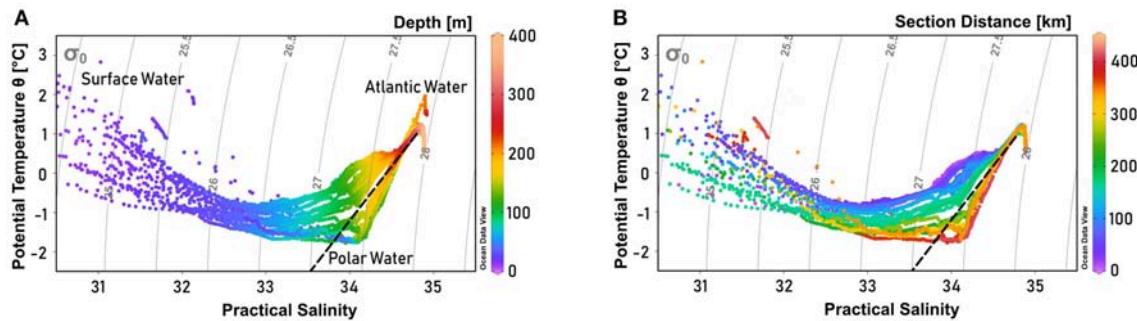


FIGURE 3 | Temperature-salinity diagram of Scoresby Sund, showing the primary water masses present in the study area (after Rudels et al., 2002). Colors indicate (A) depth and (B) section distance, while gray lines indicate isopycnals. The dashed black line represents the Gade line between the Atlantic Water ($T = 1^{\circ}\text{C}$, $S = 34.8$) and the meltwater endmember of glacier termini ($T = -90^{\circ}\text{C}$, $S = 0$). One station with a distinct Atlantic Water signal was not included in the section profiles, as it was further north on the Greenland shelf. It is therefore visible in (A), but not in (B). Potential temperature was derived from *in situ* temperature using Ocean Data View 4 software (Schlitzer, 2004).

Nordvestfjord was found at 100–200 m depth at the station closest to Daugaard-Jensen glacier, with a maximum of 3.8 NTU at 120 m depth (Figure 5D). Besides, values close to the surface and to the bottom were elevated with 0.6–0.7 and 0.5–0.8 NTU, respectively. At 120–150 km section distance, surface turbidity was almost one order of magnitude higher than within large parts of the water column (2.2–2.9 NTU), coinciding with elevated silicate concentrations (Figures 5D, 6C).

The depth of the euphotic zone as derived from the 1% depth of PAR ranged between 20 and 69 m throughout the whole study area. While light penetration varied in the Nordvestfjord between 20 and 44 m (mean = 32 m, standard deviation = 7 m), it increased toward the OSS and the adjacent Greenland shelf, ranging from 34 to 69 m (mean = 48 m, standard deviation = 11 m).

DIC and TA correlate strongly with salinity ($R^2_{\text{DIC}} = 0.906$ and $R^2_{\text{TA}} = 0.942$; $n = 54$ for DIC, $n = 46$ for TA) (Figures 7A,C). Normalization to a constant salinity of 34.5 revealed that low-salinity samples (mainly surface samples of Nordvestfjord) were profoundly affected by processes other than dilution (Figures 7B,D). They were therefore not taken into account for the extrapolation to zero salinity (i.e., representing meltwater discharge), which yields concentrations of 423 and 726 $\mu\text{mol kg}^{-1}$ for DIC and TA, respectively (Figures 7A,C). Note that these freshwater endmember concentrations were used for salinity normalization (Friis et al., 2003), but that assuming a freshwater endmember with zero concentrations of DIC and TA, respectively, resulted in the same trend for normalized low-salinity samples. Non-conservative changes in DIC can be caused by a number of processes, including uptake of atmospheric CO_2 , remineralization, and photosynthesis. No clear trend could be identified in the normalized DIC values of low-salinity surface samples (Figure 7B), indicating an interaction of several processes. Non-conservative behavior of TA, by contrast, is mainly attributed to carbonate mineral precipitation and dissolution (e.g., Cross et al., 2013). As most low-salinity surface samples had lower normalized TA values than the samples with higher salinities (which display a conservative relationship

between TA concentration and salinity) (Figure 7D), we assume that they reflect carbonate mineral precipitation.

The NCP was high in the OSS (58 $\text{mmol C m}^{-2} \text{d}^{-1}$ for phosphate deficits, 82 $\text{mmol C m}^{-2} \text{d}^{-1}$ for nitrate+nitrite deficits) compared to Nordvestfjord (32 $\text{mmol C m}^{-2} \text{d}^{-1}$ for phosphate deficits, 36 $\text{mmol C m}^{-2} \text{d}^{-1}$ for nitrate+nitrite deficits; Table 2). Visual analyses of net samples from Nordvestfjord revealed that the phytoplankton community was already in a post-bloom stage (B. Edvardsen, personal communication). Much debris, many copepods, and fecal pellets found in the sediment traps show that intense grazing already diminished the primary production. By contrast, a healthy and thriving phytoplankton community was observed in net samples of the OSS.

Camera-derived POC fluxes in Nordvestfjord and at the innermost part of OSS were high close to glacier fronts, ranging from 0.5–2 $\text{g C m}^{-2} \text{d}^{-1}$, and lower in the remaining Nordvestfjord (0.1–0.3 $\text{g C m}^{-2} \text{d}^{-1}$; Figure 4E). In the OSS, they decreased with increasing depth within the surface layer and corresponded well with the stratification of the water masses below (0.1–0.2 $\text{g C m}^{-2} \text{d}^{-1}$). It has to be noted that only one POC flux profile is available for the OSS and none for the shelf. The b value, constituting the remineralization efficiency, is higher in the OSS (0.3–0.4) than in Nordvestfjord (−0.4–0.6), indicating that a smaller share of the surface production in the OSS is transported to depth. The $\text{POC}_{100\text{m}}$: NCP ratio confirms this, showing that the POC flux at the depth of the shallowest sediment trap at 100 m makes up only 10–20 or 10–30% (for NCP_N and NCP_P , respectively) of the surface production in the OSS, while in Nordvestfjord, 30–80% of the NCP (both, NCP_N and NCP_P) are reflected in the POC flux at 100 m depth. According to the Martin curve, between 0.06 and 2.5 $\text{g C m}^{-2} \text{d}^{-1}$ of POC reached the sea floor in Nordvestfjord, which is more than the average amount fixed per day by primary production since the start of the growing season, whereas only 5–15% of the NCP in the OSS was sedimented on the seafloor (0.1–0.2 $\text{g C m}^{-2} \text{d}^{-1}$) (Table 2).

Traces of the pronounced freshwater discharge of Daugaard-Jensen glacier were detectable 8–10 km away from the glacier

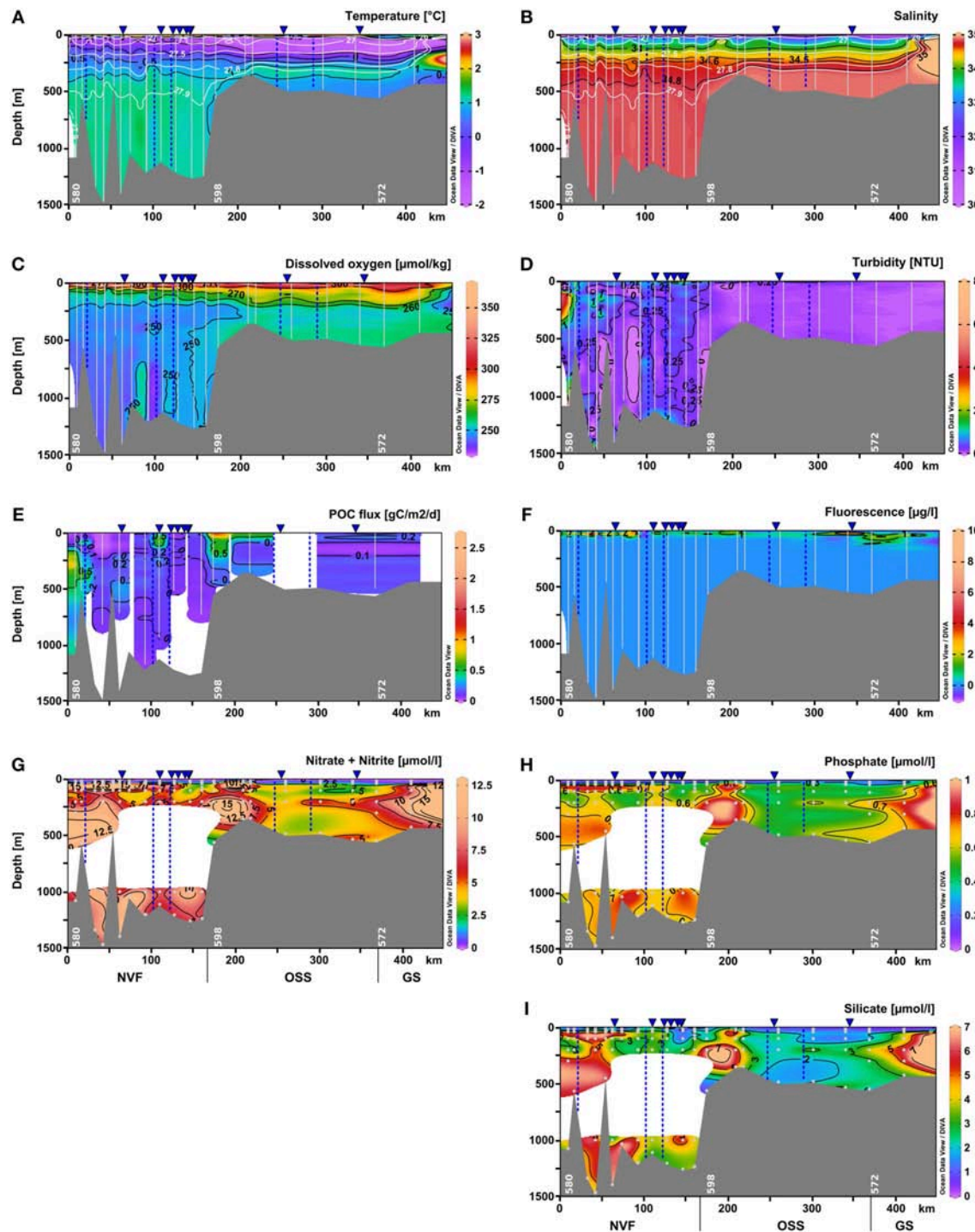


FIGURE 4 | Vertical distribution of (A) temperature (°C), (B) salinity, (C) dissolved oxygen ($\mu\text{mol kg}^{-1}$), (D) turbidity (NTU), (E) POC flux ($\text{g C m}^{-2} \text{d}^{-1}$), (F) chlorophyll *a* fluorescence ($\mu\text{g l}^{-1}$), (G) nitrate+nitrite ($\mu\text{mol l}^{-1}$), (H) phosphate ($\mu\text{mol l}^{-1}$), and (I) silicate ($\mu\text{mol l}^{-1}$) as distance from the fjord head (left) to the shelf (right) using Ocean Data View 4 software (Schlitzer, 2004). Data were interpolated by DIVA gridding, or for the POC fluxes by weighted-average gridding due to the low profile number. Bright lines indicate the CTD and camera profiles, bright dots represent water samples. The approximate positions of marine-terminating glaciers are shown by blue dashed lines, and surface meltwater discharge by blue triangles above the panels. Dagaard-Jensen glacier is situated close to the westernmost station (left side of the panels). NVF is the acronym for Nordvestfjord, OSS stands for the Outer Scoresby Sund, and GS for the Greenland Shelf.

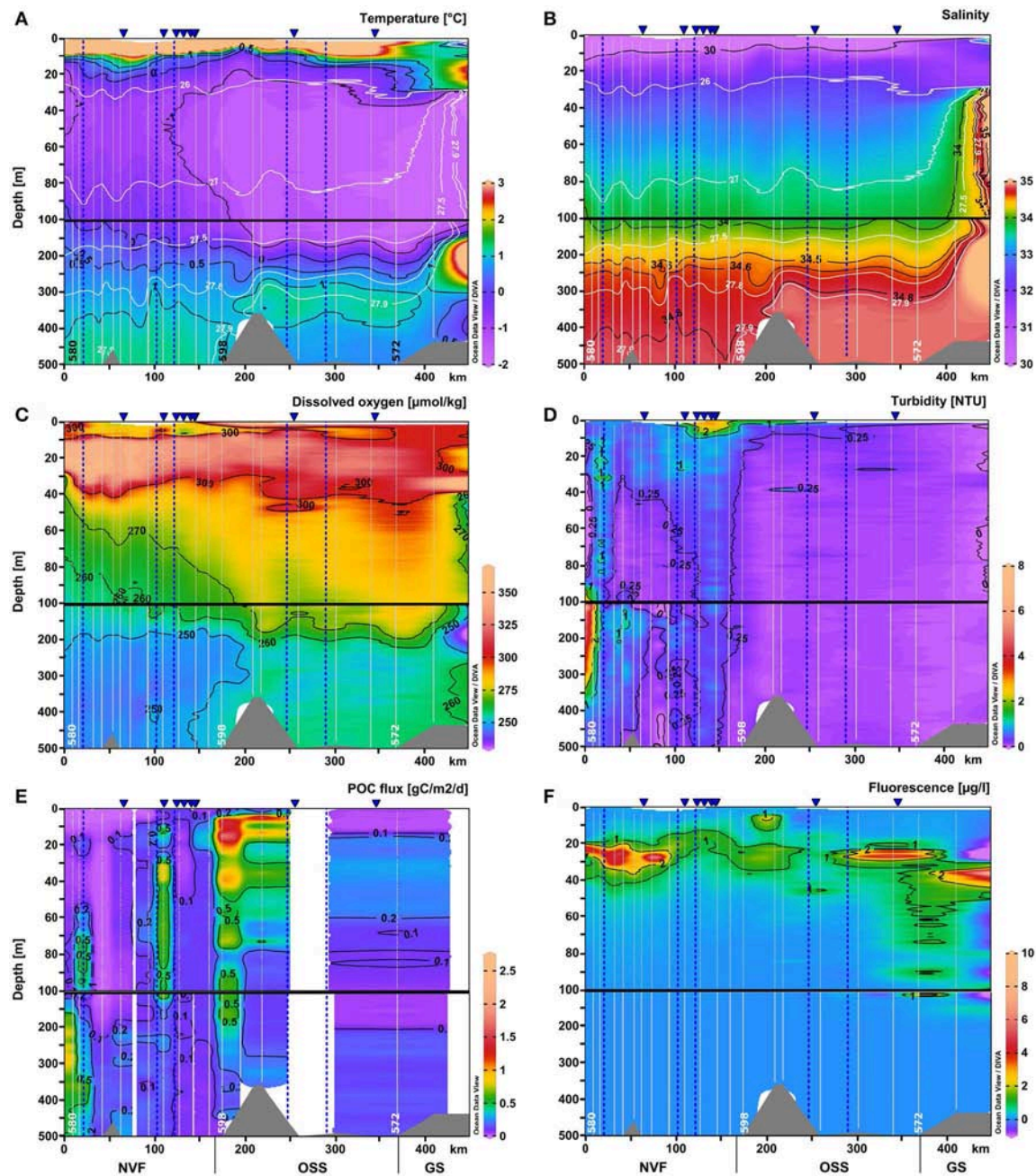


FIGURE 5 | Same as **Figure 4** for the upper 500 m of the water column: **(A)** temperature ($^{\circ}\text{C}$), **(B)** salinity, **(C)** dissolved oxygen ($\mu\text{mol kg}^{-1}$), **(D)** turbidity (NTU), **(E)** POC flux ($\text{g C m}^{-2} \text{ d}^{-1}$), and **(F)** chlorophyll a fluorescence ($\mu\text{g l}^{-1}$). Section plots of the nutrient distributions are in **Figure 6**. The scale of the upper 100 m was expanded.

front at our station closest to the terminus (station 580). In order to highlight the impact of Dagaard-Jensen's meltwater discharge on biogeochemical cycling in Scoresby Sund, we contrast measurements at two other stations (station 582 which is ~ 7 km further north of station 580, and station 599 in the OSS) in the same way as for station 580 (**Figure 8**). While at other stations at 200–240 m depth, salinity smoothly decreased with

depth (examples given in **Figures 8B,C**), a sudden salinity drop by 0.1–0.2 units could be detected at station 580 (**Figure 8A**). The temperature-salinity diagram reveals a salinity-driven density decrease, indicated by an approximately horizontal line compared to the stations 582 and 599 (**Figure 8D**). At station 580, nutrient concentrations were reduced by one third at 100–200 m depth compared to nutrient concentrations at

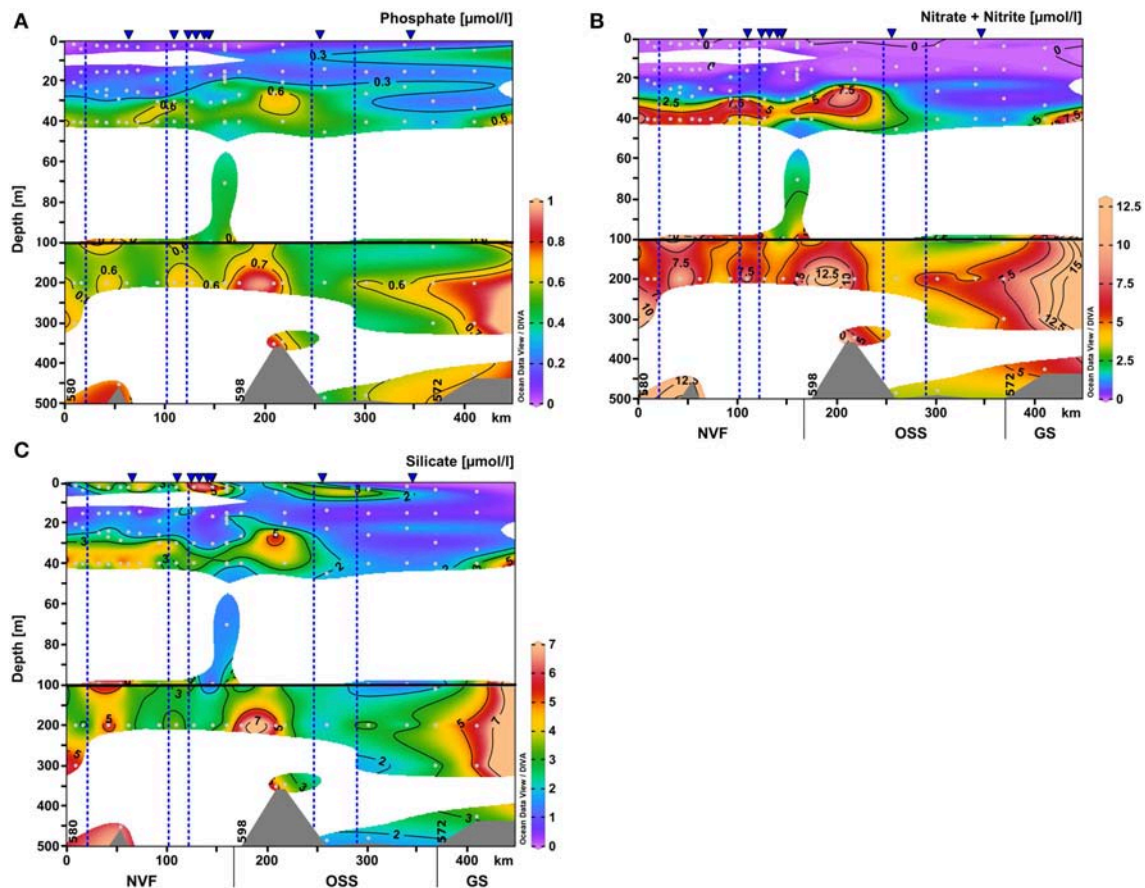


FIGURE 6 | Same as **Figure 4** for the nutrient distributions within upper 500 m of the water column: **(A)** nitrate+nitrite ($\mu\text{mol l}^{-1}$), **(B)** phosphate ($\mu\text{mol l}^{-1}$), and **(C)** silicate ($\mu\text{mol l}^{-1}$). The scale of the upper 100 m was expanded.

300 m depth. At 40–100 m depth nutrient concentrations were slightly higher. A reversed pattern was observed for turbidity, with a maximum at 100–200 m depth (2.5–3.9 NTU) and lower turbidity in the water masses above 100 m and below 200–250 m at this station. NCP, reaching 41 and 33 $\text{mmol C m}^{-2} \text{ d}^{-1}$ (for phosphate and nitrate+nitrite deficits, respectively), was not considerably higher compared to NCP at other stations (**Table 1**), but the POC flux was elevated at 250–350 m depth (up to $1 \text{ g C m}^{-2} \text{ d}^{-1}$) and with $4.0\text{--}4.9 \text{ g C m}^{-2} \text{ d}^{-1}$ (b value: -0.57) the sedimentation rate to the bottom was higher next to the glacier (station 580) than in the remaining Nordvestfjord. Maximum nutrient concentrations at the next station further outford (station 582) were measured at 100 m depth, coinciding with a POC flux maximum of $0.8 \text{ g C m}^{-2} \text{ d}^{-1}$. Turbidity was higher within the upper 250 m (~ 1 NTU) than below (~ 0.5 NTU). At a station within the shallower OSS (station 599), nutrient concentrations were increasing from the surface up to a depth of 50 m, which coincides with an elevated POC flux (up to $0.4 \text{ g C m}^{-2} \text{ d}^{-1}$), high turbidity (1.5–3.0 NTU), and high chlorophyll *a* fluorescence (**Figure 5F**), indicating active primary production and remineralization. Below, nutrient concentrations and turbidity increased toward the depth of the AW (200 m), while the POC flux stayed low throughout the water column.

4. DISCUSSION

Figure 11 summarizes the main processes that are discussed in the following chapters.

4.1. Circulation

The circulation of AW (i.e., temperatures exceeding 0°C) at the fjord mouth (sections A and B; see **Figure 1**) is characterized by an inflow of AW into Scoresby Sund at the northern part of the section and an outflow of AW in the southern part (**Figure 9**, upper panel). Thereby, the strongest flows are observed close to the northern and southern margins, suggesting boundary currents to be present along either margins. The observed circulation in the PW layer is considerably more patchy and weak overall (**Figure 9**, upper panel). In order to quantify the strength of the circulation, cumulative cross-section transports (integrated from north to south) have been computed for both sections A and B (**Figure 9**, lower panel). This has been done both based on the observed velocities (solid lines) and after a correction for barotropic tidal currents was applied (dashed lines). Despite differences between the 4 graphs, there is qualitative agreement in the sense that the inflow is found in the northern half of the section and outflow in the southern

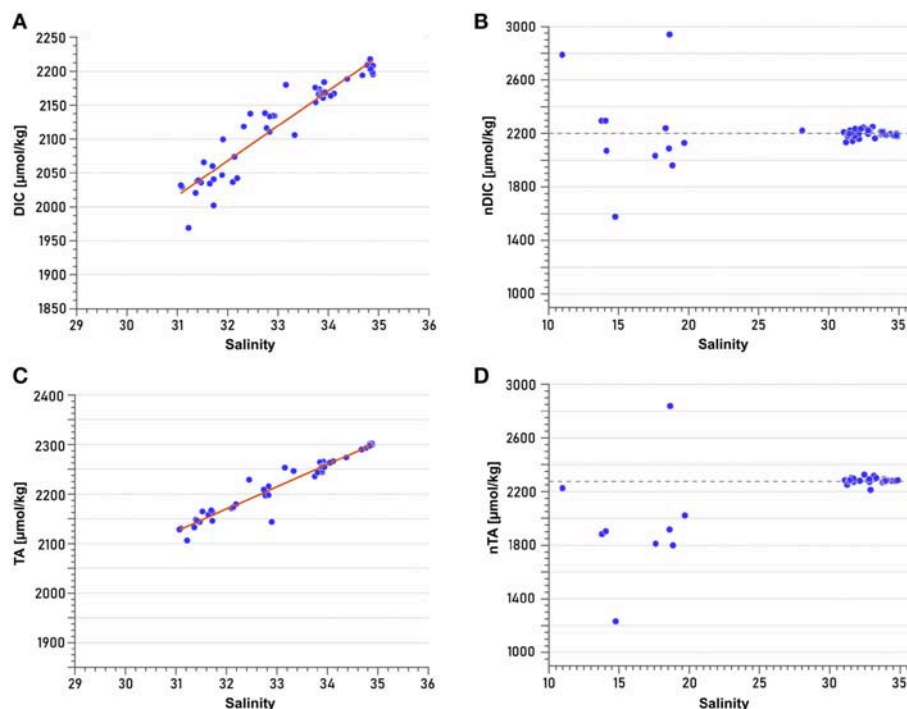


FIGURE 7 | Least-square linear regressions of **(A)** Total dissolved inorganic carbon (DIC) vs. salinity ($R^2 = 0.906$) and **(C)** Total alkalinity (TA) vs. salinity ($R^2 = 0.942$). Linear regressions were performed based only on samples with salinities >25 . Normalization of **(B)** DIC and **(D)** TA was performed according to the formula of Friis et al. (2003) for non-zero freshwater endmembers. Dashed lines in **(B,D)** represent the approximate mean values of the samples with salinities >25 . Deviations relative to this line (low-salinity samples, mainly from the surface of Nordvestfjord) indicate processes other than conservative mixing that modify TA and DIC concentrations.

TABLE 2 | Production, carbon flux, and remineralization in Nordvestfjord (NVF) and the Outer Scoresby Sund (OSS).

	NVF	OSS
NCP_P^a (mmol C m $^{-2}$ d $^{-1}$)	32 ± 6	58 ± 23
NCP_N^b (mmol C m $^{-2}$ d $^{-1}$)	36 ± 8	82 ± 32
$POC_{100m} : NCP_P$	0.3–0.8	0.1–0.3
$POC_{100m} : NCP_N$	0.3–0.8	0.1–0.2
b value	−0.4–0.6	0.3–0.4
POC_{bottom} (g C m $^{-2}$ d $^{-1}$)	0.06–2.5	0.1–0.2

All values are averaged for the respective region or were given as a range between maximum and minimum value. Because of the influence of the Dagaard-Jensen glacier, data from the closest station to the glacier were not included but instead discussed separately. The low number of profiles only allowed to give a range for POC_{bottom} and the b value, which indicates the degradation efficiency of organic matter, with high values showing high degradation, and low values showing initially increasing POC flux with depth.

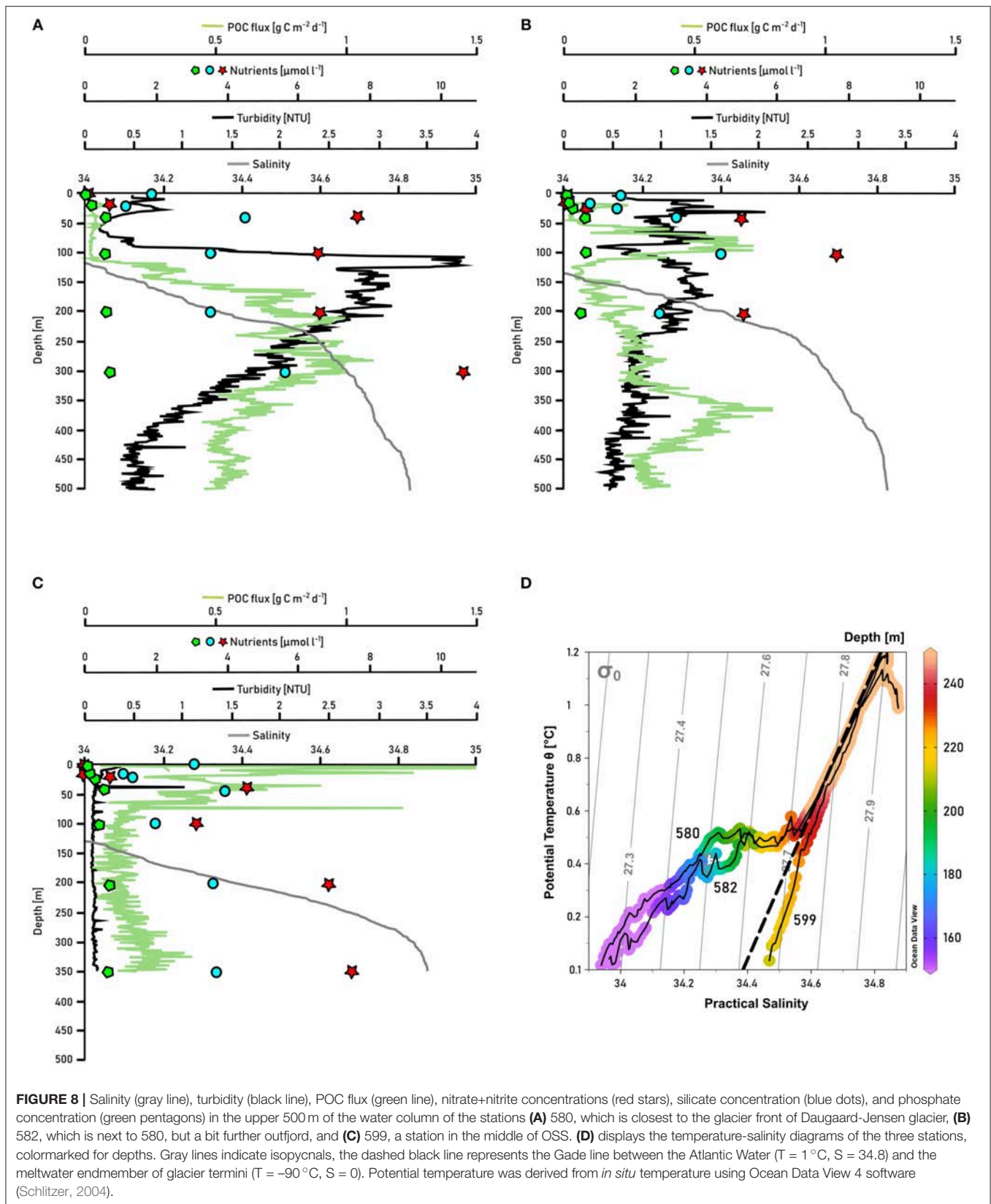
^acalculated based on phosphate deficits.

^bcalculated based on nitrate+nitrite deficits.

part. The maximum inflow lies between 110 and $190 \cdot 10^3 \text{ m}^3 \text{ s}^{-1}$ for the original data and reduces to values between 60 and $100 \cdot 10^3 \text{ m}^3 \text{ s}^{-1}$ after tidal correction (Figure 9, lower panel). Note that after tidal corrections for both sections there is a higher degree of compensation between inflow and outflow than without the correction (Figure 9, lower panel). As mass should be approximately conserved on weekly and long time scales, the tidal correction seems to add to the plausibility of the results.

Section C across the transition between the OSS and Nordvestfjord (see Figures 1, 10, left panel) is divided into two 4 km-wide channels separated by an island in the middle. The location where the section was taken is placed beyond the sill (at a distance of ~ 180 km; Figure 4A) where the sea floor slopes downward into Nordvestfjord. Here, a pronounced, bottom intensified inflow of the warmest part of AW into Nordvestfjord at densities exceeding 27.9 kg m^{-3} (and $T > 1.1^\circ\text{C}$) is found in both channels. This supports the fact that the deep part of Nordvestfjord is filled by AW with temperatures exceeding 1.0°C (Figure 4A). The outflow is found in both channels to occur mainly at middepths confined to a layer bounded by the 27.9 kg m^{-3} at the bottom and the 0°C isotherm (i.e., the AW-PW interface) at the top. At shallower depths, a weak flow toward the OSS is found. Overall, the flow across section C seems to vary strongly with depth, with an inflow of warm AW of $65 \cdot 10^3 \text{ m}^3 \text{ s}^{-1}$ at the bottom, compensated by an outflow of slightly colder AW. There is no indication of pronounced horizontal recirculation as was found at the mouth of Scoresby Sund.

In summary, our observations suggest the presence of boundary currents at the mouth of Scoresby Sund. At horizontal scales exceeding the baroclinic Rossby Radius of deformation, R_D , the Coriolis force is expected to impact the circulation such that boundary currents exist. Based on the hydrographic profiles, we estimated R_D to amount to 6 km (following Nurser and Bacon, 2014), both at the mouth of the OSS and near the sill



toward Nordvestfjord. The OSS exhibits typical widths of 35 km and exceeds 25 km at the mouth. This means that a horizontal circulation patterns with boundary currents along either margin represents plausible features of the circulation which we expect to exist throughout the OSS. The sense of the circulation (inflow along the northern margin and outflow along the southern one) can be reconciled with the fact that the Coriolis force acts on the flow to the right relative to the flow direction. At the transition of the OSS to Nordvestfjord (**Figure 10**), where the fjord becomes narrow, no evidence for horizontal recirculations are found. Here the flow seems to vary mainly in the vertical - reminiscent of estuarine circulations with an inflow at depth and outflow above this.

The inflow of warm AW into Scoresby Sund at depth and the compensatory outflow at shallower levels means that the heat, salt, and mass need to be transported upward within Nordvestfjord. The gradual warming of the subsurface layer (erosion of PW layer) may be explained by this. The fact that the isohalines are essentially flat in the upper 200 m throughout the OSS and Nordvestfjord may mean that there is a balance between salt being mixed upward and the input of freshwater from marine terminating glaciers and icebergs into the subsurface waters of the fjord.

4.2. Opposing Biogeochemical Regimes in Nordvestfjord and Outer Scoresby Sund

4.2.1. Nutrients and Turbidity

While deep nutrient concentrations in Nordvestfjord were elevated, the surface layer (up to 25–40 m depth) exhibited low nutrient concentrations (**Figures 4G–I**). Chlorophyll *a* fluorescence showed a maximum within a layer at 20–30 m depth, with laterally decreasing values in this layer with distance to the fjord head (**Figure 5F**). A surface patch with high silicate concentrations and elevated turbidity was found at 120–150 km section distance where numerous meltwater rivers drain into the fjord (**Figures 1, 5D, 6C**). Since there was no patch of other high nutrients, and the chlorophyll *a* fluorescence was not elevated, the surface meltwater must have been the source of silicate and silt. We assume that surface meltwater rivers accumulated silicate during their way across the bedrock surface.

Previous studies are not consistent in the information about the nutrient content of GrIS meltwater. While silicate has indeed been found to be transported into the system by glacial meltwater (Meire et al., 2016a; Hawkings et al., 2017), the meltwater contribution to phosphate and nitrate is unclear. The GrIS has been suggested to be a nitrogen source to phytoplankton (Hawkings et al., 2015, 2016; Wadham et al., 2016; Lund-Hansen et al., 2018). A fraction of this nitrogen might, however, not be readily bioavailable because it is bound to particles (Hawkings et al., 2015, 2016).

The indirect impact of glacier meltwater discharge on the distribution of nutrients and the resulting productivity in the fjord depends on the meltwater source. Meire et al. (2017) described two possible patterns: a fjord dominated by marine-terminating glaciers is likely to be productive because

of enhanced upwelling of nutrient-rich deep water induced by the deep meltwater plume (see also Kanna et al., 2018). By contrast, a fjord that is dominated by land-terminating glaciers discharges meltwater directly into the surface layer and is therefore characterized by low productivity because of enhanced stratification.

Nordvestfjord is influenced by both marine- and land-terminating glaciers. A third pattern besides the two described above seems to emerge here. Surface meltwater discharged into the fjord has formed a stable low-saline layer in the upper 10 m of the water column and below that the salinity increased only gradually. Also upwelling of nutrients due to meltwater release at greater depths seems to occur. Nutrient concentrations were high below 25–40 m depth, depending on the region. However, apparently they did not reach the surface layer above that. Because of the low surface layer chlorophyll *a* fluorescence at most stations, it is unlikely that such nutrients would have been consumed by primary production in the upper 10–25 m. While it appears that primary productivity in the innermost part of Nordvestfjord was still active, low chlorophyll *a* fluorescence values at stations further out (> 100 km section distance until the sill to the OSS) suggest a termination of the bloom. The latter is supported by observations of a post-bloom plankton community, many copepods and fecal pellets in net samples and sediment traps during our cruise. Critical whether meltwater plumes of marine-terminating glaciers reach the surface or not are the distance to the glacier termini, the strength of the ambient stratification, the volume of subglacial discharge, and the grounding line depths (Sciascia et al., 2013; Carroll et al., 2015; Hopwood et al., 2018). Even when not much is known about the marine-terminating glaciers in Scoresby Sund, it seems as if these factors produced plumes that obtained neutral buoyancy below the photic zone with only having a minor fertilizing effect on primary production. The depth of neutral buoyancy can be different for each marine-terminating glacier.

Within PW and AW, nutrients were transferred from the Greenland shelf to the OSS in the layer from 40 m to the bottom with concentrations of up to $12 \mu\text{mol l}^{-1}$ of nitrate+nitrite; $0.8 \mu\text{mol l}^{-1}$ of phosphate; and $6.0 \mu\text{mol l}^{-1}$ of silicate. It seems as if these waters would not supply the whole Scoresby Sund with nutrients, because nutrient concentrations decrease shortly after entering the OSS. However, our stations were located at the southern side of the OSS entrance, and thus in the outflowing water (see section 4.1). If we would have sampled further north, the connection between the inner fjord waters and the shelf waters in terms of nutrient concentrations would possibly have been clear.

Above, we discussed why no nutrients arrived in the very surface layer (upper 10–20 m), resulting in a low primary productivity in Nordvestfjord. However, the situation with the nutrients supply to the euphotic zone is more complicated than this. The euphotic zone ranged from 20 to 44 m (see section 3). In a similar depth range of 20–35 m, the chlorophyll *a* fluorescence maxima were found (**Figure 5F**). Nutrient concentrations were clearly higher in the deeper waters (>30 m) than in the near-surface water. This constellation can be explained by upwelling of nutrients which are consumed by primary producers near

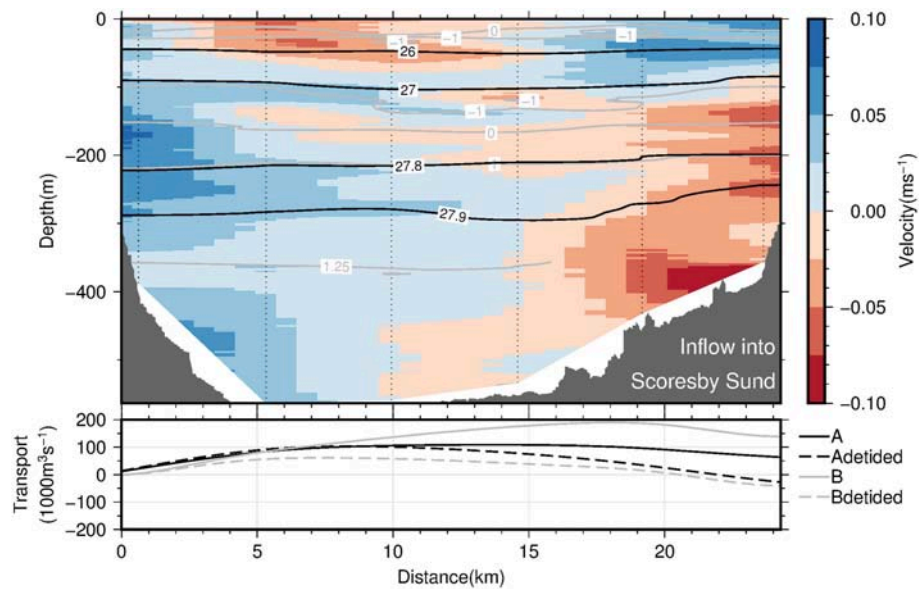


FIGURE 9 | The **(Upper panel)** displays the across-section velocity profiles (vertical, dotted lines) (interpolated onto a regular grid using 2D-spline interpolation) along the mouth of Scoresby Sund as a function of both depth and along-section distance from northern section end point. The view is out-fjord directed. Blue shading denotes inflow of waters from the continental shelf into Scoresby Sund, while red shading denotes outflow. Also shown are selected isopycnals and isotherms as black and gray solid lines, respectively. The **(Lower panel)** displays the cumulative volume transport into Scoresby Sund (precisely, the meridional integral of the vertically integrated across-section velocity along the mouth of Scoresby Sund) as a function of along-section distance from the northern section end point. The transports based on the LADCP profiles from the sections A and B are displayed as solid black and gray lines, respectively. The corresponding dashed lines denote the same transport quantities computed after subtracting barotropic tidal velocities from the LADCP profiles as predicted by the AOTIM-5 inverse tide model (Padman and Erofeeva, 2004).

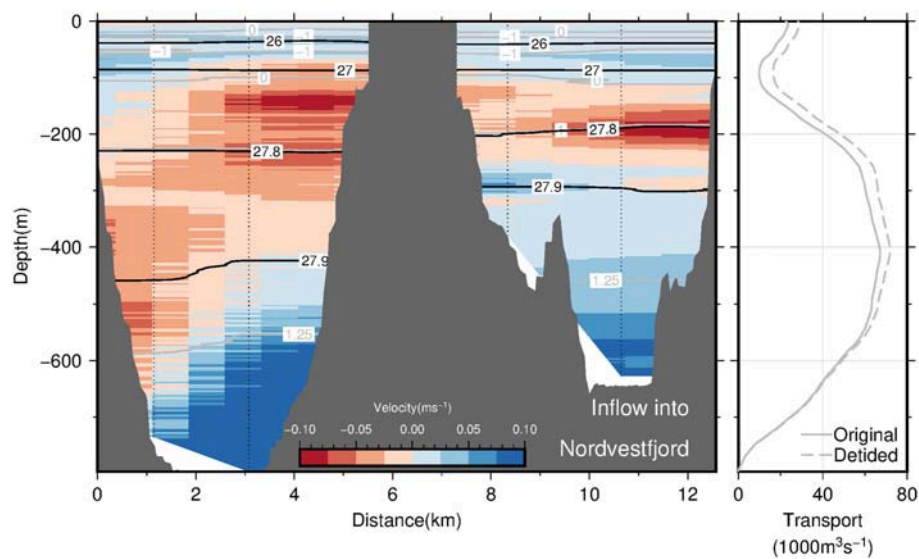


FIGURE 10 | The **(Left panel)** displays the across-section velocity based on LADCP profiles (interpolated onto a regular grid using 2D-spline interpolation) at transition between the OSS and Nordvestfjord (section C) as a function of both depth and along-section distance. The view is in-fjord directed. Blue shading denotes inflow of waters from the OSS into Nordvestfjord, while red shading denotes outflow. Also shown are selected isopycnals and isotherms as black and gray solid lines, respectively. The black, solid line in the **(Right panel)** displays the cumulative volume transport into Nordvestfjord (precisely, the cumulative integral of the along-section integrated across-section velocity from the seafloor to the sea surface) as a function of depth. The transport is based on the LADCP profiles from section C. The corresponding dashed line denotes the same transport quantity computed after subtracting barotropic tidal velocities like in **Figure 9**.

the lower boundary of the euphotic zone, identified by a chlorophyll *a* fluorescence maximum. Thus, the deep maximum of chlorophyll *a* fluorescence in the fjord is very much influenced by the different, shallow and deep, meltwater inflows which in turn determine the nutrient availability.

The sources of bulk particulates in Nordvestfjord, measured as turbidity (**Figure 4D**), can clearly be identified. GrIS meltwater discharge at the surface and at depth increased turbidity, indicating that GrIS meltwater introduced particulate material. Indeed, GrIS can carry a high load of terrestrial lithogenic matter, which has the potential to limit primary productivity due to light attenuation (Murray et al., 2015; Arendt et al., 2016; Richlen et al., 2016). Moreover, redistribution of sediments and phytoplankton cells increased turbidity at the bottom and at the surface, respectively. In the OSS, by contrast, turbidity was solely elevated at high-oxygen patches near the surface, suggesting that only plankton itself increased turbidity.

Light penetration as described by euphotic zone depth was highest where turbidity was lowest and vice versa, ranging from 20 to 69 m throughout the Scoresby Sund. Holinde and Zielinski (2016) reported 1% depths of PAR ranging from 12 to 42 m for two fjord systems at the west coast of Greenland (Uummannaq Fjord and Vaigat-Disko Bay), influenced by suspended inorganic matter concentrations and phytoplankton abundance. Lund-Hansen et al. (2010) investigated the Kangerlussuaq fjord-type estuary, also situated at Greenland's west coast, reporting on light penetration depth from <1 m near a meltwater outlet to a typical range from 6 to 39 m in the main part, again correlated with the concentration of suspended inorganic matter.

4.2.2. Dissolved Inorganic Carbon and Total Alkalinity

Estimates of DIC and TA in freshwater derived from inner fjord observations of Scoresby Sund are high, reaching 423 and 726 $\mu\text{mol kg}^{-1}$, respectively. Other studies found lower freshwater endmember concentrations of about 60–160 $\mu\text{mol kg}^{-1}$ for DIC and 160 $\mu\text{mol kg}^{-1}$ for TA in Godthåbsfjord using similar methods (Rysgaard et al., 2012; Meire et al., 2015). The reasons for high DIC and TA concentrations in freshwater are numerous. Surface meltwater can take up atmospheric CO_2 by bubble intrusion. Moreover, it has been reported that rivers flowing through the GrIS take up dissolved CO_2 from basal ice, and release it to the ocean and the atmosphere. The origin of this CO_2 is attributed to either inorganic mechanisms such as refreezing, or microbial metabolism. Even though these fluxes seem to be minor compared to other sources of CO_2 , they might strongly increase as soon as melting has reached basal ice (Ryu and Jacobson, 2012). With respect to TA, the source of meltwater is particularly important. Runoff from land-terminating glaciers carries higher TA concentrations due to stronger interaction with the bedrock than the meltwater from marine-terminating glaciers (Anderson et al., 2000; Brown, 2002; Reisdorph and Mathis, 2014; Pilcher et al., 2018). Because our TA freshwater endmember concentration was almost five times those obtained by Rysgaard et al. (2012) and Meire et al. (2015) in Godthåbsfjord, we suspect that the contribution of meltwater from land-terminating glaciers in Scoresby Sund is higher than in Godthåbsfjord.

Note that there are some uncertainties in the approach of obtaining a freshwater endmember estimate for TA and DIC, because low-salinity samples have been excluded from the linear extrapolation as they might have been influenced by biological processes.

TA and DIC concentrations from samples with salinities >25 mainly changed conservatively with salinity (**Figures 7B,D**). However, normalization to a constant salinity revealed that samples from low-salinity surface waters of Nordvestfjord must have been subject to processes other than dilution, because they deviated from a constant concentration at a salinity of 34.5. The relationship between TA and salinity suggests that precipitation of carbonate minerals plays a role, as its concentration in almost all samples was lower than it would have been expected from conservative mixing only. Because only few calcifying plankton species were present, we hypothesize that inorganic calcium carbonate was formed within the brine channels of sea ice that was formed during winter, which decreases dissolved DIC and TA in the brine (Rysgaard et al., 2009; Jones et al., 2010). When the sea ice melts during spring and summer, the brine is released to the surface layer, lowering the TA concentration of the surface water. Strikingly, the concomitant trend in DIC was more diverse with likewise higher and lower normalized DIC concentrations compared to a conservative mixing behavior. This indicates not only a depletion (which would have been expected from brine release as the only factor apart from conservative mixing changing the carbonate system), but also increasing concentrations of DIC at the surface. This increase independent from changes in salinity at the surface can be the result of several processes. On the one hand, the termination of the bloom in Nordvestfjord (see section 4.2.3) might have enhanced remineralization processes. On the other hand, a flux of CO_2 from the atmosphere to the fjord's surface water would have had more time to change DIC concentrations in Nordvestfjord compared to the OSS, because ice break-up occurred a few days earlier (**Table 1**). Finally, rising meltwater plumes from submarine glacial discharge can bring up low-DIC waters (Meire et al., 2015). However, due to the stable freshwater surface layer and the distribution patterns of nutrients, which are indicating no upwelling to the surface, we believe that the latter is the least likely cause.

4.2.3. Net Community Production

We observed a higher NCP in the OSS (58–82 $\text{mmol C m}^{-2} \text{d}^{-1}$) than in Nordvestfjord (32–36 $\text{mmol C m}^{-2} \text{d}^{-1}$, **Table 2**). However, a healthy and thriving phytoplankton assemblage in net samples taken in the OSS indicates that primary production had not been terminated at the time of the cruise. Thus, the calculated NCP in the OSS does not include the entire yearly production, and is therefore an underestimation of the annual NCP. Note that NCP was lower at the innermost station of the OSS than at the station closest to the fjord mouth (64–79 $\text{mmol C m}^{-2} \text{d}^{-1}$ at station 598 vs. 91–101 $\text{mmol C m}^{-2} \text{d}^{-1}$ at station 572, **Table 1**). In Nordvestfjord on the other hand, visual analysis of net samples and the catchment of debris, copepods, and fecal pellets in the sediment traps demonstrated that production was terminated. In the case of Nordvestfjord, remineralization of part of the organic

material after the productive period might have caused our NCP to be underestimated.

Even though chlorophyll *a* fluorescence was still high at the innermost stations of Nordvestfjord, low chlorophyll *a* fluorescence further out-fjord and a post-bloom phytoplankton community imply that primary production in Nordvestfjord had largely come to an end. Thus, annual NCP was less than half of that in the OSS. Sealing of nutrients at greater depths was observed in Young Sound (Rysgaard and Nielsen, 2006), resulting in lower phytoplankton biomass compared to areas with less meltwater discharge (Middelbo et al., 2018). In addition, silts contained in the meltwater tend to limit production by decreasing the light penetration in the water column (Murray et al., 2015; Arendt et al., 2016). For the computation of the NCP we assumed little vertical or lateral mixing which could add nutrients from adjacent water masses; homogeneity of the water column during winter; a depletion of nutrients within a realistic time frame, and a negligible winter drawdown (Jennings et al., 1984; Hoppema et al., 2007). Because these assumptions may not completely hold in a fjord system, our computed NCP may be underestimated. In contrast, an overestimation of NCP may have been introduced at some locations in the OSS where we sampled on the southern side of the fjord and, thus, in the outflowing, nutrient-poor water (see section 4.1 and 4.2.1).

The difference in the timing of the blooms (post-bloom situation in Nordvestfjord vs. active bloom in the OSS) could have been triggered by an earlier sea ice retreat in Nordvestfjord by 12–19 days compared to the OSS. While in the OSS we sampled only 19–27 days after ice break-up (except for the outermost station 572 with 35 days), it was 32–37 days in Nordvestfjord (Table 1). Meire et al. (2016b) suggest that the intensity and location of the spring bloom in the southwest Greenland Godthåbsfjord is not only controlled by the presence of sea ice, but also by the upwelling of nutrient-rich water and wind forcing. Upwelling of nutrients seems to play a role in Scoresby Sund (see section 4.2.1), but the role of wind forcing is unclear, though it might be relevant in determining the timing of the blooms. Interestingly, the earlier bloom in Nordvestfjord compared to the OSS does not tally with observations in Godthåbsfjord, where the bloom in the inner fjord occurs later than further out-fjord (Hopwood et al., 2016; Meire et al., 2016b). According to a 2D-hydrodynamic model, the establishment of the ice cover in the northeast Greenland fjord Young Sound largely depends on tides and the related current velocities (Rysgaard et al., 2003), generating openings (polynyas and leads) in the sea ice during winter. We conjecture that also the ice break-up is affected by tidal dynamics. Hence, current velocities resulting from tides, and wind forcing may have acted differently on the winter sea ice cover in Scoresby Sund and in Godthåbsfjord, ending up in different timing of the blooms from the fjord mouths to the inner fjords.

From the snapshot that we made from Scoresby Sund's primary production it is difficult to use the terms “bloom” and “post-bloom” in a strict sense, because actual bloom dynamics over the course of a year would need to be examined further. We therefore use these terms in a broader sense, referring to active

and recently terminated phytoplankton growth, respectively. Juul-Pedersen et al. (2015) described two phytoplankton blooms every year in Godthåbsfjord, a spring bloom in April/May and a summer bloom in July that was probably initiated by upwelling of nutrients from deeper layers. We could not observe such an upwelling of nutrients to the upper surface layer during the time of the expedition, but upwelling to the lower bound of the euphotic layer could be deduced from the existence of a maximum of chlorophyll *a* fluorescence. In the OSS, the import of nutrients from the shelf could have either supported a prolonged spring bloom or initiated a summer bloom. Our dataset does not allow further analysis of the temporal bloom dynamics in Scoresby Sund.

In the OSS, highest NCP values were observed at the fjord mouth, where primary producers were probably fed by nutrients from the PW and AW. High primary productivity along the shelf of Greenland sustains a high secondary production, and last but not least Greenland's export income due to efficient halibut landings (Meire et al., 2017). Estimates of NCP, especially in Arctic fjord and shelf regions which can be compared to our values in terms of methodology, are scarce. In Glacier Bay, Alaska, similar production rates as in the OSS of 54–81 mmol C m⁻² d⁻¹ were observed (Reisdorph and Mathis, 2015). Arrigo and van Dijken (2015) observed a decline in net primary production (derived by satellite chlorophyll *a* measurements, sea surface temperature, and sea ice cover) by 15% in the Greenland Sea between 1998 and 2012. The reasons for this are unclear, but an increase in productivity at the Scoresby Sund mouth seems unlikely. Shelf areas of the Chukchi Sea and the Larsen Shelf (Antarctica) that are both influenced by meltwater discharges are with 80–250 mmol C m⁻² d⁻¹ more productive than the OSS at the time of the cruise (Hoppema et al., 2000; Bates et al., 2005; Mathis et al., 2009). The reason for higher NCP in those latter regions may be that their growing season had been progressed further at the time of sampling relative to the growing season in the OSS. Thus, the NCP summed up over an entire year might be similar in Scoresby Sund compared to the other regions. Open water areas of polar regions, like the basin of the Chukchi Sea, the Arctic Ocean basin, and the Weddell Sea and Drake Passage in Antarctica, generally experience 10–100 times lower export production rates (Hoppema et al., 2000, 2007; Anderson et al., 2003; Bates et al., 2005; Mathis et al., 2009; Munro et al., 2015).

Differences in NCP estimates based on nitrate+nitrite or phosphate deficits may be a result of a deviation from the canonical Redfield ratio. This deviation may be caused by different remineralization rates of the nutrients, or a phytoplankton assemblage with a non-Redfieldian stoichiometric ratio. Also, nitrate is more prone to be altered by additional processes other than phytoplankton growth, for instance denitrification and nitrogen fixation (Anderson et al., 2003). Nevertheless, both estimates show the same trends within the fjord system.

4.2.4. Particulate Organic Carbon Flux

Within Nordvestfjord, POC fluxes were about five times higher close to glacier fronts than in the remaining fjord. Averaged over

the whole fjord, extrapolated POC fluxes show that with $0.06\text{--}2.5\text{ g C m}^{-2}\text{ d}^{-1}$ more organic carbon reached the sea floor than was produced as NCP during the growth season until the time of sampling. In the OSS, the POC flux decreased with increasing depth in the surface water, and was then dependent on the horizontal advection of the water mass present at the respective depths. Five to fifteen percent of the NCP in the OSS was exported to the seafloor (**Table 2**, **Figure 4E**).

Despite the limited number of POC profiles we believe that they may be representative for the POC fluxes during the time of the cruise as they are in good accordance to other studies. The b values in Nordvestfjord ($-0.4\text{--}0.6$), which constitute the carbon export efficiency, were low compared to the global value of 0.86 (Martin et al., 1987) and to the values proposed by Guidi et al. (2015) for Arctic provinces ($1.65\text{--}1.75$) (**Table 2**). The POC flux at 100 m depth corresponds to 30–80% of the NCP, which is high in comparison to the OSS, where only 10–20% (or 10–30%, depending on the NCP estimate) of the NCP reached the trap depth at 100 m (**Table 2**). We therefore believe that Nordvestfjord is a spot of high POC sedimentation or even burial, especially close to marine-terminating glaciers. High POC fluxes and sedimentation rates might have been caused by the high sediment concentration in meltwater from the GrIS due to its passage along the ice-bed interface (Nienow et al., 2017), which can increase the sinking velocities of particles by ballasting (e.g., Iversen and Robert, 2015; Wiedmann et al., 2016). High POC fluxes close to glacier fronts have also been observed in other fjord systems. In Adventfjorden, Svalbard, POC fluxes of $0.77\text{--}1.53\text{ g C m}^{-2}\text{ d}^{-1}$ were observed in direct vicinity to glacier fronts while they were considerably lower within the remaining fjord (Wiedmann et al., 2016). Annually-integrated POC fluxes in Kobbefjord, southwest Greenland, accounted for $19.9\text{ mol C m}^{-2}\text{ yr}^{-1}$ (Sørensen et al., 2015), which converts to a daily rate of $0.65\text{ g C m}^{-2}\text{ d}^{-1}$. Daily production must not necessarily correspond to the daily flux because strong lateral advection, the accumulation of particles at salinity gradients (Alldredge and Crocker, 1995), and the active transport of POC by vertically-migrating zooplankton (Turner, 2015) mask the sources of the particles and may bias the estimation of POC export to depth. Besides, we calculated the daily NCP rate based on the number of open water days since winter and averaged out fluctuations in production within this period, while the POC fluxes (and the resulting export to the sea floor) are snapshots of the situation during the time of the cruise.

In the OSS, the boundary between the relatively fresh water at the surface in the upper 75 m and the more saline PW acted as a trap of particles that accumulated at the density gradient (Alldredge and Crocker, 1995). Below that, the POC concentration was mainly determined by the POC concentration of the advected water mass, with PW carrying low concentrations and AW carrying slightly elevated POC concentrations (**Figure 4E**). The mean b value in the OSS was higher than in Nordvestfjord and a smaller share of the NCP was reflected in the POC flux at 100 m depth (**Table 2**), indicating a more effective remineralization within the water column. Fragmentation and ingestion by zooplankton in the upper water column is an important mechanism to increase flux attenuation, together with the timing of the bloom (Belcher et al., 2016).

The density gradients described before may have given the zooplankton additional time to feed effectively before particles sank to a depth where microbial respiration dominated over zooplankton activity.

At the sill between the OSS and Nordvestfjord, a higher POC flux at depth than in the surrounding waters was observed. Whether this is caused by the overflow of AW into the basin of Nordvestfjord (see section 4.1) would need further investigations. Generally, it might be that the sill plays an important role in the distribution of particles and solutes at the entrance to Nordvestfjord.

In summary, our data suggest that the Scoresby Sund can be divided into two parts with particular biogeochemical regimes: The outer fjord part (OSS) experiences high productivity due to the large surface area that reduces the stratifying impact of surface meltwater discharge, and the import of nutrients with shelf waters, as well as an active pelagic remineralization reducing the sedimentation of organic carbon to the sea floor. The regime in the inner fjords, in particular Nordvestfjord, is the opposite; primary production is limited by the supply of nutrients and shadowing by silts at the surface, whereas the export efficiency is high due to ballasting by exactly those silts.

4.3. Biogeochemical Cycling Close to Dagaard-Jensen Glacier

Greenland's marine-terminating glaciers vary largely in their characteristics, for instance their flow speeds, the shape of their termini, and the pattern of their meltwater discharge (Straneo and Cenedese, 2015). What is common to all is their substantial impact on the physical (e.g., Mortensen et al., 2013; Sciascia et al., 2013; Fried et al., 2015) and biological (e.g., Juul-Pedersen et al., 2015; Meire et al., 2016b, 2017) regimes within their respective fjords and, hence, the adjacent shelf areas. Understanding the processes in direct vicinity to the glacier fronts reveals important information on the dynamics further out-fjord. Dagaard-Jensen glacier is one of the largest east Greenland glaciers with a drainage basin of about $50,150\text{ km}^2$ (Rignot and Kanagaratnam, 2006). From 13 marine-terminating glaciers in east and west Greenland that were examined by Enderlin and Howat (2013), Dagaard-Jensen's submarine melt rate is high with 2.41 m d^{-1} (minimum 0.03 m d^{-1} for Petermann glacier, maximum 2.98 m d^{-1} for Jakobshavn Isbræ, both west Greenland), whereas the surface melt rate is relatively low with only 0.0014 m d^{-1} (minimum 0.0006 m d^{-1} for Yngvar Nielson glacier, maximum 0.0064 m d^{-1} for Jakobshavn Isbræ, both west Greenland). The position of Dagaard-Jensen glacier's terminus is highly variable within the year, but the mean front position has not changed from 2000 to 2010 (Walsh et al., 2012; Enderlin and Howat, 2013). Our station closest to Dagaard-Jensen glacier was about 8–10 km away from the terminus. At a depth of 200–240 m, we observed a salinity-driven density decrease, whereas at other stations nearby (e.g., 582) and in the OSS (e.g., 599) no such a freshwater sign could be detected in the temperature-salinity diagram (**Figure 8D**). Commonly, subglacial discharge and the entrainment in the buoyant plume substantially influence transport processes in direct vicinity to the glacier front ($\sim 5\text{ km}$), while transport

processes further away (~20 km distance to the glacier) are indirectly modulated by the freshwater discharge, rather than by the process of entrainment itself (Bendtsen et al., 2015). Besides, melting of ice at glacier fronts or from icebergs can be identified by the so-called Gade-slope on the temperature-salinity diagram, which takes into account the amount of energy that is required to melt ice, and its effect on the water temperature. This has to be distinguished from a horizontal line on the temperature-salinity diagram like we observed at station 580, which typically indicates the characteristic of a mixture of fjord water with water from runoff (zero temperature and salinity) (Gade, 1979; Straneo et al., 2012). We therefore attribute the temperature-salinity pattern at 200–240 m depth of station 580 mostly to liquid freshwater discharge through outlets of englacial and subglacial channels at the glacier front, and not to actual melting processes at the terminus (Chu, 2014) (Figure 8D). However, given that the values in T-S space fall in between the dense water properties of the inflowing water, a runoff endmember (as defined by the Gade line) mixing with submarine meltwater cannot be fully excluded. Due to upwelling of deep fjord waters, this discharge can result in the export of a meltwater/deep water mixture with a much larger volume than the initial meltwater release (Beairst et al., 2018). Altogether, we assume that we recorded signs of the submarine meltwater export of Dagaard-Jensen glacier; these could not be detected further outfjord due to the gradual mixing with fjord waters from depth.

Because the meltwater input was observed at a depth of 200–240 m (Figure 8A), we assume that the core of the meltwater plume of Dagaard-Jensen glacier reached neutral buoyancy at that depth. Carroll et al. (2016) showed that plumes from marine-terminating glaciers with deep grounding lines gradually increase their temperature and salinity by mixing with the surrounding water, and therefore equilibrate to their final depth within the layer of Polar Water. The grounding line depth of Dagaard-Jensen glacier is presently unknown; we observed signs of low salinity at 200–250 m depth. Because there is some distance between our innermost station and the glacier front, the plume has probably ascended from a deeper grounding line and crossed the AW/PW interface at 250–300 m depth (for depth distributions of water masses, see Figure 3). A high amount of suspended particulate material, recorded as turbidity, and low nutrient concentrations followed the freshwater plume (Figure 8A), confirming that meltwater itself does not introduce additional nutrients (see section 4.2.1), but adds silts to the fjord system.

Different to the depth distribution of nutrients and turbidity, the POC flux increased just below the depth of the meltwater plume to almost the highest values within the whole fjord system (Figure 8A). However, because NCP was not higher than at other stations (Table 1), and the maximum POC flux was at a depth where primary production is not possible due to light limitation (250–350 m), we propose that the high POC flux cannot be attributed to high primary productivity at the surface, but that organic material must have accumulated at depth and was gradually sinking down the water column. Meltwater can introduce mass mortality of zooplankton, e.g., by

osmotic pressure and the ingestion of silt particles (Wesławski and Legeżyńska, 1998), and also glacial melt itself can entrain particulate organic matter (Wiedmann et al., 2016).

If we compare the profiles of station 580 closest to Dagaard-Jensen's glacier terminus to other stations in the fjord, the special characteristic of it becomes clearer. For example, at station 582, which is further outfjord than the aforementioned one, no such a distinct melt sign in the temperature-salinity diagram could be found. Accordingly, nutrient concentrations, turbidity, and POC flux are highest at a depth below the euphotic layer, where typically remineralization is highest. Another peak in POC flux at 350–400 m depth can be the result of lateral advection of particles (Figure 8B). In the OSS at station 599, the profiles indicate active primary production and remineralization processes, and a dependence of POC and nutrient distributions on water masses (Figure 8C).

4.4. The Future of Scoresby Sund and Analogies to Other Glacially Influenced Regions

While our data only allow us to obtain a snapshot of the biogeochemical cycling of Scoresby Sund in summer, Rysgaard and Glud (2007) provided an important and extensive picture of the dynamics in the more northerly fjord Young Sound based on long-term comprehensive observations. They propose that due to climate change, conditions in Young Sound will resemble those of present-day Scoresby Sund by 2071–2100 (see also Rysgaard et al., 2003). Analyzing ecosystem structure and elemental cycling along a transect from Young Sound to a few hundred kilometers southwards (including Scoresby Sund) is thought to mirror the temporal changes that Young Sound will undergo within the next decades of climate change. We cannot fully support this statement. Of course, some conditions in Young Sound are comparable to those we observed in Scoresby Sund. Seasonal observations of the fjord system showed that the magnitude of the vertical flux of material was tightly coupled to the retreat of sea ice and the peak in freshwater discharge from a river, which imported large quantities of terrestrial matter into the fjord (Rysgaard and Sej, 2007). High POC fluxes in Scoresby Sund coincide with high turbidity close to glacier fronts, demonstrating a similar link of vertical flux and freshwater discharge. About 30% of the organic carbon reaching the sea floor in Young Sound was preserved in the sedimentary record (Thamdrup et al., 2007), which is inbetween the estimates we obtained from Nordvestfjord and the OSS. Notwithstanding, Young Sound has a completely different geometry than Scoresby Sund. The 90 km long and 2–7 km wide Young Sound fjord system has a mean depth of 100 m, a maximum depth of 360 m, and its inner part does not have a deep basin, but is even shallower than the area closer to the fjord mouth. A sill shallows the fjord to only 45 m, which has completely different implications for the circulation of water masses than the sill between the OSS and Nordvestfjord. Also important is the fact that Young Sound is only fed by surface runoff and does not receive meltwater discharge at depth (Bendtsen et al., 2007). The hydrographical settings and biogeochemical cyclings are therefore profoundly

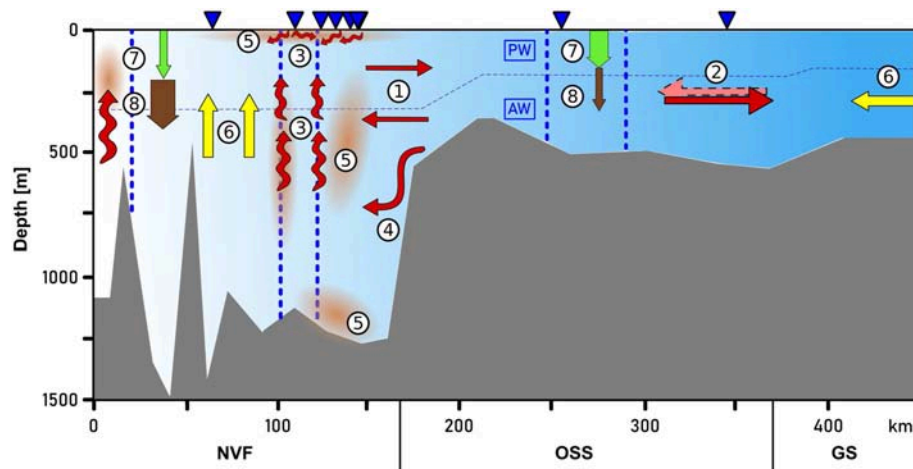


FIGURE 11 | Conceptual figure of the different regimes in Scoresby Sund influencing the fjord carbon cycle. Two-dimensional circulation was observed at the entrance to Nordvestfjord with inflowing water below 400–500 m depth, and outflowing water above (1). Due to the width of the OSS, the formation of a three-dimensional circulation pattern consisting of outflowing water at the southern side and inflowing water at the northern side was possible (2). The import of meltwater (3) consists of rising meltwater plumes from submarine discharge and surface meltwater inflow. (4) indicates the deep overflow of Atlantic Water across the sill, filling the basin of Nordvestfjord. Currents, bottom topography, and meltwater discharge result in (5) plumes of high turbidity at the depth of surface and submarine meltwater discharge as well as resuspension. The distribution of nutrients is determined by upwelling caused by rising plumes of subglacial discharge, and by the import with Atlantic and Polar Water from the shelf (6). Arrows of (7) export production and (8) POC flux are scaled to the according magnitude. PW, Polar Water; AW, Atlantic Water.

different between Young Sound and Scoresby Sund, which makes a direct transfer of Scoresby Sund's conditions to Young Sound regarding future projections difficult. We nevertheless believe that a thorough examination of fjords along the coast of Greenland reveal important information on the way Arctic glacially-influenced ecosystems are developing with ongoing climate change. Moreover, even though fjord systems can barely be compared to each other as a whole, several hydrographic and biogeochemical concepts are similar and can be related to each other.

What will finally be the effects of ongoing climate change on Scoresby Sund? We hypothesize that a further increase in glacial meltwater discharge and surface runoff would on the one hand decrease Nordvestfjord's primary production because of intensified shadowing and stratification, and increase vertical export caused by mineral ballasting. The GrIS is the largest ice body of the Arctic, but also the melting of marine-terminating valley glaciers is contributing to the Arctic freshwater budget, for example in Svalbard's fjords. Their total POC flux from glaciers to fjords, independent from glacier area and annual runoff, is considerably smaller than that of the GrIS (e.g., the POC flux of Svalbard is only 6% of that from the GrIS) (Zhu et al., 2016), but a considerable amount of terrestrial organic matter is imported into the fjord close to glaciers (Koziorowska et al., 2016). Similar to Scoresby Sund, it is projected that sedimentation will enhance with warming climate due to the enhanced inflow of silt-rich meltwater (Rysgaard et al., 2003; Arendt et al., 2010; Zajackowski et al., 2010; Murray et al., 2015). In Young Sound, a 3-fold increase in primary production is projected by the end of this century compared to present-day levels due to higher light availability and enhanced import of nutrients (Rysgaard and Glud, 2007). In Arctic fjords in general,

production largely depends on the import of nutrients from the shelf, usually by AW. In the Southern Ocean as a high-nutrient-low-chlorophyll region, by contrast, primary production depends on the input of iron. Meltwater from the largest ice body in the world, the Antarctic ice sheet, displays an important source of the micronutrient iron, which is limiting productivity (Death et al., 2014), and icebergs calved from the ice sheet can produce a trace of fertilized surface water along their track and thereby increase primary production (Duprat et al., 2016). Hence, while meltwater from the GrIS can only fuel primary production by the upwelling of nutrient-rich water from depth and modulated circulation patterns that are increasing the shelf nutrient import, the Antarctic ice sheet meltwater itself can increase primary production by adding the limiting nutrient iron. In terms of the impact of climate change on the circulation patterns and water mass distributions in fjords, Boone et al. (2018) showed that an increasing amount of freshwater at the shelf diminishes the exchange of bottom water in fjords. This might result in a longer residence time of Nordvestfjord's basin waters. Largely unknown is to what extent the meltwater sources to the fjord will change in the future. Icebergs constitute up to 30–50% of the freshwater loss from the GrIS with highest melt rates in southeast Greenland, most of it being released at a depth of 100–300 m during summer (Moon et al., 2017; Enderlin et al., 2018). Their (future) role in the regional freshwater budget is, however, barely known. Besides, marine-terminating glaciers in Scoresby Sund might become land-terminating. The speed of the glacier retreat is highly dependent on the bed geometry, slopes of the sea floor, and the presence of warm AW (Millan et al., 2018). Analyzing the topography of Scoresby Sund in more detail would therefore add significant information for making projections on the future fate of Scoresby Sund's carbon cycle.

5. CONCLUSION

The Scoresby Sund fjord system is the largest fjord system in the world, but its hydrography and biogeochemical cycling has never before been studied. We presented data from a comprehensive sampling program in summer 2016. They show that circulation and biogeochemical cycling largely depend on the kind of freshwater import from the GrIS to the fjord, and on the fjord width that defines the degree how meltwater can act on the hydrography of the fjord. We define two different regimes in Scoresby Sund:

1. The narrow Nordvestfjord is influenced by marine- and land-terminating glaciers. Meltwater does not introduce any nutrient, except for surface meltwater discharge that imports dissolved silicate. During the sampling period, the surface freshwater layer prevented the resupply of nutrients from deep upwelling with submarine meltwater discharge [Figure 11(3, 6)], and only the lower bound of the euphotic layer was presumably fed by nutrients from depth. Besides, silts that are carried by meltwater shaded the upper part of the water column [Figure 11(5)]. This leads to a relatively low primary productivity in Nordvestfjord [Figure 11(7)], which occurred earlier than in the outer fjord due to earlier ice break-up. However, meltwater plumes might supply nutrients to the entire surface layer during the period of maximum discharge later in the year. Low TA in surface waters were attributed to inorganic carbonate mineral precipitation in sea ice during winter. Relatively high DIC and TA freshwater endmember concentrations stem from land-terminating glaciers. POC flux was high [Figure 11(8)], especially close to glacier fronts, because of particle ballasting by silts. Overall, we assign Nordvestfjord to be a hotspot of carbon burial.
2. The OSS is also affected by surface and submarine meltwater discharge, but because of its greater width (35–40 km) the signs of meltwater were less pronounced. Hydrography is mainly determined by the inflowing water masses from the shelf. Atlantic Water and Polar Water import nutrients [Figure 11(6)], sustaining a relatively high NCP [Figure 11(7)] that was still flourishing during the time of our cruise. Sinking of particles was slowed down by the salinity gradients between the water masses, and the water column. Consequently, less organic carbon was sedimenting to the sea floor [Figure 11(8)].

We analyzed processes close to the glacier front of Scoresby Sund's largest marine-terminating glacier at the head of Nordvestfjord. We saw signs of a freshwater plume 8–10 km away from the terminus that obtained neutral buoyancy at 200–240 m depth. While NCP was not higher than at other locations in Nordvestfjord, the POC flux was high possibly due to meltwater-induced mass mortality of planktonic organisms.

With ongoing climate warming we anticipate an intensification of the differences between Nordvestfjord and the OSS compared to present-day conditions. Investigating the other fjord arms of the Scoresby Sund fjord system would reveal important information whether processes are similar to those we observed in Nordvestfjord. This could then be used to give an area-based estimate on production vs. export and, thus, whether Scoresby Sund is or will

be a source or a sink of atmospheric CO₂. Long-term observations are needed to understand the seasonal variability of production and remineralization within the fjord, and to assess Scoresby Sund's role in the Arctic carbon cycle. However, our observations highlight the impact of the interplay between fjord geometry and glacial meltwater discharge on hydrography and biogeochemical processes, and contribute to the understanding of Greenland's fjord systems and their carbon cycling.

AUTHOR CONTRIBUTIONS

UJ and BK planned the expedition MSM56. MS, MH, and MI designed the study. MS, CB, AF, JG, UJ, BK, CK, and HvdJ acquired the data. AF and OZ provided hydrographic and light field data. HvdJ and CK corrected the flux data, and CB and JG the nutrient data. TK and CE planned and participated in the cruise MSM76, and analyzed the LADCP data. MS, MH, and MI interpreted the data, with help from co-authors. MS wrote the manuscript with contributions from all co-authors.

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Episodic Arctic CO₂ Limitation in the West Svalbard Shelf

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The European Sector of the Arctic Ocean is characterized by low CO₂ concentrations in seawater during spring and summer, largely due to strong biological uptake driven by extensive plankton blooms in spring. The spring plankton bloom is eventually terminated by nutrient depletion and grazing. However, low CO₂ concentrations in seawater and low atmospheric resupply of CO₂ can cause episodes during which the phytoplankton growth is limited by CO₂. Here, we show that gross primary production (GPP) of Arctic plankton communities increases from 32 to 72% on average with CO₂ additions in spring. Enhanced GPP with CO₂ additions occur during episodes of high productivity, low CO₂ concentration and in the presence of dissolved inorganic nutrients. However, during summer the addition of CO₂ suppresses planktonic Arctic GPP. Events of CO₂ limitation in spring may contribute to the termination of the Arctic spring plankton blooms. The stimulation of GPP by CO₂ during the spring bloom provides a biotic feedback loop that might influence the global role played by the Arctic Ocean as a CO₂ sink in the future.

Keywords: CO₂ limitation, gross primary production, Arctic Ocean, spring blooms, plankton communities, CO₂ additions

INTRODUCTION

The shelf seas and the shelf edge of the European Arctic Sector are characterized by strong spring plankton blooms that extend between 70 and 80°N in the Barents Sea and the northern Svalbard shelf (Wassmann and Reigstad, 2011). These blooms support high net community production (NCP) rates and fuel the Arctic food web (Vaquer-Sunyer et al., 2013). The strength of the spring Arctic plankton bloom results not only from high primary productivity, but also from a very low respiratory demand of the planktonic community at that time, which leads to high NCP (Vaquer-Sunyer et al., 2013). The spring bloom is associated with increased photoperiod, and depends on light availability, ice cover, water masses and nutrient availability, which lead to extremely pronounced seasonality and spatial heterogeneity (Vaquer-Sunyer et al., 2013). The high biological CO₂ uptake in shallow stratified layers during the spring bloom results in rapid CO₂ drawdown in the surface waters of the Arctic Ocean (Chierici et al., 2011; Yasunaka et al., 2016). Values as low as 100 μatm of partial pressure of CO₂ (pCO₂) have been recorded at the end of the spring bloom (Fransson et al., 2009), which is among the lowest pCO₂ values reported across the open ocean (Takahashi et al., 2009). As a consequence, several regions of the Arctic Ocean such as the Eurasian shelves and the Barents Sea (Fransson et al., 2001, 2009) and the Bering-Chukchi shelves

(Kaltin and Anderson, 2005), act as intense carbon sink for atmospheric CO₂, taken up ~66–199 Tg C yr⁻¹ during spring and summer (Bates and Mathis, 2009).

Arctic spring plankton blooms are generally triggered by increased solar radiation with increased photoperiod, and the associated increase in temperature, melting ice and the consequent increase in underwater irradiance and water column stratification (Sakshaug and Skjoldal, 1989; Niebauer, 1991; Reigstad et al., 2002; Hodal et al., 2012; Juul-Pedersen et al., 2015). The spring bloom is usually considered to be terminated by nutrient depletion and grazing, but secondary blooms can be produced by wind-driven events that break down the weak stratification and supply nutrients to the euphotic zone (Sakshaug and Skjoldal, 1989; Niebauer, 1991; Wassmann et al., 1999; Tremblay et al., 2006; Fransson et al., 2017). However, experimental assessments suggest that low CO₂ concentrations can limit primary production (Mercado and Gordillo, 2011), such as the low CO₂ concentrations observed during spring and summer in the Arctic Ocean (Bates and Mathis, 2009).

Limitation by CO₂ in plankton communities has indeed been experimentally observed in the European Arctic sector (Engel et al., 2013; Holding et al., 2015) and in sub-ice blooms in the Baltic Sea (Spilling, 2007) as well as in temperate regions of the Atlantic Ocean (Hein and Sand-Jensen, 1997). However, Arctic CO₂ limitation seems to be temperature-dependent (Holding et al., 2015), light-dependent and acclimation of subarctic plankton productivity to high levels of CO₂ has been observed (Hoppe et al., 2017). When CO₂ is depleted, the intracellular CO₂ concentration decreases, leading to a lower diffusive CO₂ supply that reduces photosynthetic rates (Riebesell et al., 1993) and results in CO₂-limited phytoplankton production (Rost et al., 2006). In polar regions, CO₂ limitation is more likely than in temperate regions because the conversion of HCO₃⁻ to CO₂ in cold waters with high pH supplies little CO₂, <5% of the required CO₂ for one polar diatom species (Riebesell et al., 1993). Isotopic evidence also points at CO₂ limitation during peak and late bloom phases in the Arctic Ocean, reflected in heavier δ¹³C signatures in plankton (Tamelander et al., 2009). However, experimental and observational evidence of CO₂ limitation of phytoplankton production during the spring phytoplankton bloom is limited, so whether this is an episodic or chronic situation remains unclear.

Here, we test the hypothesis that the characteristically low CO₂ concentrations in seawater during the Arctic spring and early summer limit the primary productivity of plankton communities before dissolved inorganic nutrients are fully consumed. To test this hypothesis, we conducted a series of seven experiments to test the response of planktonic gross primary production (GPP) to elevated CO₂. These communities were sampled west and northwest of Svalbard (European Arctic sector), during spring and summer. The locations of the experiments were heterogeneous (Figure S1); four of the experiments were located in the path of the West Spitsbergen Current (WSC), that flows northward along the shelf edge at the west of the Svalbard Islands, and two of the experiments were located in the mouths of two western fjords. We sampled seven subsurface plankton communities in the spring and

summer of 2014 and 2015, thereby experiencing a wide range of conditions in terms of community metabolism and biogeochemical conditions. We evaluated the net biological demand for CO₂, as the NCP in the euphotic layer, compared this to the atmospheric supply of CO₂ through air-sea exchange, and assessed the experimental response of the GPP of the plankton communities sampled to elevated CO₂.

MATERIALS AND METHODS

Three cruises were conducted to the west and northwest of the Svalbard shelf where seven experiments on CO₂ addition were carried out on board R/V Helmer Hanssen in 2014 and 2015: two experiments were run in May, three in August 2014 and two in May 2015 (Figure S1). Results of the first experiment, in May 2014, were previously Holding et al. (2015).

A 50 L sample of subsurface seawater (3 m) was collected using a Rosette sampler system, which was fitted with Niskin bottles and a calibrated CTD profiler (Seabird 911plus), and located in two 25 L closed tanks using silicon tubes. Samples to measure the carbonate system parameters, chlorophyll *a* concentration (Chl *a*), nutrients concentrations and phytoplankton community composition were taken and preserved for further analysis.

To simulate the predicted scenario of atmospheric *p*CO₂ by 2,100 (IPCC Panel, 2014), 25 L of seawater was stored in a closed tank and the remaining 25 L were bubbled with CO₂ until ~1,000 ppm *p*CO₂ was reached, using an Environmental Gas Monitor (EGM-3) to measure *p*CO₂ while a water pump ensured proper mixing. The treated and untreated water were gently mixed in 10 L carboys to produce an intermediate level and a gradient of increasing *p*CO₂ between treatments. In 2014, this gradient included four *p*CO₂ levels in the experiments, but the experimental design was simplified, based on the results obtained, to have only two elevated *p*CO₂ levels in 2015. This allowed experiments with a greater number of communities to be conducted within the time available (see *p*CO₂ of each treatment in Table S1).

After every treatment reached the targeted *p*CO₂ (45 min), two sets of samples were collected. The first set was immediately preserved to determinate the initial dissolved O₂ concentration, δ¹⁸O (in dissolved O₂), total alkalinity (TA) and total dissolved inorganic carbon (DIC). The second set of samples was incubated for 24 h and subsequently preserved to determinate the same parameters at the end of the incubation. In 2014 the second set of samples was incubated in transparent methacrylate tubes which allowed the 60% transmittance of photosynthetically active radiation surface (PAR) to simulate the irradiance at 3 m depth, with flow-through surface seawater baths to maintain samples close to the *in-situ* temperature during the cruises of 2014. In May 2015, samples were incubated in a 40-L tank with circulation of surface seawater and neutral screens allowed the 80% transmittance of surface PAR.

Gross primary production (GPP) was measured from the photosynthetic production of ¹⁸O₂ following the addition of H₂¹⁸O during a 24 h incubation, according to Bender et al. (1987) and Grande (1988). Four 12-ml vials per treatment, made of

borosilicate, were immediately fixed with 100 µl of saturated HgCl₂ solution and stored in darkness for further $\delta^{18}\text{O}_{\text{initial}}$ analysis. Four other vials per treatment containing glass beads to mix, were labeled with 80 µl of 98% H₂¹⁸O, shaken to ensure mixing, incubated for 24 h on deck and subsequently fixed with 100 µl of saturated HgCl₂ solution for further analysis. At the Stable-Isotope Laboratory of the Instituto Andaluz de Ciencias de la Tierra (IACT-CSIC) Stable-Isotope Laboratory, a 4-ml headspace of Helium was generated in each vial. Vials were left to equilibrate for 24 h at room temperature letting the dissolved gases in water equilibrate with the headspace, originally Helium 100%. After 24 h, the $\delta^{18}\text{O}$ of dissolved oxygen in the headspace was measured in a Finnigan GasBench II attached to a Finnigan DeltaPlusXP isotope ratio mass spectrometer, with precision better than 0.1‰. The flow was passed through a liquid nitrogen trap to remove water vapor before entering GasBench II. Oxygen and nitrogen were separated in a Molecular Sieve 5 Å chromatographic column. Data, which were corrected with atmospheric air, are reported as $\delta^{18}\text{O}$ value (‰) relative to V-SMOW (Vienna Standard Mean Ocean Water) standard.

The $\delta^{18}\text{O}(\text{H}_2\text{O})$ composition of labeled samples was measured 3 weeks later in a liquid water isotope analyzer (Los Gatos Research) with precision of 0.2‰. In order to avoid contamination of the analyzer with highly ¹⁸O-enriched H₂O (≈3,000‰), the labeled water was diluted (approximately 1:20) with a laboratory standard of known isotopic composition. GPP was calculated from Bender et al. (1999) as:

$$\text{GPP} = [(\delta^{18}\text{O}_{\text{final}} - \delta^{18}\text{O}_{\text{initial}})/(\delta^{18}\text{O}_{\text{water}} - \delta^{18}\text{O}_{\text{initial}})] \times [\text{O}_2]_{\text{initial}}$$

where $\delta^{18}\text{O}_{\text{initial}}$ and $\delta^{18}\text{O}_{\text{final}}$ are the initial and final $\delta^{18}\text{O}$ of dissolved O₂ (‰ vs. V-SMOW), respectively, $\delta^{18}\text{O}_{\text{water}}$ is the $\delta^{18}\text{O}$ of the labeled seawater (‰ vs. V-SMOW) and $[\text{O}_2]_{\text{initial}}$ is the initial O₂ concentration (µmol O₂ L⁻¹) measured by high-precision Winkler titration.

In addition to the ¹⁸O method, the O₂ mass balance method (Carpenter, 1965; Carritt and Carpenter, 1966) was used to estimate the NCP and the community respiration (R) in darkness in the water column of the CO₂ experiments stations, as well as in 5 additional stations in the nearby area. NCP and R rates were calculated by subtracting initial dissolved oxygen concentrations from dissolved oxygen concentrations measured after incubation in the dark and light conditions, respectively. GPP measured with the O₂ mass balance method (GPP-O₂) was calculated by solving the mass balance equation $\text{GPP-O}_2 = \text{NCP} + \text{R}$ (Carpenter, 1965; Carritt and Carpenter, 1966). NCP and R was determined at 3 different depths on the euphotic layer (3 m, 15 m and 25 m, on average). Seawater samples were collected with a Rosette sampler system fitted with 10-L Niskin bottles and a calibrated CTD (Seabird 911plus). Seawater was carefully siphoned from the Niskin bottles into 100 ml narrow-mouth, borosilicate Winkler bottles. Seven replicates were used to determine the initial oxygen concentration, and seven replicates were incubated for 24 h in dark and in light. The bottles were incubated on deck, following the same procedure previously mentioned for GPP samples measured with the ¹⁸O method. Light attenuation inside each methacrylate incubator was estimated

with a Photosynthetically Available Radiation (PAR) radiometer (Biospherical Instruments Inc. QSL-101). Light attenuation was simulated using screens as a % of the on-deck PAR with 0 screen, 2 screens, 3 screens, simulating 60, 33, and 25% of surface PAR, respectively. GPP-O₂ was calculated by the difference between the mean final oxygen concentration of light incubated bottles and the mean final oxygen concentration of dark incubated bottles. Oxygen concentrations were determined by automated high-precision Winkler titration (Carpenter, 1965; Carritt and Carpenter, 1966), using a potentiometric electrode and automated endpoint detection (Oudot et al., 1988). Values that reported O₂ production in darkness were considered unviable and were discarded from the database. The communities were then characterized as autotrophic communities (GPP/R ratios > 1, NCP > 0) or heterotrophic (GPP/R ratios < 1, NCP < 0).

Sampling and analyses for the determination of the carbonate chemistry in the experiments followed the standard operating procedures from Dickson et al. (2007). Seawater for TA and DIC analyses were collected from each treatment carboy with a silicon tube and carefully siphoned in two 250 mL borosilicate bottles per treatment. Initial samples were preserved with 60 µL of mercury chloride and stored in dark and cold until analysis onboard and the final samples were preserved after 24 h of incubation and analyzed onboard. TA was determined using potentiometric titration in open cell with 0.05 mol l⁻¹ hydrochloric acid using a Titrino system (Metrohm, Switzerland). The precision was ±2 µmol kg⁻¹, obtained by triplicate analysis of one sample on a daily basis and Certified Reference Material provided by Dr. Andrew Dickson (Scripps Institution of Oceanography, University of California) was used for accuracy check of the TA analyses. pH was determined spectrophotometrically, using m-cresol purple and a diode-array spectrophotometer, HP8453 (Clayton and Byrne, 1993). The analytical precision was estimated to ±0.002 pH units, which was determined by triplicate analysis of one sample every day. The pH of the indicator solution was measured daily using a 0.2-mm flow cell, this was then used as correction for the perturbation caused by the addition of the indicator solution (Chierici et al., 1999).

The CO₂ concentration was calculated from TA and DIC analysis using the program CO2SYS (Pierrot et al., 2006) and output parameters were standardized to standard pressure and *in situ* water temperature. We used the carbonate dissociation constants (K₁ and K₂) of Mehrbach et al. (1973) as refitted by Dickson and Millero (1987), and the KSO₄ determined by Dickson (1990). The CO₂ removal rates were calculated from the difference in CO₂ concentration during 24 h incubation.

The air-sea CO₂ flux (F) was calculated using the measured *f*CO₂ according to the gas flux formulation:

$$F = K_0 \times k \times (f\text{CO}_2 - f\text{CO}_2_{\text{air}}) \\ k = 0.31 \times u^2 \times (\text{Sc}/660) - 0.5$$

Where K₀ is the solubility, k is the transfer velocity for air-sea CO₂ exchange, *f*CO₂_{air} and *f*CO₂ are the atmospheric and sea surface *f*CO₂, respectively, u is the wind speed (mean daily) and Sc is the Schmidt number. The solubility (K₀) was calculated according to Weiss (1974) using the measured sea surface

temperature (SST) and salinity values. The transfer velocities (k) and the Schmidt number (Sc) were calculated according to Wanninkhof (1992) for monthly and daily average observed wind speed (Equation 3) and are based on wind speed (u). The $f\text{CO}_2$ air was estimated from the monthly $x\text{CO}_{2\text{air}}$ from Ny-Ålesund (www.nilu.no). The dry atmospheric mole fraction was converted into the atmospheric $p\text{CO}_2$ ($p\text{CO}_{2\text{air}}$) in wet air using the relative air humidity, air pressure and air temperature for the date when the fluxes based on ship data were estimated.

Chlorophyll *a* concentration (Chl *a*) was collected from the same depth at which seawater was collected for the experiments conducted in May 2015 and was determined fluorometrically by filtering 200 mL of the sub-surface seawater sampled through Whatman GF/F filters and extracted in 90% acetone for 24 h before spectrofluorometric determination using a Shimadzu RF-5301PC spectrofluorometer, following Parsons et al. (1984). For the experiments conducted in May and August 2014, Chl *a* was derived from the fluorescence measured in a calibrated CTD (Seabird 911plus) at the depth of the sampled seawater using linear regression equations between results of Chl *a* and fluorescence measured in from previous vertical profiles in same stations ($R^2 > 0.67$ and $n = 12$ for every regression equation).

Samples of unfiltered 50 mL seawater was collected at the same depth of the experiments conducted in May 2015 for analysis of phosphorus, nitrate-nitrite, and silicate concentrations and vials were kept frozen until analysis using standard seawater methods using a Flow Solution IV analyzer from O.I. Analytical, USA. The analyzer was calibrated using reference seawater from Ocean Scientific International Ltd. UK. Nutrients concentrations of the experiments conducted in May and August 2014 were analyzed in a previous vertical profile from the same station.

Samples of 100 mL of untreated plankton community were collected from each experimental community, at the onset of the experiment, and fixed with glutaraldehyde (at 1–1.5%). Cells were counted following the Utermöhl method, while also measuring the linear dimensions of the different taxa present to allow biovolume calculations by approximation to the nearest geometrical figure. Samples were concentrated in 50-ml chambers for 48 h and counted in a transmitted-light inverted microscope (Zeiss Axiovert 200) at 200x or 400x magnification depending on cell size. Phytoplankton cells were differentiated into species or genus, and their contribution to the communities is presented as % of the community biovolume.

The response of GPP to increased CO₂ was compared among experiments using the Ln-transformed effect size:

$$\text{Ln effect size GPP} = \text{LnGPP}_E - \text{LnGPP}_C$$

Where GPP_E and GPP_C are the mean response in the experimental and control treatments, respectively ($n = 3$ –4). The effect size is frequently used in experimental ecology to quantify the proportional effect of a treatment and to facilitate the comparison of biological responses across experiments (Hedges et al., 1999). An Ln effect size of GPP of zero is

interpreted as having no effect on GPP, whereas a positive value indicates a positive effect of CO₂ on GPP and a negative value indicates a negative effect of CO₂ on GPP. The variance in the Ln effect size was calculated following Kroecker et al. (2010). Moreover, comparisons based on the Ln effect size GPP did not assume normality and were heterogeneous because the experiments encompassed distinct phases of blooms, which occur rapidly and yield extreme data (i.e., very low $p\text{CO}_2$ and high GPP; R Core Team, 2014). The analyses were carried out using RStudio 0.98.945 and the “Metafor package” designed for meta-analyses (Viechtbauer, 2010).

RESULTS

Community Metabolism and CO₂ Demand

GPP-O₂ within the euphotic layer increased with increasing Chl *a* concentration ($p < 0.0001$, $R^2 = 0.81$, Figure S2), resulting in low-CO₂ waters (ranging from 281 to 128 μatm of $p\text{CO}_2$, Table 1). GPP, measured with the ¹⁸O method, of these low-CO₂ communities ranged from 5.8 to 82.4 $\mu\text{mol O}_2 \text{ L}^{-1} \text{ d}^{-1}$ in spring, under blooming conditions, while in summer GPP was much lower (0.4–1.4 $\mu\text{mol O}_2 \text{ L}^{-1} \text{ d}^{-1}$), reflecting a recycling phase. The GPP-O₂/R ratio was extremely high in the euphotic layer in spring (43.4 ± 0.85 , with a maximum value of 244.6) compared with low values in summer (2.67 ± 0.73). As a result, the waters sampled were consistently undersaturated in CO₂ and with a broad range of primary productivity rates. Consistent with the role of biota as a CO₂ sink, there was oceanic uptake of atmospheric CO₂ at the stations sampled, which increased with increasing NCP in the euphotic layer (Figure 1, Table 1). However, the resulting input of atmospheric CO₂ was much smaller than the net CO₂ demand by the plankton community, calculated assuming a 1:1 ratio between O₂ and C, accounting for 19%, on average, of the net biological removal (Figure 1, Table 1).

Response to Experimental CO₂ Additions

In situ $p\text{CO}_2$ ranged from 128 to 281 μatm (Table 1, Table S1), within reported *in situ* $p\text{CO}_2$ across the Arctic Ocean (78 to 765 μatm ; Bakker et al., 2016), and the experimentally-elevated $p\text{CO}_2$ ranged from 178 to 1,096 μatm (Table S1), consistent with predicted scenarios of atmospheric CO₂ by 2,100 (IPCC, 2014). The experimentally tested plankton communities represented variable biogeochemical parameters, from low-productivity communities supported by nutrient recycling sampled in August 2014, to pre-bloom, blooming and decay phases, sampled in May 2014 and 2015. All of the waters sampled were characterized by low salinity (<34.3) and low temperatures (<0.1°C), except in August 2014-1 (7°C), probably due to the proximity of surface waters to the WSC that transports warm Atlantic water mass.

Three of the experiments showed positive responses to CO₂ additions, all of them for communities sampled in May (May 2014-1, May 2015-1, May 2015-2). These were characterized by the highest *in situ* GPP (6.2, 46, and 82.4 $\mu\text{mol O}_2 \text{ L}^{-1} \text{ d}^{-1}$, respectively), high Chl *a* concentration (7.9, 10.6, and 13 $\mu\text{g Chl a L}^{-1}$), low $p\text{CO}_2$ (<193 μatm) and either low nutrient

TABLE 1 | *In situ* conditions and results of the seven experiments conducted in the west and northwest of Svalbard.

Variables	Experiments						
	May2014-1	May2014-2	Aug2014-1	Aug2014-2	Aug2014-3	May2015-1	May2015-2
Date (d)	5/23/2014	5/25/2014	8/7/2014	8/12/2014	8/14/2014	5/2/2015	5/4/2015
Depth (m)	2.4	3.2	5.7	2.9	3.0	5.0	5.0
Temperature (°C)	−0.8	−1.2	7.0	−0.4	−0.1	−1.0	−1.3
Salinity (psu)	33.9	33.6	34.3	31.5	31.6	34.2	34.2
GPP ± SE (μmol O ₂ L ^{−1} d ^{−1})	6.2 ± 0.1	5.8 ± 0.6	1.4 ± 0.1	0.4 ± 0.03	0.8 ± 0.1	46.0 ± 6.0	82.4 ± 11.4
Avg. LNES GPP (μmol O ₂ L ^{−1} d ^{−1})	0.5	−0.5	−1.5	−0.1	−0.6	0.2	0.2
pCO ₂ (μatm)	142.5	127.9	281.2	170.8	185.7	167.5	192.5
Chl <i>a</i> (μg L ^{−1})	7.9	1.8	1.1	0.3	0.4	10.6	13.0
NO ₃ + NO ₂ ± SE (μmol N L ^{−1})	0.7 ± 0.0	0 ± 0.0	10.3 ± 0.6	0.7 ± 0.0	0.5 ± 0.0	0.0	1.7
PO ₄ ± SE (μmol P L ^{−1})	0.1 ± 0.0	0.0 ± 0.0	0.7 ± 0.0	0.1 ± 0.0	0.1 ± 0.0	0.1	0.3
SiO ₄ ± SE (μmol Si L ^{−1})	0.9 ± 0.1	na	4.8 ± 0.6	0.6 ± 0.0	0.7 ± 0.0	0.4	1.5
Total phytoplankton (cell L ^{−1})	47,300	19,400	870	1,870	2,910	10,180	147,302
<i>Phaeocystis</i> spp. (%)	99.4	79.2	0.0	8.2	26.2	0	0
Diatoms (%)	0.6	11.6	97.3	90.5	69.9	68.6	80.28
Dinoflagellates (%)	0	0	0.0	0.0	0.0	0.0	0
No identified (%)	0	9.2	0.0	0.0	2.4	31.0	19.7
Air-sea CO ₂ flux (μmol C m ^{−2} d ^{−1})	1,504	37,927	12,613	33,655	14,823	8,450	13,224
Integrated NCP ± SE (μmol O ₂ m ^{−2} d ^{−1})	236,302 ± 4,097	290,586 ± 11,732	41,755 ± 7,814	191,310 ± 17,888	44,962 ± 10,460	na	na
Integrated NCP/Air-sea CO ₂ flux (No units)	157.1	7.7	3.3	5.7	3.0	na	na
Air-sea CO ₂ flux /Integrated NCP (%)	0.6	13.1	30.2	17.6	33.0	na	na
Ice conditions	Very open drift ice	Open drift ice	Open waters	Open drift ice	Open drift ice	Fjord mouth, no ice	Fjord mouth, no ice

Na indicates not available and the phytoplankton abundance is reported as the % of the microphytoplankton biovolume.

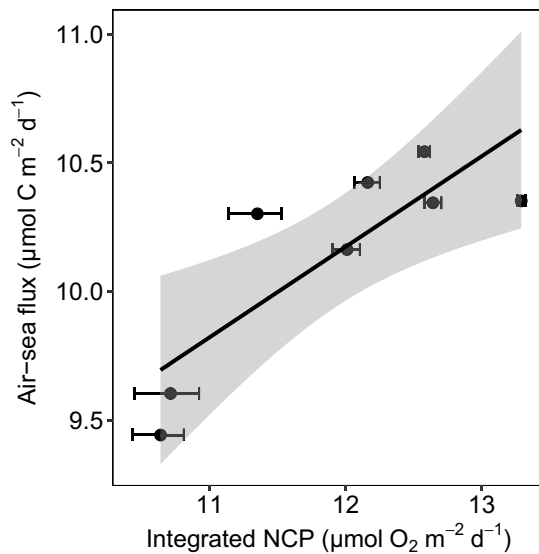


FIGURE 1 | Oceanic uptake of CO₂ shown by the relationship between the Ln-transformed air-sea CO₂ flux and the Ln-transformed NCP integrated in the water column from 3 to 25 m and the regression equation [$\ln$ air-sea flux = $0.35 (\pm 0.1) + 5.95 (\pm 1.1)$; $p = 0.01$, $R^2 = 0.64$, $df = 6$]. The shaded area represents the confidence interval (CI).

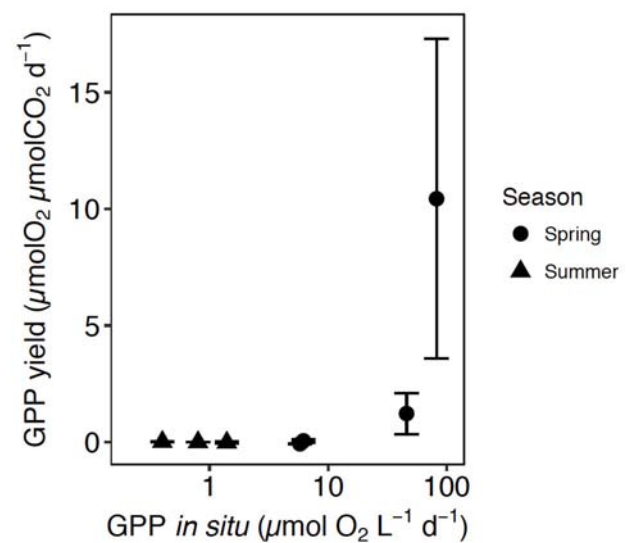


FIGURE 2 | The relationship between the average ($\pm$ SE) GPP yield per μmol of added CO₂ in each community tested and the GPP at *in situ* pCO₂. The shape corresponds with the communities tested in spring (circles) and summer (triangles).

concentrations ($0.7 \mu\text{mol N L}^{-1}$, $0.1 \mu\text{mol P L}^{-1}$, and $0.9 \mu\text{mol Si L}^{-1}$, in May 2014-1), depleted in nitrite and nitrate ($0 \text{ NO}_3 + \text{NO}_2$, 0.1 PO_4 , 0.4 SiO_4 , in May 2015-1) or slightly higher nitrate, phosphate and silicate ($1.7 \text{ NO}_3 + \text{NO}_2$, 0.3 PO_4 , 1.5 SiO_4 , in May 2015-2) (Table 1). In these three experiments the phytoplankton communities supported high cell density, with a dominance of diatoms in May 2015-1 and 2, such as the centric diatoms *Thalassiosira* sp. and *Chaetoceros* sp., and a community dominated by *Phaeocystis* sp. in May 2014-1 (Table 1). The GPP yield per μmol of added CO₂ of every community tested was calculated as the slope of the fitted regression equations between GPP and the concentration of added CO₂ (Table S1, Figure 2). The GPP yield per μmol added CO₂ increased with increased GPP at *in situ* CO₂ concentration, being 10-fold higher in spring than in summer (Figure 2).

The response of GPP to CO₂ addition was negative in four of the seven experiments, including all of the experiments conducted in August and one experiment in May 2014 (2014-2, Table 1), with communities generally characterized by low GPP (from 5.8 to $0.4 \mu\text{mol O}_2 \text{ L}^{-1} \text{ d}^{-1}$), low Chl *a* concentration (1.8 to $0.3 \mu\text{g L}^{-1}$), low pCO₂ (ranging from 128 to $281 \mu\text{atm}$) and low abundance of phytoplankton, dominated by diatoms such as *Chaetoceros* sp. and a presence of dinoflagellates, such as *Protoperidinium* sp. (Table 1). Dissolved inorganic nutrients concentrations were generally low (nitrite and nitrate $\sim 0.7 \mu\text{mol N L}^{-1}$, phosphate $\sim 0.1 \mu\text{mol P L}^{-1}$, and silicate $\sim 0.6 \mu\text{mol Si L}^{-1}$), except for the experiment conducted in August 2014 (2014-1), which showed high nitrate ($10.3 \mu\text{mol N L}^{-1}$) and silicate concentrations ($4.8 \mu\text{mol Si L}^{-1}$), despite low *in situ* GPP ($1.4 \mu\text{mol O}_2 \text{ L}^{-1} \text{ d}^{-1}$).

A meta-analysis of the experimental results revealed consistent patterns in the responses observed. In particular, the response to CO₂ enrichment, measured as the Ln effect size for GPP, increased significantly with the biomass of the communities tested ($p = 0.002$, $R^2 = 0.36$, Figure 3A). The Ln effect size of GPP became positive, indicative of an increase in GPP under elevated CO₂, during dense blooms with Chl *a* concentrations in excess of $7 \mu\text{g Chl } a \text{ L}^{-1}$ (Figure 3A). The Ln effect size for GPP declined with increasing *in situ* pCO₂ and became positive when the *in situ* pCO₂ was below $150 \mu\text{atm}$ (Figure 3B). The strongest GPP stimulation was found in a community with intermediate GPP ($6.2 \pm 0.1 \mu\text{mol O}_2 \text{ L}^{-1} \text{ d}^{-1}$, experiment May 2014-1) and dominated by *Phaeocystis* sp. (99.4% of the biovolume, Table 1, Table S1, Figure 4). Two diatom-dominated communities (51.5% and 76.6% of the microphytoplankton biovolume) with high GPP (46 ± 6 and $82.4 \pm 11.4 \mu\text{mol O}_2 \text{ L}^{-1} \text{ d}^{-1}$) were also stimulated by CO₂ enrichment (May 2015-1 and May 2015-2 respectively, Table 1, Table S1). As a result of the CO₂ unsaturated waters and the low atmospheric CO₂ input (Figure 1), the turnover of CO₂ pool in the communities tested, calculated as the slopes of fitted regression equations between the CO₂ removal rates (in units of $\mu\text{mol CO}_2 \text{ L}^{-1} \text{ d}^{-1}$) and the concentration of added CO₂, increased with increasing *in situ* GPP (Figure 5, Table S1).

DISCUSSION

The atmospheric resupply of CO₂ was far too slow to compensate for the observed biological drawdown of CO₂ (19% of removal, Figure 1), resulting in low-CO₂ waters at the end of the Arctic spring bloom (Kaltin et al., 2002; Bates et al., 2006; Bates and

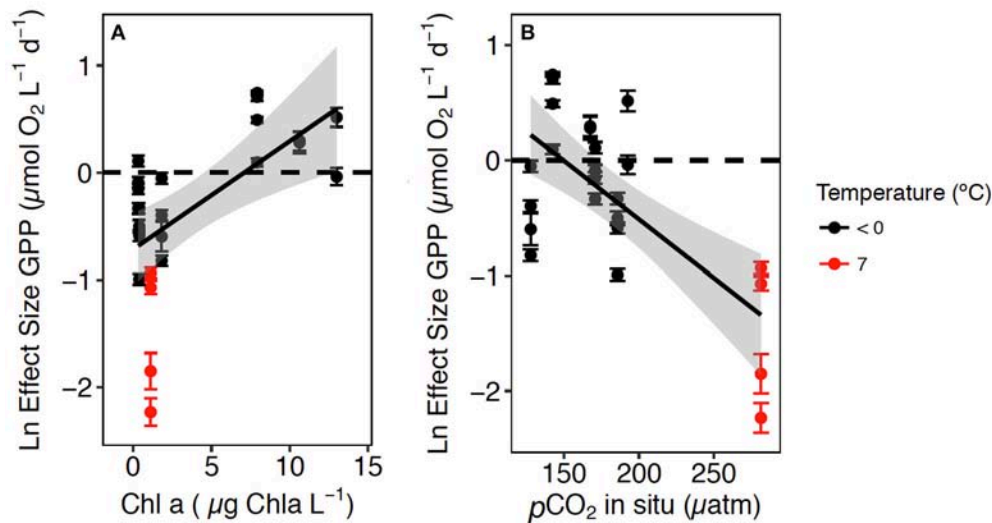


FIGURE 3 | The relationship between the Ln Effect Size of GPP ($\pm$ SE) and: **(A)** the *in situ* Chl a concentration in the communities tested and the regression equation [$\text{Ln Effect Size of GPP} = -0.7 (\pm 0.17) + 0.10 (\pm 0.3) \text{ Chl a}$; $R^2 = 0.36$, $p = 0.002$]; and **(B)** the *in situ* $p\text{CO}_2$ and the regression equation [$\text{Log Effect Size of GPP} = 1.52 (\pm 0.43) - 0.01 (\pm 0.00) \text{ in situ } p\text{CO}_2$; $R^2 = 0.50$, $p = 0.0001$] at temperature $< 0^\circ\text{C}$ in black and 7°C in red. The shaded area represents the CI indicates the 95% confidence interval (CI) of the regression equation.

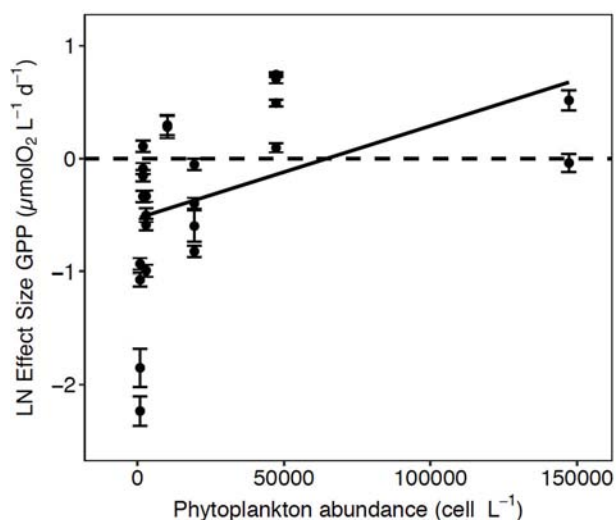


FIGURE 4 | The Ln effect size of GPP ($\pm$ SE) in relation to the total abundance of phytoplankton. The solid line represents the regression equation ($p < 0.05$, $R^2 = 0.20$).

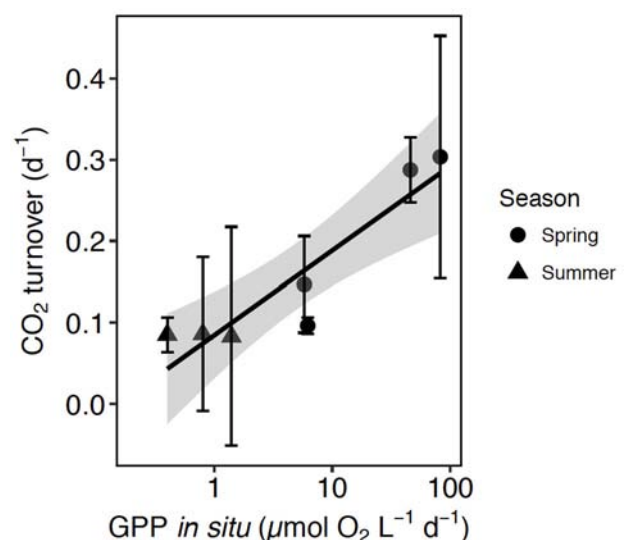


FIGURE 5 | The relationship between CO₂ turnover ($\pm$ SE) and GPP at *in situ* $p\text{CO}_2$ and the regression equation [$\text{CO}_2 \text{ turnover} = 0.10 (\pm 0.02) + 0.003 (\pm 0.0005) \text{ GPP in situ}$, $R^2 = 0.87$, $p\text{-value} = 0.001$], the shaded area indicates the 95% confidence interval (CI) of the regression equation. The shape corresponds with the communities tested in spring (circles) and summer (triangles).

Mathis, 2009; Fransson et al., 2009, 2017). Upward CO₂ supply from deeper layers was also likely to be low because the seasonal stratification produced by melting sea ice in the same area leads to small upward diffusive fluxes (Randelhoff et al., 2016). The large imbalances that we observed between net biological CO₂ consumption and supply explain the sensitivity of the Arctic phytoplankton community to CO₂ limitation. The time for photosynthetic removal of the CO₂ pool, in the absence of recycling mechanisms, ranged from more than 10 days for the

least productive communities to 3 days for communities in the most active phase of the spring bloom (Figure 5). Respiratory remineralization of CO₂ was characteristically low during the spring bloom (40-fold lower than photosynthetic uptake, i.e., $P/R = 43$) as is the atmospheric input of CO₂, leading to CO₂ depletion, thereby creating the conditions for CO₂ limitation

during the spring bloom. The peak of the spring Arctic bloom was characterized by autotrophic communities with high net biological CO₂ demand and high P/R ratios on average (43 ± 0.8) showed consistent with previous reports (Vaquer-Sunyer et al., 2013), with the communities acting as strong CO₂ sinks during spring. In August, when recycling processes drive primary production, the average GPP-O₂/R ratio (3 ± 0.7) was more than 10-fold lower than that in spring.

The plankton communities tested spanned a range of bloom stages according to the season and the location and yielded a broad diversity of responses to increased CO₂, from increased GPP, generally observed (3 of 4 experiments) in the spring, along with a very high GPP yield per unit CO₂ added, to suppression of GPP in the summer experiments. This is consistent with expectations, as high net biological demand for CO₂ in spring, along with low resupply from low respiration rates and air-sea exchange, lead to a rapid CO₂ depletion. In contrast, a closer balance between community production and respiration during the recycling mode, in summer, when communities are strongly nutrient-limited, relieves them from CO₂ limitation. The finding of a prevalence of suppression of GPP with CO₂ enrichment in the summer was unexpected, as we expected no effect but not a negative one, which we are unable to explain and may in fact reflect pH-dependent processes, as CO₂ enrichment leads to decrease in pH, rather than negative effects of CO₂ itself.

The broad diversity of responses observed further allowed us, through a meta-analysis approach, to explore the conditions associated with CO₂ limitation. In particular, we found that these divergent results were dependent on the biological demand for CO₂ and the extent of CO₂ depletion in the water column. These findings point at a shifting role of CO₂ with seasons, supporting the hypothesis of the existence of transient time windows of CO₂ limitation during highly productive periods in spring.

We observed the most negative effect size (i.e., suppression of GPP with addition of CO₂) in a community sampled in warm surface water and slightly influenced by melting sea ice (with 7°C temperature and 34.3 salinity), likely indicating an influence of the WSC, transporting warm Atlantic water mass. This community supported low Chl *a* concentration and the highest *p*CO₂ (281 μatm) observed in this study (Figures 3A,B). This negative result is consistent with the temperature-dependence of the response of GPP to CO₂ reported by Holding et al. (2015), as well as with the temperature threshold of 5°C at which Arctic plankton communities have been shown to shift from autotrophic to heterotrophic (Holding et al., 2013). However, the mechanism through which added CO₂ suppresses GPP is unclear. It may involve indirect effects of changes in pH on cellular composition (Taraldsvik and Mykkestad, 2000) or the pH-dependence of the availability of other nutrients, such as trace metals (Saito and Goepfert, 2008; Shi et al., 2010; Xu et al., 2010, 2012). No or little response to CO₂ enrichment was expected in waters with *p*CO₂ near atmospheric equilibrium (Mercado and Gordillo, 2011). In turn, an increase in GPP with CO₂ enrichment was expected in cold waters depleted in CO₂ relative to atmospheric equilibrium but still containing enough dissolved inorganic nutrients to support primary production (Holding et al., 2015).

Our results showed that GPP increased by 32–72% (Table S1) on average when CO₂ was supplied to blooming phytoplankton communities (Chl *a* > 7 μg L⁻¹) supporting high CO₂ demand (GPP > 6 μmol O₂ L⁻¹ d⁻¹), and growing under low *p*CO₂ (<150 μatm) and in the presence of low, but inorganic nutrients concentrations. These conditions, found during the Arctic spring bloom, therefore, define those under which episodes episodic CO₂ limitation is expected. It was previously found that the CO₂ concentration limits photosynthesis of phytoplankton bloom episodes in semi-enclosed systems (Mercado and Gordillo, 2011), but the environmental conditions for CO₂ limitation in Arctic communities have not yet been defined. Moreover, previous experimental results showed that increased CO₂ concentrations may increase primary production in nutrient-poor communities (Hein and Sand-Jensen, 1997) and during nutrient-depleted conditions resulting in “carbon-overconsumption” (Taucher et al., 2015). Such carbon-overconsumption has been observed (Sambrotto et al., 1993; Banse, 1994) and has been associated with experimental nutrient stress (Taucher et al., 2012, 2015), suggesting that episodes of CO₂ limitation could extend into the later phases of a bloom.

Enhanced GPP in response to elevated CO₂ was observed in highly productive communities, one dominated by *Phaeocystis* sp. and two communities dominated by diatoms (Figure 4). However, the strongest enhancement was observed in the community dominated by *Phaeocystis* sp. (Table 1, Table S1), which is an important Arctic haptophyte that tends to be dominant close to drifting ice (Wassmann et al., 1999), and with increasing salinity and temperature following ice melt events (Lasternas and Agustí, 2010). *Phaeocystis* sp. is considered to have less-efficient carbon concentration mechanisms (CCMs) than diatoms do (Rost et al., 2008). Elevated CO₂ produces a decrease in inorganic carbon affinity and leads to strong downregulation in the expression of CCMs in some eukaryotic algae, such that the diffusive entry of CO₂ can be facilitated (Giordano et al., 2005; Reinfelder, 2010; Raven et al., 2011). This suggests a possible mechanism through which the GPP of *Phaeocystis* sp. and diatom communities are stimulated during CO₂-enriched conditions. Besides, the abundance of *Phaeocystis* sp. was greatest when *p*CO₂ concentrations were lower than 150 μatm, which can potentially influence competitions among phytoplankton species (Tortell et al., 2002), a possibility that was not evaluated in our study. *Phaeocystis* sp. replaces diatoms when the growth of diatoms is limited by the availability of silicic acid while other nutrients remain available to support growth of non-diatom taxa (Lasternas and Agustí, 2010). Recently, an under ice bloom in the Arctic dominated by *Phaeocystis pouchetii* was detected earlier than expected with subsequent decline of DIC (Assmy et al., 2017). Our results indicate that both *Phaeocystis* sp. and diatoms are sensitive to CO₂ limitation during highly productive periods in the west of Svalbard shelf. Although we cannot extrapolate our results beyond the study area, they are nevertheless relevant because the European sector of the Arctic contributes 50% of the annual Arctic Ocean plankton production (Arrigo, 2007).

Our results suggest that increased atmospheric CO₂ and the resulting increased air-sea CO₂ supply may stimulate Arctic gross

production of spring algal blooms under conditions of high biomass, high phytoplankton abundance, presence of nutrients and low $p\text{CO}_2$. In contrast, increased CO₂ may suppress gross production during summer conditions, when phytoplankton biomass and production are low, although the mechanisms involved are unknown. Moreover, our results are consistent with previous reports that the response of primary production to increased CO₂ is suppressed at water temperatures above 7°C (Holding et al., 2015). The expectation of GPP stimulation with increased CO₂ during spring blooms assumes that the nutrient supply will not be affected by concurrent changes. Increased stratification, due to Arctic warming and freshening may reduce vertical nutrient supplies from deeper layers (Sarmiento et al., 2004; Wassmann, 2011; Randelhoff et al., 2017), possibly reducing the intensity and timing of the spring algal bloom and, therefore, its carbon demand and potential CO₂ limitation. In contrast, areas currently covered by ice would, as the extent of ice continues to decline, support stronger algal spring blooms (Arrigo et al., 2008), which may experience episodic CO₂ limitation. The greatest increases in primary production in a future Arctic are expected in the Eurasian perimeter (Slagstad et al., 2015). However, current models do not consider the effects of episodic CO₂ limitation during the Arctic spring.

The global increase in CO₂ seems to have stimulated the primary production of terrestrial plants on a global scale due to CO₂ fertilization, possibly affecting the rate of increase in atmospheric CO₂ concentration and global temperatures (Denman et al., 2007; Leggett and Ball, 2015) during the last 10 years (Keenan et al., 2016). However, the existence of this slow-down remains controversial (Cowtan and Way, 2014; Karl et al., 2015). Given the relevant role that the Arctic Ocean plays as a sink for atmospheric CO₂ (Bates and Mathis, 2009), stimulation of Arctic GPP by CO₂ during highly productive periods in spring may strengthen the Arctic CO₂ sink and add, modestly, to biotic feedbacks that may affect global trends in atmospheric CO₂. However, negative effects of CO₂ on primary production of Arctic plankton

communities in summer suggest that the “fertilization effect” of CO₂ on Arctic plankton, resulting in enhanced primary production during the short, 2–3 weeks, period of the spring bloom, maybe offset by negative effects through the much longer, 2–3 months, recycling phase, with potentially negative effects for the ecosystem. Whereas the mechanisms leading to enhanced GPP in Arctic plankton with increased CO₂ during spring appear clear, the mechanisms leading to suppression of GPP with CO₂ enrichment during summer need be resolved.

AUTHOR CONTRIBUTIONS

CD and MS-M designed the fieldwork and experiments. MS-M and PC executed the fieldwork and experiments. MS-M, PC, MC, EM, SK, and SA executed laboratory analyses. MS-M and CD analyzed the data and all authors contributed to the writing and editing of the manuscript.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: <https://www.frontiersin.org/articles/10.3389/fmars.2018.00221/full#supplementary-material>

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Relationship Between Carbon- and Oxygen-Based Primary Productivity in the Arctic Ocean, Svalbard Archipelago

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Phytoplankton contribute half of the primary production (PP) in the biosphere and are the major source of energy for the Arctic Ocean ecosystem. While PP measurements are therefore fundamental to our understanding of marine biogeochemical cycling, the extent to which current methods provide a definitive estimate of this process remains uncertain given differences in their underlying approaches, and assumptions. This is especially the case in the Arctic Ocean, a region of the planet undergoing rapid evolution as a result of climate change, yet where PP measurements are sparse. In this study, we compared three common methods for estimating PP in the European Arctic Ocean: (1) production of ¹⁸O-labeled oxygen (GPP-¹⁸O), (2) changes in dissolved oxygen (GPP-DO), and (3) incorporation rates of ¹⁴C-labeled carbon into particulate organic carbon (¹⁴C-POC) and into total organic carbon (¹⁴C-TOC, the sum of dissolved and particulate organic carbon). Results show that PP rates derived using oxygen methods showed good agreement across season and were strongly positively correlated. While also strongly correlated, higher scatter associated with seasonal changes was observed between ¹⁴C-POC and ¹⁴C-TOC. The ¹⁴C-TOC-derived rates were, on average, approximately 50% of the oxygen-based estimates. However, the relationship between these estimates changed seasonally. In May, during a spring bloom of *Phaeocystis* sp., ¹⁴C-TOC was 52% and 50% of GPP-DO, and GPP-¹⁸O, respectively, while in August, during post-bloom conditions dominated by flagellates, ¹⁴C-TOC was 125% of GPP-DO, and ¹⁴C-TOC was 175% of GPP-¹⁸O. Varying relationship between C and O rates may be the result of varying importance of respiration, where C-based rates estimate net primary production (NPP) and O-based rates estimate gross primary production (GPP). However, uncertainty remains in this comparison, given differing assumptions of the methods and the photosynthetic quotients. The median O:C ratio of

4.75 in May is within the range of that observed for other regions of the world's ocean. However, the median O:C ratio for August is <1 , lower than in any other reported region. Our results suggest further research is needed to estimate O:C in Arctic waters, and at different times of the seasonal cycle.

Keywords: primary production, Arctic Ocean, oxygen method, carbon methodology, Svalbard (Arctic) and plankton

INTRODUCTION

Plankton photosynthesis contributes half of the primary production (PP) in the biosphere (Field et al., 1998) and is the main source of carbon for the Arctic Ocean food web (Matrai et al., 2013). Because photosynthesis is a fundamental process affecting, either directly or indirectly, the functioning of marine ecosystems, from their capacity to take up atmospheric CO₂ to the distribution and breeding success of higher trophic levels, quantification of PP has long been a core measurement in biological oceanography (Robinson et al., 2009; Regaudie-de-Gioux et al., 2014). Measurements of PP over the last decades, both remote and *in situ*, have provided critical insight into the spatial and temporal variability of phytoplankton growth in the Arctic. Although the Arctic Ocean is strongly seasonal, some of its regions rank among the most productive in the oceans (Gosselin et al., 1997; Tremblay et al., 2002; Vaquer-Sunyer et al., 2013), which results in high pelagic and benthic secondary production (Grebmeier and Mcroy, 1989; Grebmeier et al., 2006, 2013). While recent modeling and remote sensing studies have also suggested climate-driven changes in the rates of PP in the Arctic (Pabi et al., 2008; Slagstad et al., 2015; Kahru, 2017), methodological differences in PP measurements nevertheless introduce uncertainty in these future projections. To evaluate PP responses, appropriate estimations and evaluations of PP based on comparable methods are fundamental (Robinson et al., 2009; Regaudie-de-Gioux et al., 2014). Until a consensus is reached or an unambiguous method is developed, comparisons between measurements originating from different methods can provide insight on the ecological and physiological processes involved as well as help constrain the uncertainties (Robinson et al., 2009; Regaudie-de-Gioux et al., 2014).

Three primary methods have historically been used to estimate planktonic PP, each with different underlying assumptions. Gross photosynthesis (or gross primary production rate, GPP) estimates the total photosynthetic rate before any losses, like phytoplankton respiration. GPP has been quantified using two oxygen-based methods as the photosynthetic production of ¹⁸O from ¹⁸O-labeled water additions (GPP-¹⁸O) as well as using the Dissolved Oxygen method. The determination of GPP-¹⁸O through mass spectrometry, which measures the O₂ produced during a 24-h incubation (Bender et al., 1987), has previously been identified as the best approach to estimate GPP (Regaudie-de-Gioux et al., 2014). However, not all the oxygen-producing metabolic processes measured with the ¹⁸O method are directly related to carbon assimilation (Bender et al., 1999; Laws et al., 2000; Dickson et al., 2001; Marra, 2002). The Dissolved Oxygen method (Carpenter, 1995), on the other

hand, measures the change in dissolved oxygen in light/dark incubations over 24 h. In this case, GPP, (hereafter GPP-DO) is derived by summing the rate of change of oxygen in dark bottles (an estimate of community respiration, CR) and that in clear bottles (an estimate of net community production, NCP) (Carritt and Carpenter, 1966; Duarte et al., 2011). This procedure assumes that respiration in the dark is the same as that in the light. Recent studies have shown that this assumption may not hold in the Arctic Ocean during spring and summer, where 24-h daylight lead to increased respiration rates (Mesa et al., 2017).

The third and most widely used method to resolve plankton PP is the ¹⁴C method (Steemann-Nielsen, 1952), which traces the incorporation of inorganic carbon into live phytoplankton cells, or particulate organic carbon (¹⁴C-POC). This method can also be used to track the release of recently incorporated ¹⁴C as dissolved organic carbon (¹⁴C-DOC). The total carbon incorporation by the ¹⁴C method is ¹⁴C-TOC, the sum of ¹⁴C-POC and ¹⁴C-DOC. High variability in incubation times has resulted in significant uncertainty as to how to interpret ¹⁴C rate measurements. In daily incubations, ¹⁴C-POC is expected to reflect net primary production (¹⁴C-NPP) (Marra, 2002, 2009). NPP rates may account for a minimum of ~35% of GPP-¹⁸O in 24-h incubations (Bender et al., 1996; Duarte and Cebrián, 1996) and about 48% of GPP-DO in short incubations, as a consequence of losses attributed to algal respiration, and DOC production (Del Giorgio and Duarte, 2002).

Comparison of estimates derived from these various methods have led to a wide range of carbon uptake estimates across spatial scales (Robinson et al., 2009; Regaudie-de-Gioux et al., 2014). While in previous studies in the North Pacific, the Dissolved Oxygen and the ¹⁸O methods provided similar estimates of GPP (Grande et al., 1989b), in global comparisons (Robinson et al., 2009; Regaudie-de-Gioux et al., 2014), as well as in the Arctic Ocean (Mesa et al., 2017), the GPP-¹⁸O estimates were higher than GPP-DO. In contrast, ¹⁸O values can be significantly lower than GPP-DO rates in nutrient-rich areas with low dissolved oxygen concentrations (Gazeau et al., 2007). This large variability indicates that the ability of methods to estimate PP is dependent on environmental conditions, and the use of multiple methods has been recommended as a regional solution (Robinson et al., 2009).

Comparisons between the C-based method and the O₂-based methods have indicated lower rates of ¹⁴C incorporation than O₂ production (Robinson et al., 2009; Regaudie-de-Gioux et al., 2014). These discrepancies are likely due to variability in the assumed photosynthetic quotient (PQ), a critical parameter quantifying the amount of oxygen evolved per unit of photosynthetically fixed carbon into organic matter. PQ values

range widely, from 1.0 to 1.8, with values 1.0 to 1.4 in non-polar oceanic areas (e.g., Bender et al., 1987; Grande et al., 1989b; Laws et al., 2000; Dickson et al., 2001) and from 1.1 to 1.8 in the Southern Ocean (i.e., Williams et al., 1979; Aristegui et al., 1996; Robinson et al., 1999). Although no PQ value has been derived for the Arctic Ocean, a value of 1.25, proposed by Williams et al. (1979), has been widely applied in this region to convert O_2 molar stoichiometry units into C (i.e., Vaquer-Sunyer et al., 2013; Duarte and Agustí, 1998). However, $PQ = 1$ is also frequently considered when comparing C and O_2 -based PP rates (Duarte et al., 2011; Regaudie-de-Gioux et al., 2014).

Historically, ^{14}C -POC measurements have primarily been collected across the Arctic Ocean, with O_2 -based rates collected only in select regions (Matrai et al., 2013). Average ^{14}C -POC rates in Arctic surface waters, compiled over 50 years (1954–2007), are 70 and 21 $mg\ C\ m^{-3}\ d^{-1}$ in spring and summer, respectively (Matrai et al., 2013). By comparison, O_2 -based GPP-DO productivity rates of surface waters, collected in the European sector of the Arctic between 2007 and 2011, average 168 and 55 $mg\ C\ m^{-3}\ d^{-1}$ in spring and summer, respectively (Vaquer-Sunyer et al., 2013), twofold higher than those derived for ^{14}C -POC rates. Whether these differences are due to spatial gradients or temporal changes in the system, or a result of bias in the methods of measurement remains unknown due to a lack of comparison between concurrent C-based and O_2 -based measurements of PP in Arctic waters.

In this study, we report on rates of PP derived using ^{14}C , Dissolved Oxygen, and ^{18}O methods in the northwestern Svalbard Archipelago in the European Arctic and focus on comparing these rates. We also consider the pathways of carbon and oxygen within the plankton and provide an assessment of the ecological and physiological processes underlying the methods' assumptions. We aim to facilitate future PP studies in the region and to highlight improvements needed in order to interpret results from the various methods in the Arctic Ocean ecosystems.

MATERIALS AND METHODS

Sampling

Two cruises were conducted in the north and northwestern Svalbard region during May and August 2014 aboard R/V Helmer Hanssen (Figure 1). Our aim was to analyze the underlying assumptions of primary productivity rate measurements through two different pathways: the carbon assimilation and the oxygen production. In order to achieve this, we measured PP rates in 24-h incubations using three different methods (the ^{14}C method, the Dissolved Oxygen method, and the ^{18}O method). Although the cruise sampled six "P" stations, P6 was not included in this study as GPP-DO measurements are not available. Similarly, no sampling is available from P2 as this station was aborted due to loss of the mooring with the ^{14}C incubations. Five remaining stations were occupied during the May cruise (P1, P3, P4, D1, and D6) and four remaining stations in the August cruise (P5, P7, D1, and D6), with sampling including hydrographic profiling with a calibrated Seabird 911plus CTD (conductivity, temperature, and depth). Discrete water samples for PP incubations were

collected from CTD casts, for ^{14}C rate measurement and oxygen measurements (DO and ^{18}O). Seawater for PP analysis was sampled from the same cast at four stations (D1 and D6 in both May and August), while logistical constraints on hydrographic deployments forced collection of water from separate CTD casts at three stations (P1, P3, and P4) in May and two stations (P5 and P7) in August, with time lag between casts ranging from minutes to 32 h (see section "Sampling Time Lag" below). Seawater for all O_2 -based PP and for ^{14}C at the D stations was sampled at the surface (1 or 3 m), the deep chlorophyll maximum layer (DCM) depth (20–30 m depending on stations), and an intermediate depth (10 or 15 m). Seawater for ^{14}C -based PP determination at the P stations was sampled at 1–3, 5, 10, 15–20, and 25–30 m, with exact sampling depths varying depending on the presence and depth of the DCM. Rate measurements at a given station were matched by closest depths, with depth differences reaching a maximum of 3 m.

Primary Production Incubations

Primary production rates were measured using three methods: the ^{18}O method (Bender et al., 1987), the Dissolved Oxygen method (Carpenter, 1995), and the ^{14}C method (Steemann-Nielsen, 1952). Samples measured with O_2 methods were incubated on deck with running seawater from the ship's seawater intake (Supplementary Figure S1), following the incubation protocols used in previous studies (Regaudie-de-Gioux and Duarte, 2010; Vaquer-Sunyer et al., 2013; Holding et al., 2015; Garcia-Corral et al., 2016; Mesa et al., 2017). The seawater intake was at ~6 m depth, within the mixed layer. Depending on the station, the mixed layer reached depths between 9 and 15 m (Randelhoff et al., 2018). For deep samples collected below the mixed layer, temperature differences between circulated water and *in situ* temperature ranged from 0.03°C to 4.5°C (Supplementary Figures S2, S3). Samples measured with the ^{14}C method were incubated both on deck (D stations, Supplementary Figure S1), using the incubation system of the O_2 samples, and *in situ* (P stations, see below for additional details).

The ^{18}O Method

GPP- ^{18}O was measured as the photosynthetic production of $^{18}O_2$ following the addition of $H_2^{18}O$ after 24 h incubations (Bender et al., 1987; Table 1). Samples were distributed into eight 12-ml vials, allowing them to overflow to avoid contamination with atmospheric O_2 . Borosilicate vials were ultraviolet A and B (UVA/B) opaque. Four replicate vials were immediately preserved with 100 μl of saturated mercury chloride ($HgCl_2$) solution for further determination of natural $\delta^{18}O$ in seawater and the vials stored inverted, in darkness. The other four replicate vials, containing glass beads, were labeled with 80 μl of 98% $H_2^{18}O$ and shaken to ensure mixing. The labeled samples were incubated for 24 h on deck in transparent methacrylate tubes that are also UVA/B opaque with flow-through surface seawater. To simulate light attenuation in the water column, methacrylate tubes were wrapped with screen. Screening resulted in an attenuation of 60, 33, and 25% of surface PAR for these

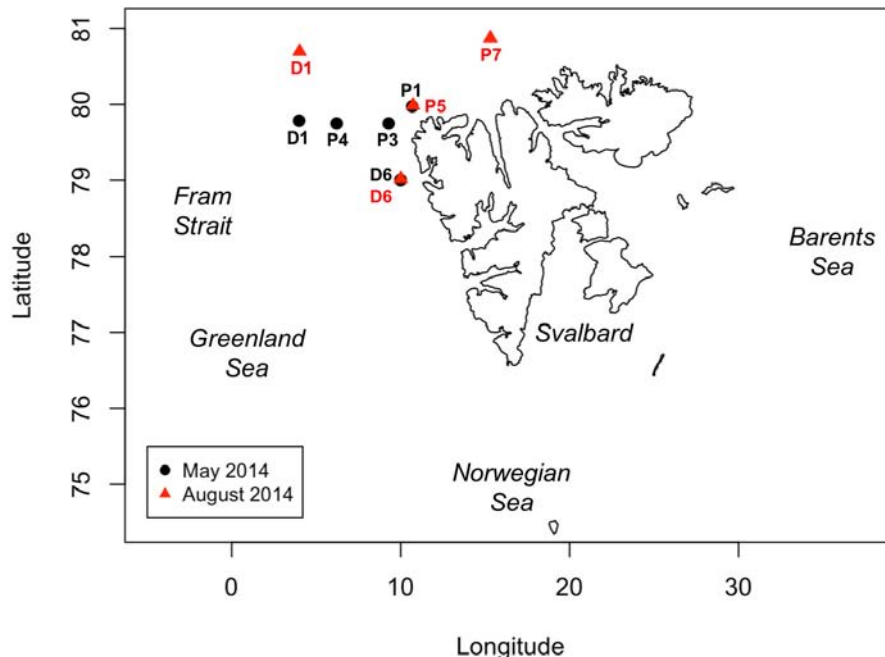


FIGURE 1 | Map of the Svalbard Archipelago, showing the locations of sampling stations occupied in May (stations D1, D6, P1, P3, and P4, black dots) and August 2014 (stations D1, D6, P5 and P7, red triangles). Note that stations P2 and P6 are not included as no data was available for the analysis (see section “Materials and Methods”).

bottles (as measured with a portable photosynthetically available radiation (PAR) radiometer, Biospherical Instruments Inc. QSL-101), equivalent to light levels at 1, 10, and 20–30 m depth (Randelhoff et al., 2018). After 24 h, incubation vials were spiked with 100 μ l of saturated HgCl_2 solution and stored for further analysis.

Samples were analyzed 2 weeks later at the Stable-Isotope Laboratory in IACT-CSIC, Armilla, Spain. A 4-mL headspace with 100% Helium was generated in each vial and left for 24 h at

room temperature, letting the dissolved gases in water equilibrate with the headspace. After 24 h, the $\delta^{18}\text{O}$ of dissolved oxygen in the headspace was measured in a Finnigan GasBench II attached to a Finnigan DeltaPlusXP isotope ratio mass spectrometer. We used a gas bottle of oxygen as our internal standard and atmospheric air injected in helium vials as an external standard. The analysis of the $\delta^{18}\text{O}$ of oxygen from the gas bottle had a standard deviation of 0.05%. Atmospheric air, which was measured following the same route as the samples, had a standard deviation of 0.2%. The flow was passed through a liquid nitrogen trap to remove water vapor before entering into the GasBench II. Molecules of O_2 and N_2 were separated in a Molecular Sieve 5Å chromatographic column. Corrected data with atmospheric air was reported as $\delta^{18}\text{O}$ value (‰) relative to V-SMOW (Vienna Standard Mean Ocean Water) standard.

The $\delta^{18}\text{O}$ (H_2O) composition of labeled samples was measured in a liquid water isotope analyzer (Los Gatos Research), with precision of 0.2%. In order to avoid contamination of the analyzer with highly ^{18}O -enriched H_2O ($\approx 3000\text{‰}$), the labeled sample was diluted (approximately 1:20) with a laboratory standard of known isotopic composition. $\text{GPP-}^{18}\text{O}$ was calculated using the Eq. (1) from Bender et al. (1999):

$$\text{GPP-}^{18}\text{O} = \left[(\delta^{18}\text{O}_{\text{final}} - \delta^{18}\text{O}_{\text{initial}}) / (\delta^{18}\text{O}_{\text{water}} - \delta^{18}\text{O}_{\text{initial}}) \right] \times [\text{O}_2]_{\text{initial}} \times (1/\delta t) \quad (1)$$

Where $\text{GPP-}^{18}\text{O}$, in units of $\text{mmol O}_2 \text{ m}^{-3} \text{ d}^{-1}$, is the gross PP measured with the ^{18}O method, $\delta^{18}\text{O}_{\text{initial}}$ and $\delta^{18}\text{O}_{\text{final}}$ are the initial and final $\delta^{18}\text{O}$ of dissolved O_2 (‰), respectively,

TABLE 1 | Acronyms for primary production variables used in this study, including their definition and source.

Acronyms	Significance	References
$\text{GPP-}^{18}\text{O}$	Gross primary production measured with the ^{18}O method adding H_2^{18}O	Bender et al., 1987
GPP-DO	Gross primary production measured with O_2 mass balance method ($\text{GPP-DO} = \text{NCP} + \text{CR}$)	Carritt and Carpenter, 1966
NCP	Net community production measured with O_2 mass balance method in light bottles	Carpenter, 1995
CR	Community respiration with O_2 mass balance method in dark bottles	
$^{14}\text{C-TOC}$	Primary production of total organic carbon measured with the ^{14}C method ($^{14}\text{C-TOC} = ^{14}\text{C-POC} + ^{14}\text{C-DOC}$)	Steemann-Nielsen, 1952
$^{14}\text{C-POC}$	Primary production of particulate organic carbon measured with the ^{14}C method	
$^{14}\text{C-DOC}$	Primary production of dissolved organic carbon measured with the ^{14}C method	

$\delta^{18}\text{O}_{\text{water}}$ is the $\delta^{18}\text{O}$ of the labeled seawater (‰), $[\text{O}_2]_{\text{initial}}$ is the initial O_2 concentration ($\mu\text{mol O}_2 \text{ L}^{-1}$) measured by high-precision Winkler titration (see below) and δt is the incubation time in days (d).

The Dissolved Oxygen Method

GPP-DO, an acronym previously applied for GPP evaluated with this method (i.e., Regaudie-de-Gioux et al., 2014), also called GP(O_2), (i.e., Robinson et al., 2009) was calculated by solving the daily change in dissolved oxygen in equation $\text{GPP-DO} = \text{NCP} + \text{CR}_{\text{dark}}$ where NCP is net primary production and CR_{dark} is community respiration in darkness, in units of $\text{mmol O}_2 \text{ m}^{-3} \text{ d}^{-1}$. NCP and CR_{dark} were calculated by subtracting initial dissolved oxygen concentrations from the dissolved oxygen concentrations measured after 24-h incubation in light and dark conditions, respectively (Carritt and Carpenter, 1966; Carpenter, 1995; **Table 1**). For this incubation, water samples were distributed into 21 UVA/B opaque 100 mL narrow-mouth borosilicate Winkler bottles. Seven replicates were used to determine the initial oxygen concentration, and seven replicates were incubated in dark and seven in light for 24 h on deck. O_2 concentrations were determined using an automatic titrator (808 Tritando, Metrohm) (Carritt and Carpenter, 1966; Carpenter, 1995), a potentiometric electrode and automated endpoint detection (Oudot et al., 1988). Values that reported O_2 production in darkness (Pamatmat, 1997) were flagged as unreliable and discarded (Holding et al., 2013).

The ^{14}C Method

Primary production using ^{14}C method included estimates of particulate (^{14}C -POC) and total (^{14}C -TOC) organic carbon production in 24 h incubations (Steeemann-Nielsen, 1952; Vernet et al., 1998; **Table 1**). Water samples were distributed in four UVA/B opaque 150-mL polycarbonate bottles. Treatments included 2 light bottles, 1 dark, and one Time Zero. Ten μCi of ^{14}C -labeled bicarbonate was dispensed into each bottle, and the Time Zero filtered immediately. In addition, for each depth, a 100 μL aliquot was sampled into a 6-mL scintillation vial containing 0.1 mL 6N NaOH in order to estimate the initial ^{14}C -bicarbonate concentration, or Specific Activity. In the P stations (**Figure 1**), samples were incubated *in situ*: light and dark bottles were hung from a line anchored to an ice floe and deployed for approximately 22 h. In D stations (**Figure 1**), samples were incubated on deck for 24 h, in UVA/B opaque methacrylate tubes (Plexiglas®), with surface water temperatures maintained with running seawater from the ship's intake. To simulate light attenuation in the water column, screens covered the methacrylate tubes placed inside the incubator (**Supplementary Figure S1**). Light attenuation was simulated using screens as a % of the on-deck photosynthetically available irradiance (PAR), simulating 100, 50, 25, and 12% of surface PAR, respectively. Attenuation within the methacrylate tubes was quantified with a Biospherical Instruments Inc QSL-101. After 22–24 h, bottles for *in situ* or on deck incubations were recovered and sampled, keeping the bottles refrigerated. 200 μL of 20% HCl was dispensed into each 6-mL scintillation

vial containing either a Whatman GF/F filter (for particulate, ^{14}C -POC) or 2 mL of seawater (for total production, ^{14}C -TOC) in order to release any inorganic ^{14}C remaining in the sample. After 24 h, 5 ml of Ultima Gold (Perkin Elmer, United States) was added and the samples stored in the dark for further analysis. One week later, each vial was shaken and the ^{14}C activity measured in a Perkin Elmer scintillation counter at the University of Tromsø. PP was calculated as ^{14}C incorporation into the sample, measured in units of disintegrations per minute (DPM). The intensity of the signal is proportional to the beta particle emission from the ^{14}C incorporated into the cells. The total C-based production rates were then calculated as:

$$^{14}\text{C} - \text{TOC} = \frac{(\text{DPM}_L - \text{DPM}_D) / \text{Vol} \times \text{DIC} \times 1.05 \times \left(\frac{1}{\delta t}\right)}{\frac{\text{DPM Sp Act}}{\text{Vol}}} \quad (2)$$

where ^{14}C -TOC is production or $\text{mg C m}^{-3} \text{ d}^{-1}$, DPM_L is disintegration per minute in the samples incubated in the light, DPM_D is disintegration per minute for the samples incubated in the dark, Vol refers to the sample volume (100 ml filtered for POC, 2 ml seawater for TOC and 0.1 ml for determination of Specific Activity) and δt the incubation time in days (d). DIC or dissolved inorganic carbon was measured in every sample (see section “Dissolved Inorganic Carbon”). The value of 1.05 is the discrimination factor between incorporation of ^{14}C and ^{12}C . The ^{14}C incorporation in the light bottle is thought to account both for biotic (i.e., photosynthesis and CaCO_3 incorporation) and for abiotic (i.e., adsorption) processes (Banse, 1993). Adsorption processes were accounted for by the Time Zero bottle. The incorporation of ^{14}C into CaCO_3 is corrected by conversion to CO_2 following 24-h acidification. Thus, ^{14}C incorporation rates are corrected by subtracting the ^{14}C incorporation in the dark bottle, accounting for biological ^{14}C uptake that can occur outside photosynthesis, and yielding carbon uptake by photosynthesis. The C-based rates were obtained in weight units, $\text{mg C m}^{-3} \text{ d}^{-1}$, and divided by the molar mass of C (12 g/mol) to obtain final units of $\text{mmol C m}^{-3} \text{ d}^{-1}$.

Dissolved Inorganic Carbon

Samples for dissolved inorganic carbon (DIC) were measured at the Norwegian Polar Institute (M. Chierici, PI). Seawater for DIC analysis was collected from the same CTD casts as the water for C-based estimates. Seawater was sampled and distributed into 100-mL borosilicate bottles, which were then preserved with 20 μL of HgCl_2 and stored in dark and cold until analysis. DIC was determined using gas extraction of the acidified sample followed by coulometric titration and photometric detection using a Versatile Instrument for the Determination of Titration carbonate (VINDTA 3C, Marianda, Germany) following the standard operating procedures from Dickson et al. (2007). Certified reference material provided by Dr. Andrew Dickson (Scripps Institution of Oceanography, University of California San Diego, La Jolla, CA, United States) was used to control accuracy of the analyses. The limit of detection is estimated at approximately $1.0 \text{ mg C m}^{-3} \text{ d}^{-1}$.

Volumetric and Integrated Primary Production Rates

Volumetric ^{14}C and O_2 -based rates were estimated for each depth at every station, yielding a total of 21 volumetric rates for each method (data available in **Supplementary Table S1**). Units of volumetric rates are $\text{mmol C or O}_2 \text{ m}^{-3} \text{ d}^{-1}$. Integrated ^{14}C and O_2 -based rates, integrated to a depth equal to the 90% of accumulated ^{14}C -POC (which was significantly correlated with the euphotic depth; p -value < 0.05 and $R^2 = 0.85$) were calculated from the volumetric rates by the quadratic method, where the volumetric value of PP at two consecutive depths were averaged and multiplied by the depth differential. The resulting units for integrated rates are in $\text{mmol C or O}_2 \text{ m}^{-2} \text{ d}^{-1}$. Details of euphotic zone depth calculations are described in Randelhoff et al. (2018).

Data Analysis

Primary production rates for each method were $\log_{10}$ -transformed to meet the assumption of normality. Normality of data was tested using the Shapiro-Wilk test, appropriate for small sample size (Shapiro and Wilk, 1965), with $p > 0.05$ for volumetric and integrated rates within each method for the full dataset (i.e., aggregating both cruises; **Supplementary Table S2**). Despite the non-normal nature of the untransformed data, we present PP rates as scatterplots in both untransformed and transformed (i.e., log) space in order to facilitate comparison with results from previous studies (see section “Discussion” below).

Comparison between the ^{14}C - and O_2 -based methods were performed for samples collected at similar depths (maximum difference of ~ 3 m). Seawater for ^{14}C and O_2 -based analysis was sampled with time lags between casts ranging from 4 to 32 h for stations P, and no time lag for stations D (i.e., they were sampled from the same CTD cast, **Supplementary Figures S4, S5**). Similarity in sampled water masses, considering time lag between casts, was examined by comparing cast temperature-salinity characteristics (**Supplementary Figures S6, S7**), with water masses as defined in Randelhoff et al. (2018) and references therein. While sampling at the majority of P stations indeed occurred within the same water mass, samples collected in P1 originated from different water masses (**Supplementary Figure S6A**). This station was subsequently omitted from the comparison analysis, resulting in a total of 19 rates ensembles across 8 stations (i.e., $n = 19$).

Relative contributions of factors (method, cruise, depth and casts) to variability in PP rates were assessed using ANOVA. Examination of scatterplots of log-transformed PP rates (see section “Results” below) suggested wider variance in May than in August within the factor “cruise” (i.e., season, May and August). Levene’s test within the factor season (using differences between observations and group median) rejected the null hypothesis of homoscedasticity between log-transformed PP rates in May and August [i.e., homogeneity of variances; $F(1,74) = 9.76$, $p < 0.01$]. By comparison, the assumption of homoscedasticity of log-transformed PP data held for methods, casts and depths (values not shown). To account for inhomogeneity of variances, relative contribution of factors to variability in PP rates was

therefore assessed using a 4-way ANOVA (type II) using a heteroscedasticity-corrected coefficient covariance matrix, omitting interactions after insuring they were not significant (not shown). The analysis was run using the “car” package (Fox and Weisberg, 2011), implemented in R software version 1.0.44 (R Core Team, 2014). Given an assumption that neither time differences between cast nor depth were significant in explaining variability in the productivity data, we also ran a 2-way ANOVA analysis focusing on method and cruise (or season) alone, omitting casts and depth, using the same “car” package and in the same way as the 4-way ANOVA. This analysis was performed to independently confirm the results obtained by the 4-way ANOVA relative to differences between seasons.

Regression was applied to $\log_{10}$ -transformed data, with a regression equation of the form:

$$\log_{10} PP_1 = a + b \log_{10} PP_2 \quad (3)$$

Where PP_1 and PP_2 correspond to rates from two different PP methods (e.g., GPP-DO and ^{14}C -TOC) and a and b are fitted intercept and slope parameters. Note that fitting this linear regression in log space is equivalent to fitting a power function in untransformed space:

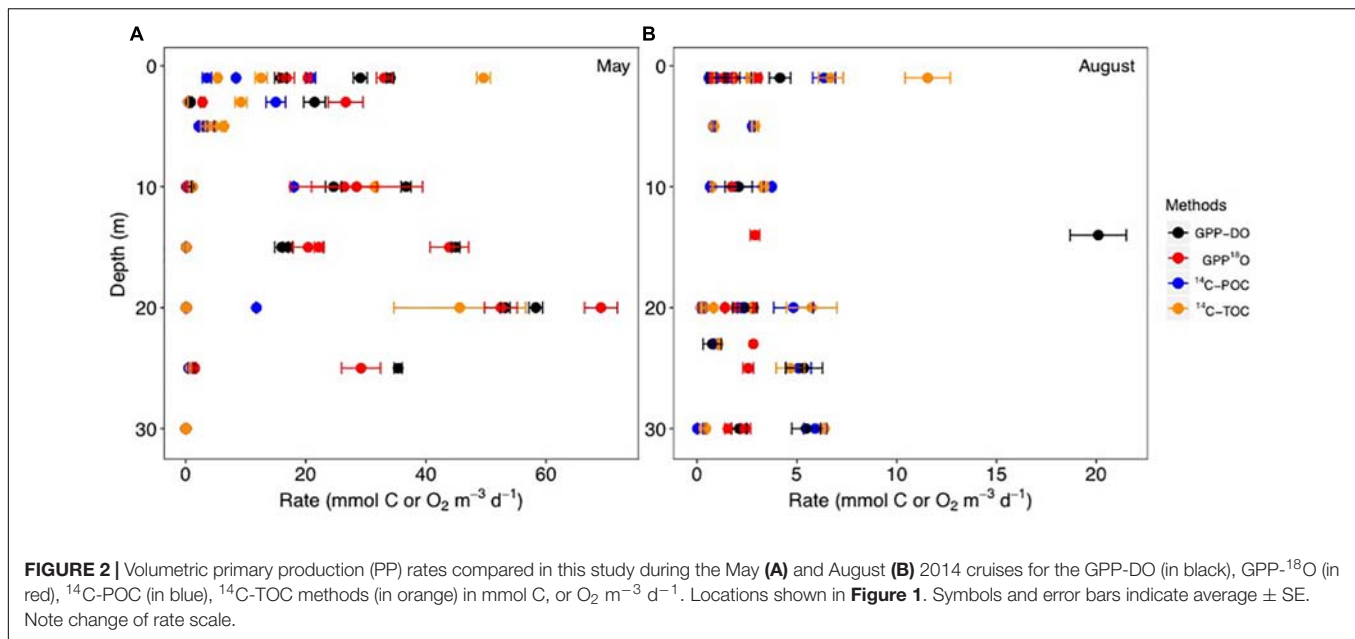
$$PP_1 = 10^a PP_2^b \quad (4)$$

Multivariate normality of the input data was assessed with the MVN package in R (Korkmaz et al., 2014). Assuming symmetry in the relationship between PP rates derived by the methods under consideration, reduced major axis regression (RMA) was employed to examine relationships between productivity rates (Legendre and Legendre, 1998). Statistical analyses were completed using the lmodel2 R package (Legendre, 2014). Estimates from the pooled data presented in this study were then compared to previous regressions derived from a global PP synthesis aimed at predicting O rates from C rates (Regaudie-de-Gioux et al., 2014).

RESULTS

During May, PP rates based on GPP- ^{18}O and GPP-DO averaged $21.0 \text{ mmol O}_2 \text{ m}^{-3} \text{ d}^{-1}$ while the ^{14}C -TOC averaged $10.7 \text{ mmol C m}^{-3} \text{ d}^{-1}$ (combined ^{14}C uptake in particulate and dissolved carbon) (**Figure 2** and **Table 2**). In August, PP rates based on GPP- ^{18}O and GPP-DO averaged $2.4 \text{ mmol O}_2 \text{ m}^{-3} \text{ d}^{-1}$ while the ^{14}C -TOC was $3.5 \text{ mmol C m}^{-3} \text{ d}^{-1}$. Seasonally, the O_2 -based rates decreased $\sim 90\%$ from May to August, while the ^{14}C -based rates decreased $\sim 60\%$ (**Figure 2** and **Table 2**). Particularly in August, the ^{14}C -TOC decreased 68% while ^{14}C -POC decreased 48% from May. As a result, volumetric PP rates in May were approximately six times higher than in August while integrated rates were on average three times higher in May than in August, with variability among specific methods.

For all data combined, our results indicate that volumetric ^{14}C -TOC estimates were 40% of the oxygen-based GPP rates in the study region (calculated as the ratio of averages shown in **Table 2**). However, this relationship also varied seasonally.



In May, ¹⁴C-TOC volumetric rates were on average 51% of the O₂-based rates (**Table 2**). In August, ¹⁴C-TOC rates were on average 125% of the GPP-DO rates and 175% of the GPP-¹⁸O volumetric estimates. This relationship was also evident when examining scatterplots of the untransformed data (**Figure 3**) and O:C ratios (**Figure 4**), with O:C ratios in the spring generally higher than 1.25:1 and in some cases higher than 3:1, yet below 1:1 in the summer (see section “Photosynthetic Quotient” discussion below). On average for each season, the variability in O:C was larger in May than in August.

Considering all factors in a 4-way ANOVA, differences between rates of PP were statistically significant for cruise (i.e., season; $F = 4.25$, $p < 0.05$; **Table 3** and **Supplementary Figure S8**). Considering only factors method and cruise in a 2-way ANOVA yielded a similar result, with differences between PP rates proving significant only for the latter, confirming results from 4-way ANOVA [$F(3,71) = 0.17$ and $F(1,71) = 5.49$, $p < 0.05$, respectively]. These results are consistent with those

presented in **Figures 3, 4**, as well as **Table 2**, given the large variability within a particular method but larger seasonal differences in productivity rates. In summary, most of the variability in O:C ratios originates from the seasonal evolution of the phytoplankton community and to a lesser extent, the methods employed in measuring PP. However, examination of **Table 2**, where in some cases the distribution of the volumetric (and integrated) rates for different methods do not overlap, suggests that differences among methods cannot be discounted. Specifically, these observations, alongside difference in median O:C ratios presented in **Figure 4** and regressions analyses (see below), suggest that an interaction between Method x Season is likely, and may not have been detected in ANOVA as a result of limitations of both dataset and statistical method.

f) GPP-DO vs ¹⁴C-TOC."

Regression of log-transformed PP rates serves to further highlight differences in the relationship between O and C rate estimates in aggregate, but also as a function of season, as well as differences between this Arctic dataset and previous global syntheses. While rates within a particular method class (i.e., C or O) fell approximately along the 1:1 line in log-log space ($0.82 < r^2 < 0.85$, $p < 0.01$, **Figures 5A,B** and **Supplementary Table S3**), far more scatter was apparent when considering relationships across methods (**Figures 5C–F**), with O:C ratios amongst estimates for a particular sampling location sometimes exceeding a factor of 100 (identified as outliers in **Figure 4**). As observed in the untransformed data (**Figure 3**), higher variability was apparent during the spring bloom (May cruise) compared to summer (August cruise). While positive linear relationships between log O and log C rates were apparent, the relationships were sometimes weak (**Figures 5C–F** and **Supplementary Table S3**). Significant correlations were found for linear relationships between log-transformed oxygen and

TABLE 2 | Mean and standard error of the mean for volumetric and integrated rates of GPP-DO, GPP-¹⁸O, ¹⁴C-TOC, and ¹⁴C-POC in units mmol C or O₂ m⁻³ d⁻¹ for the volumetric rates and mmol C or O₂ m⁻² d⁻¹ for the integrated rates.

	GPP-DO	GPP- ¹⁸ O	¹⁴ C-TOC	¹⁴ C-POC
Volumetric May	20.5 ± 5.7	21.4 ± 6.3	10.7 ± 4.9	5.9 ± 2.2
Aug	2.8 ± 0.6	2.0 ± 0.2	3.5 ± 0.8	3.2 ± 0.8
Total	12.1 ± 3.6	12.2 ± 4.0	7.3 ± 2.7	4.6 ± 1.2
Integrated May	288.9 ± 124.2	293.6 ± 121.9	146.3 ± 106.3	81.8 ± 56.8
Aug	26.6 ± 14.2	47.3 ± 4.0	94.2 ± 25.8	81.5 ± 22.1
Total	176.5 ± 85.1	188.1 ± 82.0	124.0 ± 58.6	81.7 ± 31.5

Values shown indicate rates separated by season (May, August) as well as the aggregate of all data (Total). ¹⁴C-DOC production is calculated by subtracting ¹⁴C-POC from ¹⁴C-TOC (data in **Supplementary Table S1**).

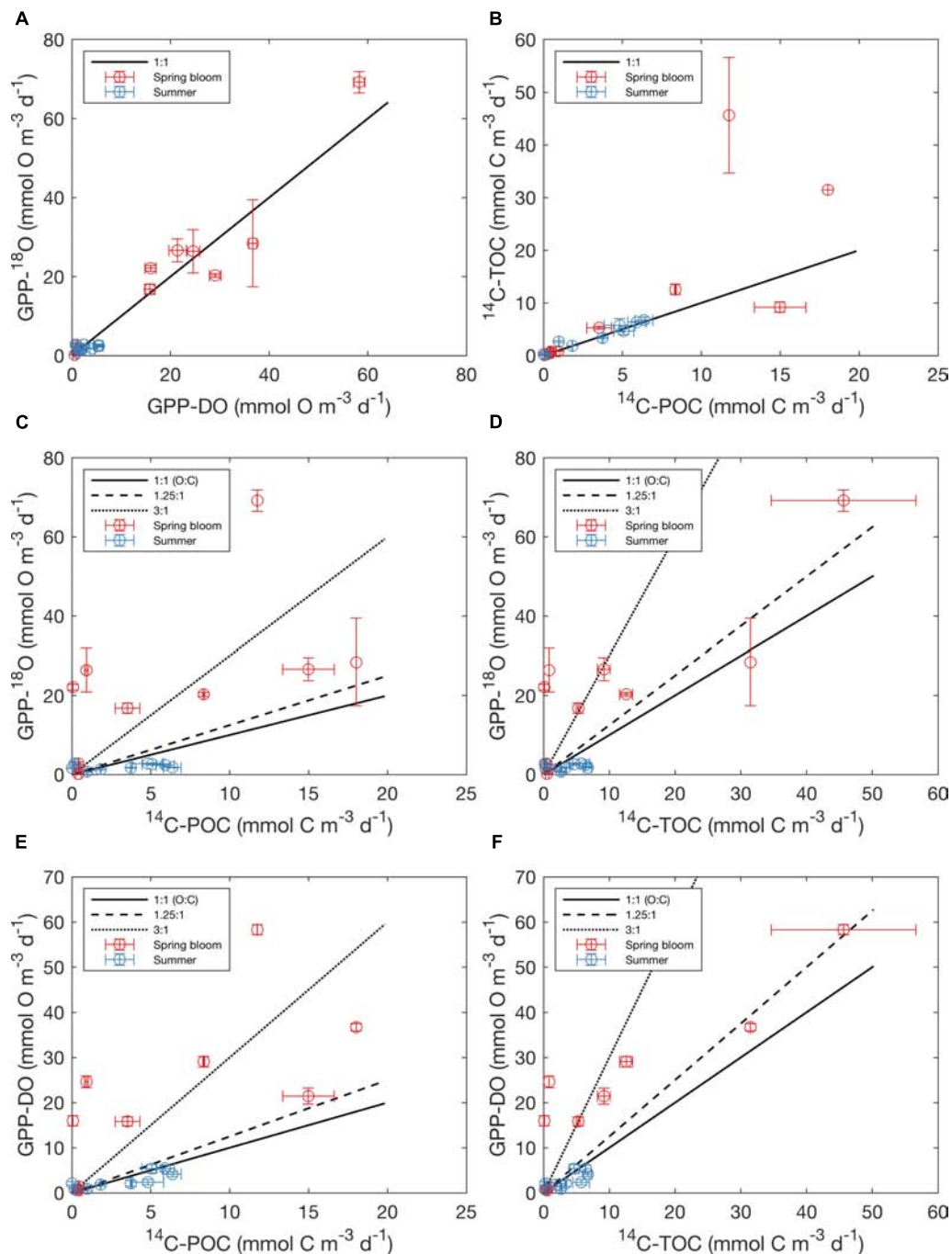


FIGURE 3 | Relationship amongst O- and C-based primary production rates reported in this study, showing mean values (circles) and standard errors on both x and y (error bars). **(A)** GPP- ^{18}O vs. GPP-DO, **(B)** ^{14}C -TOC vs. ^{14}C -POC, **(C)** GPP- ^{18}O vs. ^{14}C -POC, **(D)** GPP- ^{18}O vs. ^{14}C -TOC, **(E)** GPP-DO vs. ^{14}C -POC and **(F)** GPP-DO vs. ^{14}C -TOC. Colors indicate sampling season (the spring bloom in May and summertime in August), with the solid black line indicating a 1:1 relationship, the dashed line 1.25:1, and the dotted line 3:1 (O:C). Note that the rates are untransformed and reported in native units ($\text{mmol O m}^{-3} \text{d}^{-1}$ for oxygen and $\text{mmol C m}^{-3} \text{d}^{-1}$ for carbon).

carbon rates ($r = 0.92$, $p < 0.001$ and $r = 0.91$, $p < 0.001$, respectively), as well as between C-based productivity rates and GPP-DO ($r = 0.50$, $p < 0.05$ and $r = 0.58$, $p < 0.01$ for ^{14}C -POC and ^{14}C -TOC, respectively). Confidence intervals on the slope

in log-log regressions (i.e., the power slope “b” in Eqs 3 and 4) included 1 (one) in all cases (**Supplementary Table S3**). While this suggests an isometric relationship in untransformed (i.e., O:C) space, this result may also be a consequence of the tendency

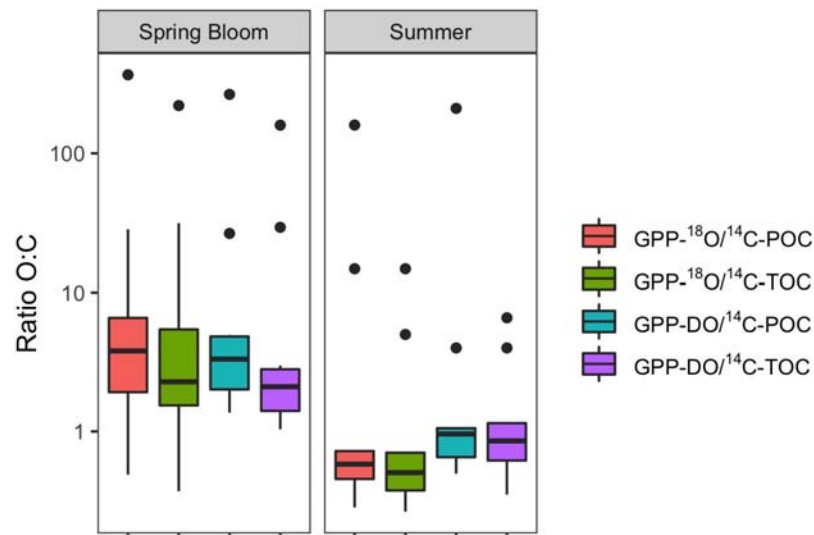


FIGURE 4 | Box plots of O:C ratios of PP estimates, by season (May – spring bloom $n = 10$; August – summer $n = 9$). Box plot showing the median (horizontal line), as well as the 25 and 75th percentiles, with vertical lines going to extremes, and outliers denoted by points.

of RMA slopes to tend to 1 for weak linear relationships (Legendre and Legendre, 1998). In several cases, fitted intercepts “a” were however significantly different from 0 (i.e., for ^{14}C -POC vs. ^{14}C -TOC, ^{14}C -POC vs. GPP- ^{18}O , ^{14}C -POC vs. GPP-DO, and ^{14}C -TOC vs. GPP-DO; **Supplementary Table S3**). Linear relationships derived for log O and log C PP rates from a previous global data synthesis (Regaudie-de-Gioux et al., 2014), while reasonable within O and C methods (**Figures 5A,B**), also proved a poor fit to the data when comparing methods. In summary, the data demonstrate that there is a large source of variability in these relationships as a function of season, further confirmed when PP methods are compared by cruise (**Supplementary Figure S9**) and that a global conversion equation likely is a poor fit to specific regions in the ocean, including in this case the Arctic.

DISCUSSION

In the spring of 2014, the waters NW and N of Svalbard Archipelago were dominated by a bloom of large chain-forming

diatoms and the colonial form of *Phaeocystis* sp. [M. Reigstad, pers. comm.]. Average integrated chlorophyll concentration was $236.7 \pm 88.8 \text{ mg chlorophyll } a \text{ m}^{-2}$. By August, toward the end of the growth season, phytoplankton abundance was low and small flagellates dominated the community. Integrated chlorophyll *a* had decreased to $57 \pm 22.6 \text{ mg m}^{-2}$. The phytoplankton community was dominated by cryptomonads, coccolithophorids, dinoflagellates, and few small diatoms. These two scenarios correspond to periods of nitrate-based new production in May, followed by a period of recycled, or ammonium-based, production in August (Randelhoff et al., 2018; Svensen et al., 2019). The C-based and O-based techniques all noted a sharp decrease in primary productivity estimates between May and August, representative of the change in phytoplankton abundance and composition (**Table 2**). The high C-based and O_2 -based rates of PP in May corresponded to the boreal spring bloom, at the ice edge, where high rates of productivity are expected (Vaquer-Sunyer et al., 2013).

Our results indicate that the average volumetric O-based PP, as measured by ^{18}O method ($12.2 \pm 4.0 \text{ mmol O}_2 \text{ m}^{-3} \text{ d}^{-1}$) is ~ 1.7 higher than the C-based estimates such as ^{14}C -TOC ($7.3 \pm 2.7 \text{ mmol C m}^{-3} \text{ d}^{-1}$), which includes particulate and dissolved carbon uptake (**Table 2**). This difference is consistent with other measurements on open ocean phytoplankton, where GPP- ^{18}O was ~ 1.5 higher than ^{14}C -POC (Juranek and Quay, 2005). Based on similar productivity methods as in this study, Regaudie-de-Gioux et al. (2014) showed that GPP- $^{18}\text{O} > \text{GPP-DO} > ^{14}\text{C-TOC} > ^{14}\text{C-POC}$. In our case, the average GPP- $^{18}\text{O} \approx \text{GPP-DO} > ^{14}\text{C-TOC} > ^{14}\text{C-POC}$ as previously reported by Grande et al. (1989b) for the North Pacific. It is only in May that our results agree with those of Regaudie-de-Gioux et al. (2014), with GPP- $^{18}\text{O} > \text{GPP-DO} > ^{14}\text{C-TOC} > ^{14}\text{C-POC}$ (**Table 2**).

Seasonal dynamics of the pelagic ecosystem's metabolism could play a key role in the difference between C- and O-based

TABLE 3 | Results of the 4-way (type II) ANOVA testing for significance of treatment by method, cruise (or season), cast, and depth for log10-transformed.

Source	Df	F	Pr (>F)	Significance
Method	3	1.68	0.18	
Cruise	1	4.25	0.04	*
Cast	1	0.69	0.41	
Depth	1	1.01	0.32	
Residuals	69			

Significance is indicated for $*p < 0.05$. Df is degrees of freedom, F is the F statistic, Pr (>F) is the significance probability associated with the statistic F and Sig denotes significance.

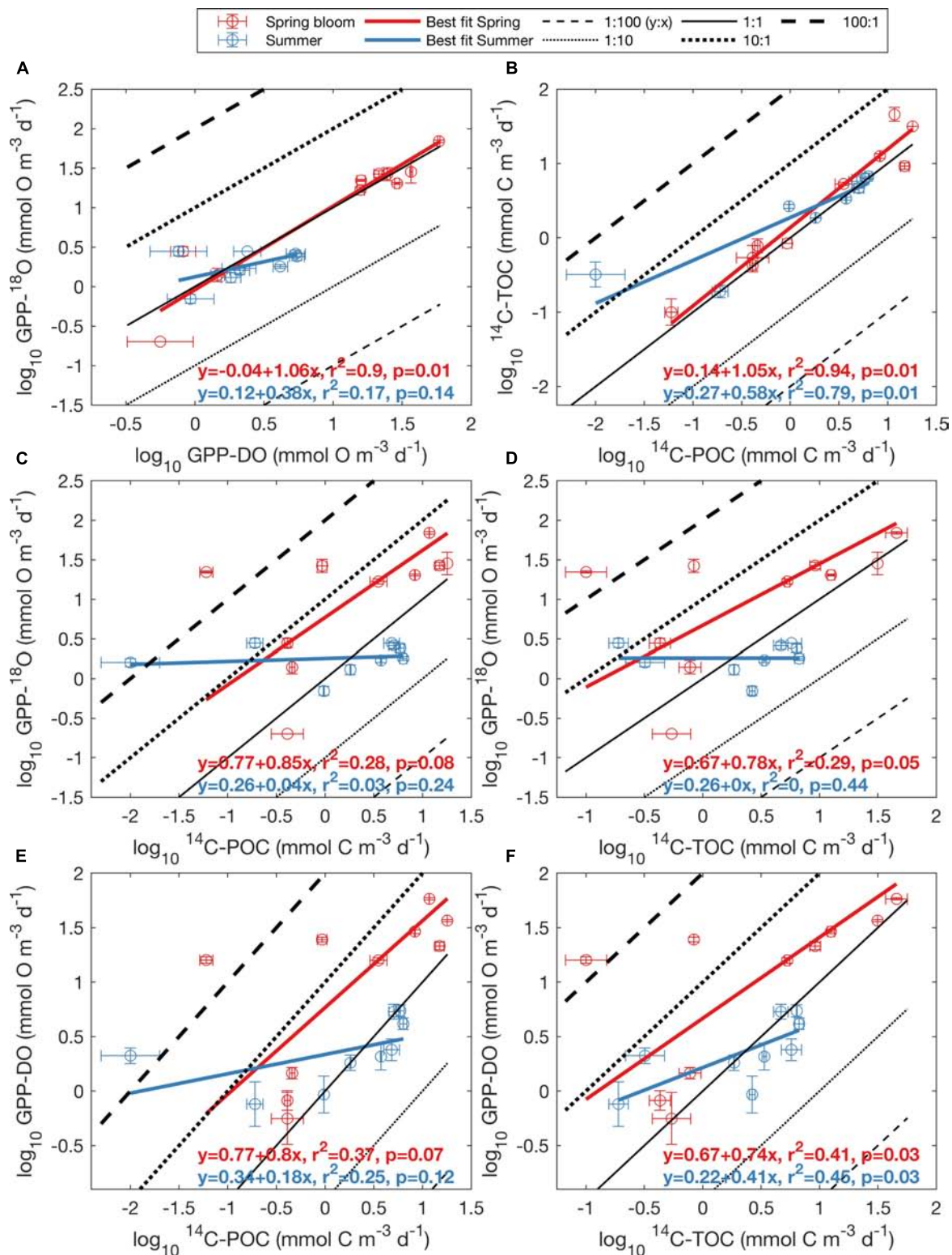


FIGURE 5 | Log-log relationship between oxygen- and carbon-based methods for May (red dots) and August (blue dots), presented as average $\pm$ standard error for each depth (Figure 2). (A) GPP- ^{18}O vs. GPP-DO, (B) $^{14}\text{C-TOC}$ vs. $^{14}\text{C-POC}$, (C) GPP- ^{18}O vs. $^{14}\text{C-POC}$, (D) GPP- ^{18}O vs. $^{14}\text{C-TOC}$, (E) GPP-DO vs. $^{14}\text{C-POC}$, and (F) GPP-DO vs. $^{14}\text{C-TOC}$. All rates are volumetric in units of $\text{mmol O m}^{-3} \text{d}^{-1}$ for oxygen and $\text{mmol C m}^{-3} \text{d}^{-1}$ for carbon. Black lines represent ratios of y to x ranging from 1:100 to 100:1, with the solid line indicating a 1:1 relationship. The bold teal line represents the best linear fit to the aggregate dataset (i.e., including both seasons), while the orange line, if present, represents the best fit line calculated by Regaudie-de-Gioux et al. (2014), based on a global synthesis of PP observations.

rates of primary productivity. In spring, during the ice-edge phytoplankton bloom, ^{14}C -TOC rates equalled 52% and 50% of GPP-DO and GPP- ^{18}O estimates, respectively (Table 2). A similar difference is observed in the integrated productivity estimates, where ^{14}C -TOC ($146.3 \pm 106.3 \text{ mmol C m}^{-3} \text{ d}^{-1}$) were 50% of the average GPP estimates from ^{18}O method ($293.6 \pm 121.9 \text{ mmol O}_2 \text{ m}^{-3} \text{ d}^{-1}$; Table 2). In August, when overall rates were low, integrated ^{14}C -TOC was 125% and 175% of DO-GPP and GPP- ^{18}O estimates, respectively (Table 2). Hence, in low productive waters with low abundance of large phytoplankton and when recycling processes dominate (Olli et al., 2019), the relationship between volumetric C- and O-estimates was reversed, ^{14}C -TOC > ^{14}C -POC > GPP-DO > GPP- ^{18}O (Table 2). In this way, seasonality not only affected overall PP rates and the absolute amount of the difference between methods, but the sign as well. Possible sources of observed variability in productivity estimates by the various methods are discussed below.

Cellular Processes Affecting Primary Production Estimates

O_2 -based GPP rates are higher than ^{14}C -based estimates as the latter excludes respiration (Bender et al., 1987). In this way, our results confirm that similar to lower latitude estimates, the C-based techniques in the Arctic better approximate net primary production (NPP) (Marra, 2002; Robinson et al., 2009; Regaudie-de-Gioux et al., 2014). As ^{14}C -TOC includes both particulate and dissolved C uptake, it is expected to be higher than ^{14}C -POC which only includes the ^{14}C retained in phytoplankton, concentrated on a filter after incubation (see section “Materials and Methods”) (Juranek and Quay, 2005; Matrai et al., 2013). ^{14}C -POC is the most common productivity technique when using radioactive carbon (Steemann-Nielsen, 1952). However, the difference between ^{14}C -TOC and ^{14}C -POC can be substantial. ^{14}C -DOC, calculated as the difference between ^{14}C -TOC and ^{14}C -POC (Table 2 and Supplementary Table S1), was higher in May than in August due to high PP rates in spring, accounting for $4.8 \pm 3.6 \text{ mmol C m}^{-3} \text{ d}^{-1}$ or approximately 45% of the ^{14}C -TOC and $0.3 \pm 0.2 \text{ mmol C m}^{-3} \text{ d}^{-1}$ or 9% of the ^{14}C -TOC in August, similar to rates previously observed in the Barents Sea (Table 2; Vernet et al., 1998) and productive areas of the Nansen Basin, Arctic Ocean (Gosselin et al., 1997).

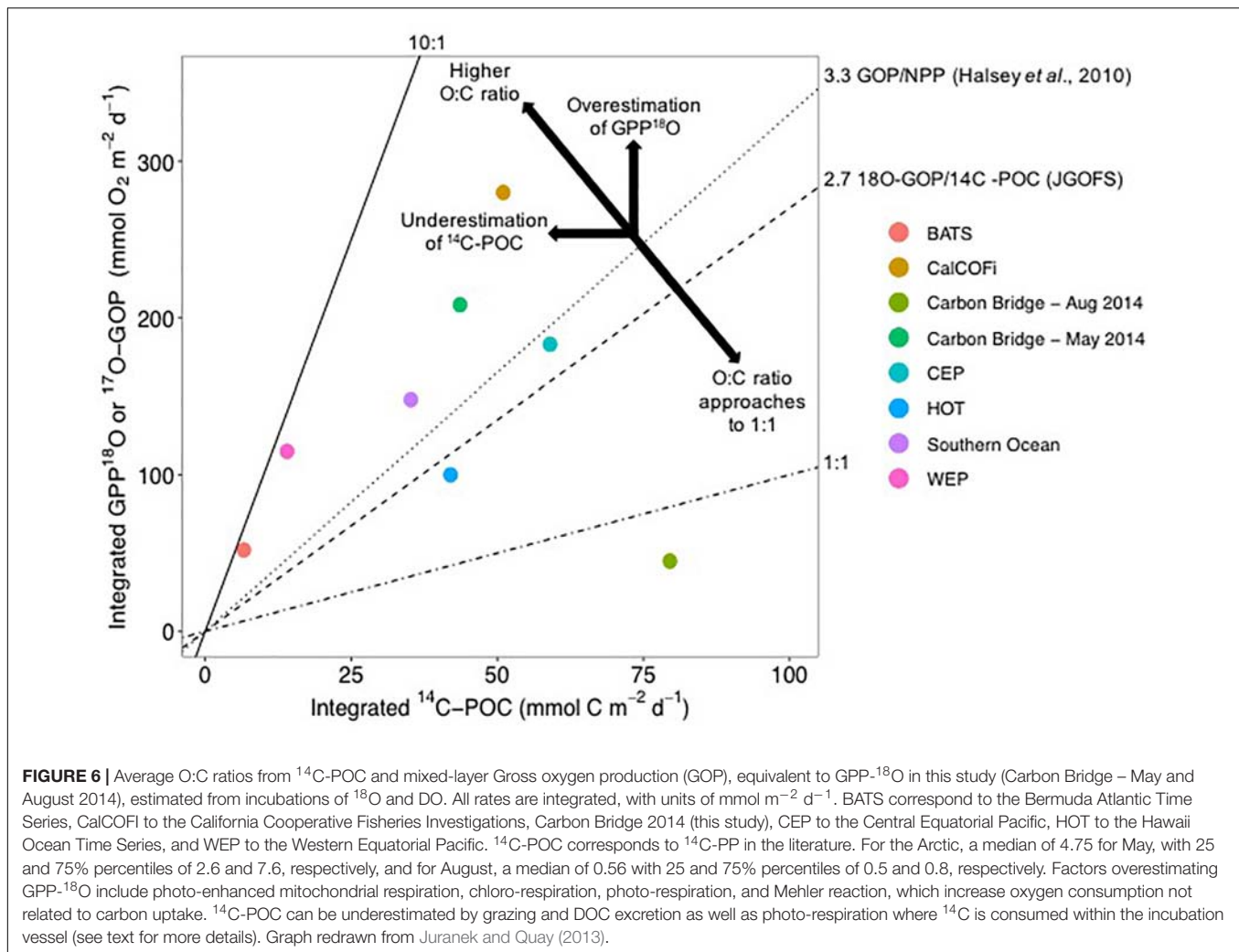
For the North Atlantic, Robinson et al. (2009) highlighted that the difference between the techniques depended on the magnitude of basal (or dark) respiration. Hence, the significant difference between GPP- ^{18}O and ^{14}C -POC rates found in this study (Tables 2, 3) could be explained by losses resulting from respiration by autotrophs (Grande et al., 1989b). In May, the basal respiratory losses accounted for $2.52 \pm 0.31 \text{ mmol O}_2$ or $\text{C m}^{-3} \text{ d}^{-1}$ (Table 1 in Mesa et al., 2017) or $\sim 10\%$ of the GPP (Table 2), in agreement with the expectation that basal respiration rates in European Arctic communities are characteristically low (i.e., Vaquer-Sunyer et al., 2013). However, the 24-h photoperiod that helps support rapid growth and high rates of photosynthesis may impose higher daily respiratory losses than in temperate regions. Higher respiration rates in the

light might be due to the contribution of autotrophic metabolic processes, such as photo-enhanced mitochondrial respiration, chlororespiration, photorespiration, and/or the Mehler reaction (Bender et al., 1999). For example, phytoplankton exposure to higher light irradiances in the shallow mixed layers created by sea ice melt, combined with low temperatures, might lead to the increase of the Mehler reaction, a defense mechanisms to overcome photoinhibition (Laws et al., 2000; Beer et al., 2014). Indeed, high respiration rates have been reported for the Beaufort Sea, in the summer, during periods of high-light exposure (Nguyen et al., 2012).

For the European Arctic, phytoplankton respiration rates during summer, characteristic of continuous daylight, are higher in the light than in the dark (Mesa et al., 2017). These authors found that community respiration rates evaluated in the light increased with increasing GPP- ^{18}O rates, establishing a threshold of $10 \text{ mmol O}_2 \text{ m}^{-3} \text{ d}^{-1}$ beyond which the light compared with the dark process prevail. Respiration in the light was on average 1.37 higher than in the dark and at maximum respiration rates, the light respiration was 17.56 higher. This non-linearity of respiration in relation to productivity rates is expected to underlie the non-linearity of the O:C relationship (Figure 5). For the area around Svalbard, the average respiration in the light is $5.2 \pm 0.52 \text{ mmol O}_2 \text{ m}^{-3} \text{ d}^{-1}$ (Table 1 in Mesa et al., 2017). Combining these light respiration rates with a GPP of $21.4 \pm 6.3 \text{ mmol O}_2 \text{ m}^{-3} \text{ d}^{-1}$ (Table 2) we can predict an O_2 -based net production of $\sim 16.2 \text{ mmol O}_2 \text{ m}^{-3} \text{ d}^{-1}$, while the ^{14}C -TOC is $10.7 \pm 4.9 \text{ mmol C m}^{-3} \text{ d}^{-1}$, with a difference of $\sim 5.5 \text{ mmol O}_2$ or $\text{C m}^{-3} \text{ d}^{-1}$ after accounting for respiratory losses.

Remaining differences between O- and C-based measurements after correcting for respiration suggests other processes are at play in Arctic plankton communities. The ^{14}C method can underestimate C assimilated due to release $^{14}\text{CO}_2$ by photorespiration that results when O_2 binds ribulose-1,5-bisphosphate carboxylase/oxygenase (Rubisco) leading to the excretion of glycolate, though photorespiration is apparently low in many phytoplankton (Peterson, 1980; Laws et al., 2000). In the case where PP is estimated with ^{14}C -POC, it differed by 17.7 mmol C or $\text{O}_2 \text{ m}^{-3} \text{ d}^{-1}$ from GPP-DO (Table 2). Processes that affect the release of ^{14}C -DOC will diminish the ^{14}C -POC estimate. “Sloppy” feeding and photorespiration might release ^{14}C -DOC as well (Laws et al., 2000). Microzooplankton grazers impact the estimation of ^{14}C -POC to the extent that grazed carbon is not only respired but also excreted (Laws et al., 2000). During our study period, average microzooplankton grazing rate was 0.23 d^{-1} (Lavrentyev et al., 2019). On the other hand, consumption by heterotrophic prokaryotes leads to a loss in ^{14}C -DOC, decreasing ^{14}C -TOC estimates (Steemann-Nielsen, 1952; Marra, 2002). Short incubation times ($<4 \text{ h}$) are recommended to minimize this loss.

The GPP- ^{18}O and triple oxygen isotope method are considered the most accurate measurements of gross photosynthesis available (Laws et al., 2000; Regaudie-de-Gioux et al., 2014) since GPP is best defined on the basis of oxygen evolution rather than carbon fixation (Falkowski and Raven, 1997). However,



this technique also has inherent errors where $\text{GPP-}^{18}\text{O}$ can be overestimated, increasing the difference with DO and ^{14}C techniques. $\text{GPP-}^{18}\text{O}$ rates are thought to overestimate GPP due to the decoupling of O_2 -production and C-assimilation through the Mehler reaction and photorespiration (Grande et al., 1989b; Laws et al., 2000). In the Mehler reaction, a molecule of labeled O_2 is produced and a molecule of unlabelled O_2 is consumed, accounting for an estimated 10% increase in $\text{GPP-}^{18}\text{O}$ rates (Falkowski and Raven, 1997; Laws et al., 2000). Photorespiration leads to the excretion of glycolate, also increasing $\text{GPP-}^{18}\text{O}$ estimates by 10% (Falkowski and Raven, 1997; Beardall et al., 2009). Higher C than O_2 -based rates during August may also be due to the presence of *Synechococcus* spp. (Paulsen et al., 2016). Indeed, Grande et al. (1989a) demonstrated elevated rates of respiration in light conditions due to photorespiration in *Synechococcus* spp. cultures from the Arabian Sea. Accounting for these sources of gains and losses, the combined effect of the Mehler reaction and photorespiration, increasing $\text{GPP-}^{18}\text{O}$ by 20%, and the impact of grazing on ^{14}C -assimilation, contributing to differences of 15% after 24 h (Laws et al., 2000), could account for ~35% of the 51% difference observed in our $\text{GPP-}^{18}\text{O}$ and

^{14}C -TOC estimates in May (Table 2). The rest is accounted for by a minimum of ~10% respiration losses.

Oxygen: Carbon Ratios in Arctic Phytoplankton

For the Arctic, median O:C ratios of 4.75 and 0.56 can be estimated for May and August, respectively, based on integrated $\text{GPP-}^{18}\text{O}$ and ^{14}C -POC rates (calculated as the median of the ratios of the integrated C and O productivity estimates for each station, data in **Supplementary Table S1**). The 25 and 75% percentiles for May and August are 2.6 and 7.6, and 0.5 and 0.8, respectively. The May ratio in the Arctic is higher than the average 2.7 of a multidisciplinary study (JGOFS, Joint Global Ocean Flux Study in the Arabian Sea, North Atlantic, Equatorial Pacific, and Southern Ocean), an O:C ratio also based on ^{18}O -GOP, or gross oxygen production, and 24-h ^{14}C incubations of the particulate matter (labeled ^{14}C -PP in JGOFS studies) (Figure 6; Juranek and Quay, 2013). This ratio is within the range of other oceanic regions where the ratio of O-based to C-based productivity estimates range from 3.1 to

8.2 (**Figure 6**; data obtained from Table 1 in Juranek and Quay, 2013). In the Southern Ocean a similar ratio of 4.2 ± 2.5 was observed (**Figure 6**; Hamme et al., 2012). These measurements were obtained at the Polar Front, at $\sim 50^\circ\text{S}$, during late summer (March), a time of the year more comparable to the August Arctic cruise of 2014 albeit with a difference of 30° in latitude. In all these studies, ^{18}O -GOP is incubation-independent, based on ^{18}O : ^{17}O ratio in surface waters and modeling of physical properties of the mixed layer and mixing processes (Bender et al., 1999, 2000; Laws et al., 2000) while ^{14}C estimates are from incubations, as in this study. Nevertheless, Marra (2002) and Marra and Barber (2004) found a robust relationship between these ^{18}O and ^{14}C measurements, where ^{14}C -POC estimations were $\sim 50\%$ lower than ^{18}O -GOP, as found for the Arctic (**Table 2**). These field O:C ratios were confirmed by laboratory experiments where Halsey et al. (2010) found a consistent O:C of 3.3 for the green microalga *Dunaliella tertiolecta* (**Figure 6**).

The low O:C ratio observed in August (median 0.56) does not have corresponding values in the literature. O:C ratios < 1 could be characteristic of high latitudes, not found in the tropics where most of the available measurements originate (e.g., Juranek and Quay, 2013). Assuming C uptake or loss do not change substantially from spring to summer (e.g., Lavrentyev et al., 2019), what decreases O_2 production with respect to carbon uptake? Possible processes decreasing O_2 production have been mentioned above, such as higher photorespiration by the abundant *Synechococcus* and higher Mehler reaction under conditions of high light (Nguyen et al., 2012; Paulsen et al., 2016). It is possible that coccolithophorids and dinoflagellates, together with *Synechococcus*, have higher basal respiration than the bloom-forming large diatoms or the colonial *Phaeocystis* sp., either due to their smaller cell size or other physiological response. The drastic change in phytoplankton composition from spring to summer suggests that phytoplankton community structure could be an important factor determining the O:C ratio. However, additional experiments are needed to substantiate this hypothesis.

High inter- and intra-seasonal variability characterizes Arctic primary productivity rates (**Figures 2, 3**). Part of the seasonal variability could originate from a variable proportion of light- and dark respiration, discussed above, as during productive periods of high phytoplankton biomass the proportion of light to dark respiration could be as high as ~ 18 (Mesa et al., 2017). This large variability in respiration, potentially affecting the O:C ratio in polar phytoplankton, could explain in part the differences we observed between May and August. As the days shorten the respiration in the light decreases, decreasing O_2 - based GPP estimates, such that in the Arctic the O:C ratio in August was < 1 (**Figures 4, 6**). These large discrepancies in O:C ratios between seasons and with the global dataset suggest that more experiments are needed before large-scale regional and seasonal patterns can be determined.

Conclusion

The O_2 -based methods and the ^{14}C method provide understanding of different processes critical to describe ecosystem function such as *gross and NPP* and *respiration* at

the plankton community level. The choice of either method should be guided by the specific question being addressed. In this way, the methods are complementary. For example, the combination of ^{14}C -TOC and ^{14}C -POC provides information of food supply (as DOC) for the microbial food web, not available from the oxygen methods. Furthermore, ^{14}C -POC represents the phytoplankton carbon production needed when quantifying the food available for higher trophic levels. The DO methods provide independent estimates of community respiration (CR) and net community production (NCP) (Carritt and Carpenter, 1966; Carpenter, 1995). The main difference among methods is the inclusion of respiration in GPP estimates, that in the Svalbard region seems to account for $\sim 20\%$ of the primary production (Mesa et al., 2017).

In this study we emphasize that (1) the relationship between O and C in the Arctic are relatively weak, with seemingly variable relationship; (2) there is evidence for seasonality in this relationship, mediated in part by rates of productivity; and (3) that this relationship differs from previous ones derived from an aggregation of global datasets. In demonstrating seasonal variability in the O to C relationship, as well as variability between types of O and C methods, our study contributes significantly to the state of the art, while doing so raising a number of interesting questions. One of these is this notion of PQ which relates moles of O released and moles of C produced. This relationship appears variable temporally and perhaps spatially, while the state of the art has been to apply a single number, often with no regional parametrization let alone temporal component. Further exploration of O:C ratios in Arctic and global phytoplankton, and the impact of respiration on rate estimates, will provide valuable insight to better constrain primary production, and ultimately provide a means to track long-term change in the evolving Arctic environment.

DATA AVAILABILITY

All datasets generated for this study are included in the manuscript and/or the **Supplementary Files**.

AUTHOR CONTRIBUTIONS

CD, MS-M, MV, and MR designed the fieldwork. MS-M, MV, EM, and MC carried out the fieldwork and the laboratory analysis. MS-M, CD, MV, and MC analyzed the data. All authors contributed to the writing and editing of the manuscript.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: <https://www.frontiersin.org/articles/10.3389/fmars.2019.00468/full#supplementary-material>

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Influence of Phytoplankton Advection on the Productivity Along the Atlantic Water Inflow to the Arctic Ocean

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Northwards flowing Atlantic waters transport heat, nutrients, and organic carbon in the form of zooplankton into the eastern Greenland Sea and Fram Strait. Less is known of the contribution of phytoplankton advection in this current, the Atlantic Water Inflow (AWI) spanning from the North Atlantic to the Arctic Ocean. The *in situ* and advected primary production was estimated using the physical-biological coupled SINMOD model over a region bounded by northern Norway coast (along the Norwegian Atlantic Current, NAC), the West Spitsbergen Current (WSC) and the entrance to the Arctic Ocean in northern Fram Strait. The simulation results show that changes in phytoplankton biomass at any one location along the AWI are supported primarily by advection. This advection is 5–50 times higher than the biomass photosynthesized *in situ*, seasonally variable, with minimum contribution in June, at the time of maximum *in situ* primary production. Advection in the NAC transports phytoplankton biomass from areas of higher production in the south, contributing to the maintenance of phytoplankton productivity further north. *In situ* productivity further decreases north of Svalbard Archipelago, at the entrance to the Arctic Ocean. Excess *in situ* annual production in northern WSC is exported to the Arctic Ocean during the growth season (April to September). The balance between *in situ* and advected primary production defines three main regions along the AWI, presumably modulated by the spatial and temporal variability of copepod grazing. As the sea ice reduces its annual extent and warmer waters enter the Arctic Ocean, ecological characteristics of the ice-free WSC with its AWI signature could extend north and east of Svalbard and into the central Arctic. Advection thus constitutes an important link connecting marine ecosystems of the Arctic and Atlantic Ocean, mainly at the gateways.

Keywords: advection, phytoplankton, carbon, Atlantic water inflow, Arctic Ocean, Fram Strait, West Spitsbergen Current

INTRODUCTION

The northward movement of Atlantic Water from the North Atlantic into the Arctic Ocean constitutes a major pathway of ocean circulation, contributing to transports of heat and salt into the Arctic with implications for the physical structure of the Arctic Ocean (Rudels et al., 2004, 2005, 2015). Atlantic Water advected along this pathway undergoes cooling and freshening as it is transported northwards along the western coast of Norway, across the Barents Sea Opening (BO), and west of the Svalbard Archipelago before finally entering the Arctic Basin north of Svalbard (NSv) (Figure 1a; Walczowski et al., 2012). In the north, the West Spitsbergen Current (WSC) is a rather complex circulation feature. North of 79°N, the current contains two separate warm cores that follow different isobaths. The western core moves north west of the Yermak Plateau and north of 80°N; part of this current detaches from the Yermak Plateau and enters the Fram Strait recirculation (Aagaard et al., 1987; Marnela et al., 2013). The inside branch follows the shelf break into the Arctic Ocean; past northwestern Spitsbergen, this water mass loses heat. Together with some freshening, this process converts the Atlantic water into Arctic Intermediate water within ~600 km of the Fram Strait.

The WSC flow has seasonal variability, with maximum in winter and minimum in summer. At 78° 50' N, before entering the Arctic, the WSC delivers 6.6 ± 0.4 Sv of water (average 1997 – 2010), 45% of which is $>2^\circ\text{C}$ in temperature. Overall, the mean temperature of the WSC is $3.1 \pm 0.1^\circ\text{C}$ (Beszczynska-Möller et al., 2012) and characterized by salinity of ~35 (Rudels et al., 1994). Two-thirds of the heat transported north of 78°N flowing through the Fram Strait is lost by the westward transport and sea surface cooling; the other third is injected into the Arctic Ocean (Kawasaki and Hasumi, 2016). In addition to an interannual variability with 5 – 6-year cycles, the Atlantic Water has a 20-year warming trend at 150 – 900 m depth, with exceptionally high temperatures in the decade of the 2000's (Polyakov et al., 2012).

With the Atlantic Water Inflow (AWI) from Norway's coast into the Arctic Ocean, phytoplankton are transported northward through 14 degrees of latitude where shorter days and lower sun angle progressively delay the onset of primary productivity (Longhurst, 2010). Phytoplankton biomass values in these northern latitudes can vary by a factor $>100\times$ between winter [$0.1 \text{ mg chlorophyll } a \text{ (chl}_a\text{) m}^{-3}$] and summer ($>10 \text{ mg chl}_a \text{ m}^{-3}$) (Nöthig et al., 2015), with maximum biomass accumulation during boreal spring and summer, the period of minimum water transport. The average primary production in this European sector of the Arctic Ocean from 1995 to 2007 was estimated at $>100 \text{ g C m}^{-2} \text{ yr}^{-1}$, with the seasonal Sea Ice Zone contributing $30\text{--}100 \text{ g C m}^{-2} \text{ yr}^{-1}$ and the Perennial Ice Zone $<30 \text{ g C m}^{-2} \text{ yr}^{-1}$ (Wassmann et al., 2010).

The Central Arctic Ocean pelagic ecosystem is net heterotrophic, and relies on a net input of organic matter from southerly latitudes to survive (Olli et al., 2007). In this way, advection constitutes an important link of the marine

ecosystems of the Arctic Ocean with the Atlantic and Pacific Oceans, from nutrients to plankton to marine mammals, in particular at the gateways (Wassmann et al., 2015; Hunt et al., 2016). Popova et al. (2013) estimated that about 20% of the Arctic Ocean primary production is supported by advective processes with simulations linking nutrient-rich Pacific and Atlantic waters to the subsurface chlorophyll maximum in the central Arctic Ocean on a timescale of 15–20 years and with deep advective enrichment of nutrients occurring on a timescale of 5–6 years. Ocean connectivity has been examined further with respect to zooplankton communities. The supply of zooplankton by advection from the Atlantic Ocean is 2–3 times larger than from the Pacific Ocean; most abundant is the boreal copepod *Calanus finmarchicus* (Carstensen et al., 2012). Local consumption reduces the influence that advected zooplankton biomass has in the Amerasian Arctic sector while having a basin-scale influence in the European sector of the Kara, Laptev and East Siberian Seas (Grebmeier et al., 2015). *C. finmarchicus* originates from the North Atlantic, with adult populations reproducing successfully in the Norwegian Sea, where they develop and are transported north in the following spring and summer (Basedow et al., 2018). By the end of the summer and during winter, *C. finmarchicus* goes into diapause, migrating below the Norwegian Current-WSC to 600–1000 m depth (Kosobokova and Hopcroft, 2010). This zooplankton cannot reproduce when introduced to Arctic waters and disappears after a few months, where it is replaced by *Calanus glacialis*, a polar shelf-associated overwintering species, that is transported further into the Arctic shelf along the AWI boundary current (Kosobokova, 2012; Wassmann et al., 2015). Less is known about the influence of advection of phytoplankton on carbon cycling and/or planktonic ecology.

While physical processes associated with AWI into the Arctic have been the subject of extensive study (Pérez-Hernández et al., 2017), the implications of water mass advection and transformation for primary producers at the bottom of the food web remain poorly examined. In particular, potential changes in the biomass and productivity of phytoplankton communities as they are advected along the AWI, from northern Norway into the Arctic Ocean NSv, and the contributions of these changes to local carbon cycling along the pathway have not been investigated. The benefits that the current provides to the phytoplankton productivity and losses in this region remain unknown. This study attempts to answer the following questions: What is the contribution of advection to phytoplankton primary production along the AWI? How much carbon is available from locally produced and advected phytoplankton and how do their relative contributions vary spatially during the growth season? Using a well-tested model for Arctic plankton (Babin et al., 2015; Lee et al., 2016), we have addressed these questions from a community and ecosystem perspective (Wassmann et al., 2006, 2010, 2015). Furthermore, we provide a context of the potential changes in carbon cycling in this transition region at a time of warming northward water flow.

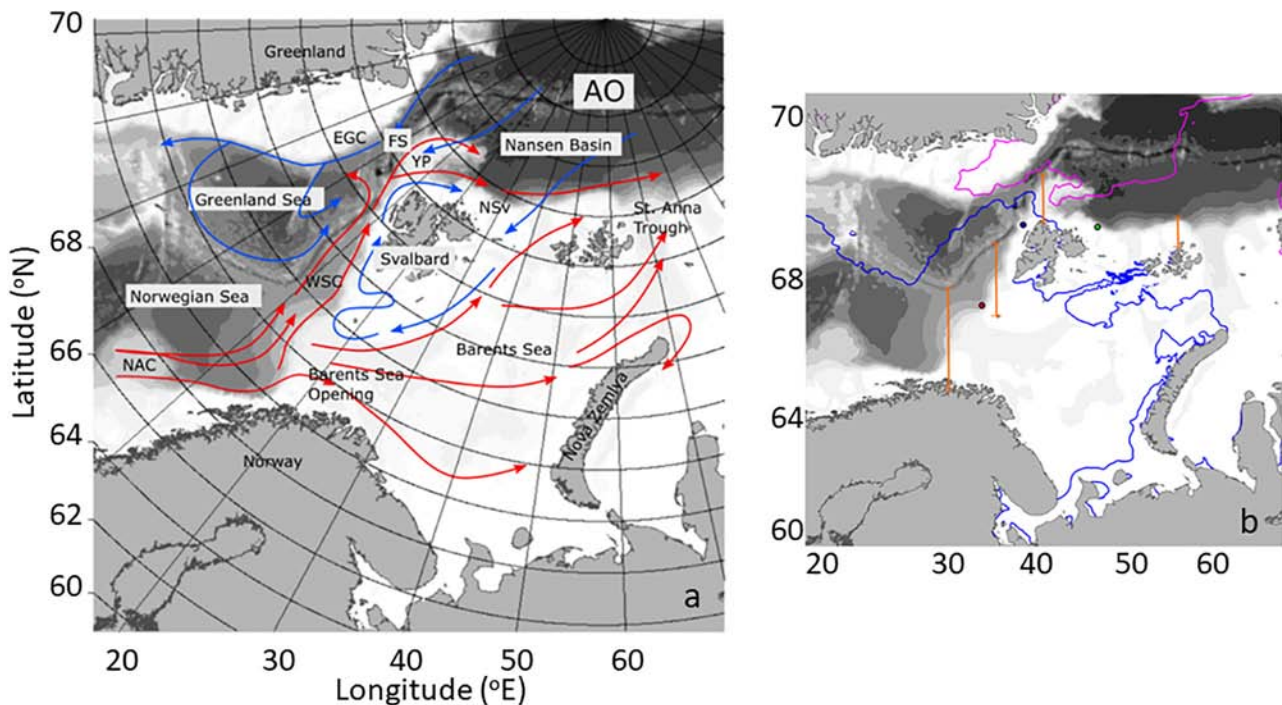


FIGURE 1 | (a) Main oceanographic features of the study area, including currents. The Atlantic water inflow (AWI) from the Norwegian Atlantic current (NAC) to the Barents sea opening (BO), the West Spitsbergen current (WSC), the area North of Svalbard (NSv), the Yermak Plateau (YP), Fram Strait (FS), the East Greenland current (EGC), and the Arctic Ocean (AO). Warm currents are depicted in red and cold currents in blue. **(b)** Map of the study area depicting sea ice extent in May (blue line) and September (pink line) of 2012. Four transects along the AWI (orange) depict the locations where phytoplankton carbon flux was estimated (see **Table 1**) and the dots correspond to locations where NCP (see **Figure 8**) was calculated.

MODEL

The phytoplankton dynamics along the AWI to the Arctic Ocean was studied with the physically-biologically coupled, nested 3D SINMOD model configurations with a 4 km horizontal grid size and with 61 vertical layers. The vertical level thickness increases from 5–10 m near the surface to 500 m below 1000 m. SINMOD is a fully coupled hydrodynamic-ice-chemical-biological model system. A comprehensive description of the physical and ecosystem and food web model is found in Slagstad and McClimans (2005) and Wassmann et al. (2006). A short description is given here. The hydrodynamic component of the model system, which is responsible for calculating the basic physical properties of the ocean like velocity, water temperature and pressure, is based on the so-called primitive Navier–Stokes equations and established on a z-grid (Slagstad and McClimans, 2005; Slagstad et al., 2015).

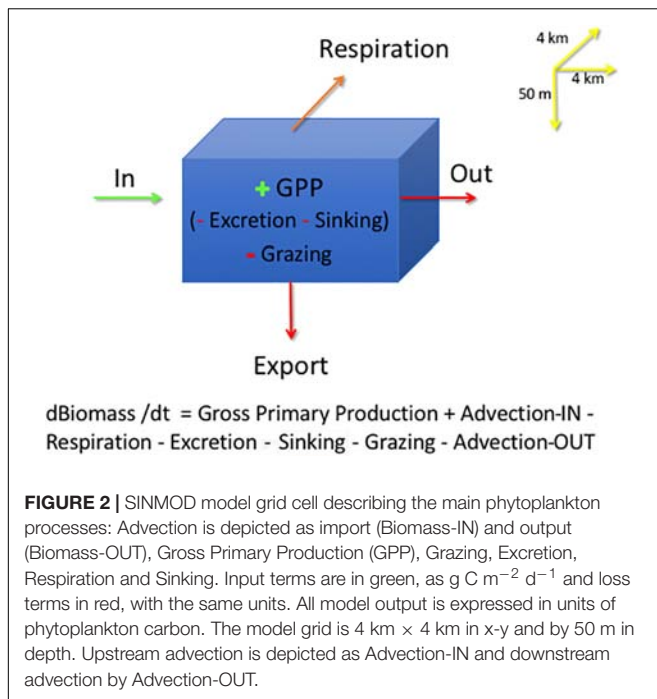
The model is forced by atmospheric data: wind, heat exchange, tides and freshwater run-off from land [for more details see Slagstad and McClimans (2005)]. The ice model is similar to that of Hibler (1979) and has two state variables, ice thickness and ice concentration, and allows ice interaction to depend on these. The ice momentum equation is solved together with an equation for the ice internal stress, using the elastic-viscous-plastic (EVP) dynamical model of

Hunke and Dukowicz (1997). The model simulates changes in ice mass and fraction of open water due to advection, deformation and thermodynamics effects. Initial values of temperature and salinity were taken from World Ocean Circulation Experiment (WOCE) Global Data Resource Version 3.0¹ using a spin-up phase of 26 years prior to the start of the simulation in this work. A comprehensive description of the WOCE data system can be found in Lindstrom and Legier (2001).

The model is forced by atmospheric output from the European Center for Medium-Range Weather Forecasts (ECMWF) reanalysis data from 2012. The model is also forced with freshwater fluxes (river discharges and diffuse run-off from land). Freshwater run-off along the Norwegian coast and in the Barents Sea is based on data from simulations by the Norwegian Water Resources and Energy Directorate². The simulations were performed using a version of the HBV-model in 1 km horizontal resolution (Beldring et al., 2003; Dankers and Middelkoop, 2008). For Arctic rivers, data are obtained from R-ArcticNet (Vörösmarty et al., 1996, 1998) available through <http://www.r-arcticnet.sr.unh.edu/v4.0/main.html>. Boundary conditions for biological, chemical and physical states are produced by a large-scale model with 20 km horizontal resolution. This includes tidal forcing. The large-scale model

¹<http://www.nodc.noaa.gov>

²www.nve.no



runs with a total of eight tidal components based on data from the TPXO 7.2 model of global ocean tides³.

The ecosystem module is formulated in an Eulerian framework and includes state variables for nutrients (nitrate - NO_3 , ammonium - NH_4 , and silicate - SiO_4), the microbial loop, heterotrophic nanoflagellates, diatoms and autotrophic flagellates, ciliates and two key mesozooplankters: the Atlantic *C. finmarchicus* and the arctic *C. glacialis*. SINMOD calculates Gross Primary Production (GPP), new production (NP), the f-ratio (NP/GPP) and secondary production of the two mesozooplankton species. For details of the biological model, see Wassmann et al. (2006). The model contains additional compartments for sinking detritus (fast and slow), dissolved organic carbon and the sediment.

The SINMOD model has been validated with field data (Wassmann et al., 2006; Ellingsen et al., 2008; Slagstad et al., 2011) where parameterization of the different variables can be found. The SINMOD model was found to be one of the best models to estimate primary production in the Arctic Ocean during an inter-comparison among ocean biogeochemical coupled models and Earth system models (Lee et al., 2016), as well as with satellite-derived primary production algorithms (Babin et al., 2015).

In each grid cell, phytoplankton are modeled in the 50 m surface layer of the water as:

$$\begin{aligned} dB/dt = & \text{GPP} - \text{Respiration} - \text{Sinking} - \text{Excretion} - \text{Grazing} \\ & + \text{Advection-IN} - \text{Advection-OUT} \end{aligned} \quad (1)$$

where B is Biomass, t is time in days, GPP is Gross Primary Production, or total carbon uptake by phytoplankton through photosynthetic process; Respiration is phytoplankton biomass lost as CO_2 ; Excretion is the production of Dissolved Organic Matter (DOC) released by phytoplankton; Grazing is phytoplankton consumption by zooplankton, both micro- and meso-zooplankton; and Sinking is diatoms lost from the 50-m surface layer as vertical sedimentation by cell flocculation and cell death; Export loss is accounted for in Sinking and Grazing and not included in calculations, all in units of carbon, $\text{g C m}^{-2} \text{d}^{-1}$. The model output is in units of Nitrogen, converted to carbon using a constant C:N ratio of 7.6, average data from the Barents Sea (Reigstad et al., 2002). Sinking is only related to phytoplankton cells, a slow export of organic carbon from the surface layer. On the other hand, Export of organic matter (Figure 2) comprises mostly the sedimentation of zooplankton fecal pellets and molts, considered to be a fast export. The model does include a module on the microbial loop where bacteria consume DOC from phytoplankton excretion and are predated upon by nanoflagellates. The model does not consider viruses as a separate compartment or cell lysis as a separate process (Wassmann et al., 2006); all phytoplankton cell death not related to grazing is included as Sinking out of the 50-m surface layer, which constitutes a portion of population mortality. DOC production from phytoplankton, expressed as Excretion, includes DOC from viral lysis, not expected to be high in polar waters (Agustí and Duarte, 2013; Mojica et al., 2016).

Model results are for the year 2012, a year of minimum sea ice extent in the Arctic Ocean (Figure 1b; Stroeve and Notz, 2018), maximizing ice-free primary production in the West and NSv Archipelago. These rates are calculated for a 6-month period during the growth season, from April to September, and are considered representative of yearly estimates (Wassmann et al., 2010). Several experiments were performed to determine the contribution of (a) phytoplankton biomass advection to local primary production, (b) phytoplankton growth parameters, (c) the relative importance of phytoplankton biomass advection on *in situ* phytoplankton production at each grid cell, and (d) the balance between sources and sinks of biomass as a function of advection. Model experiments are explained in each corresponding section of the “Results.” The SINMOD model was run and the variables of interest saved as output and later mapped within the domain of interest. Results are shown as maps in units of phytoplankton carbon and as tables with discrete values at fixed points along the AWI. The results are presented and discussed only for the AWI, from the NAC to the BO, the WSC and the area NSv (Figure 1a). The remaining data are shown to give context to the phytoplankton dynamics observed in the AWI.

RESULTS

Phytoplankton Growth

Phytoplankton Gross Primary Production

Gross Primary Production relates to the total amount of organic carbon newly incorporated by photosynthesis, thus

³<http://www-po.coas.oregonstate.edu/~poa/www-po/research/po/research/tide/global.html>

an index of production. As this process is based on the existing phytoplankton biomass, it depends on the physiological response of high-latitude microalgae to irradiance, temperature and inorganic nutrients within the surface mixed layer. Mapping the average GPP during the boreal growth season, from April to September, as calculated by the SINMOD model (Eq. 1), we observe a range spanning from 40 to 160 g C m⁻² 6mo⁻¹ (Figure 3a). Along the AWI, a gradient in GPP is observed, where close to the Norwegian shelf gross production is ~160 g C m⁻² 6mo⁻¹, maintaining high rates of ~140 g C m⁻² 6mo⁻¹ toward the BO. West of Svalbard, on the WSC, GPP is on average ~120 g C m⁻² 6mo⁻¹, decreasing to ~60 g C m⁻² 6mo⁻¹ in the NSv. These GPP annual rates are within estimates extrapolated from field samples with low March production and high June production (Vernet et al., 1998). Based on the decreasing rates of GPP toward the north, three regions can be defined along the AWI: NAC including the BO, the WSC and the NSv. However, it is notable that the WSC shows higher seasonal production than surrounding waters in the Greenland Sea and also NSv along the shelf break in the Arctic Ocean, in comparison to the Nansen Basin (Figure 1a). Superimposed on the spatial variability in GPP, there is a strong seasonality (Supplementary Figure S1 and Supplementary Table S1). GPP starts earlier in the Norwegian shelf, reaches a maximum everywhere in June, decreasing in July, with exception of the regions influenced by the AWI where GPP remains high. By September, GPP is <15 g C m⁻² mo⁻¹. Thus, the contribution of the AWI to regional GPP is most pronounced early and late in the growth season.

Phytoplankton Growth Rate

In addition to GPP, phytoplankton Growth Rate (μ) gives an indication of the speed of phytoplankton population renewal within the upper 50-m layer of the water column. The model simulations provide a unique opportunity to estimate this variable along the AWI, as carbon-specific net primary production within each model grid cell, or (GPP – Respiration)/Biomass (Figure 2) in units of d⁻¹. This is a difficult parameter to measure in the field, as phytoplankton biomass in units of carbon is often contaminated by bacteria and other heterotrophs. The modeled rates are within the range expected for seasonally averaged field samples in high-latitude environments, e.g., 0.22 d⁻¹ to 0.40 d⁻¹ (Garibotti et al., 2003). For the 6-month productive period (Figure 3b and Supplementary Table S2), between April and September, average growth rates varied from 0.02 d⁻¹ to 0.15 d⁻¹, with highest rates found in the NAC and remaining high along the WSC. Growth rates decreased in the NSv to intermediate values (~0.1 d⁻¹), although these remained higher than surrounding waters of the Nansen Basin in the Arctic Ocean and in the central Barents Sea (~0.02 d⁻¹).

Advection of Phytoplankton by the Atlantic Water Inflow Phytoplankton Biomass

Phytoplankton Biomass at any given location along the AWI can increase by transport from another location and/or from

in situ growth processes (Supplementary Table S3). In the field, assessments of *in situ* primary production concurrent to advection estimates of primary production are challenging. Here, we use the model's output to understand the possible effect of advection to phytoplankton processes by estimating phytoplankton Residence Time. For each model cell, we calculate the ratio of *in situ* biomass to phytoplankton advected into the grid cell, in units of days [d] (Biomass/Advection-IN, Figure 2). Residence Time represents the time a particle spends within the model grid cell of 4 km × 4 km × 50 m, from the time it enters (Advection-IN) to the time it leaves (Advection-OUT), in relation to the concentration of particles within a single model grid cell (Biomass). This variable is sensitive to the model grid cell size, thus, this experiment provides only relative comparisons among locations.

When the spatial distribution of phytoplankton Residence Time in each location is mapped, we observe consistently lower residence time along currents, such as the northward AWI where the average time of phytoplankton Residence Time at each location is shorter than elsewhere by a factor of ~5 or more (Figure 4). Within the flow, phytoplankton is carried north relatively fast and the Residence Time is limited to 0.05 days to 0.3 days, while phytoplankton biomass lasts 1 day or more in the open ocean. These numbers compare favorably with transport from a WSC current speed of 0.1 to 0.3 m s⁻¹ (Kolås, 2017). Comparing this Residence Time map to the distribution of GPP in Figure 3a, it suggests that the low Residence Time in the currents is mainly due to high advection of phytoplankton biomass as *in situ* GPP changes only by a factor of 2 or 3.

An alternative to estimating the effect of advection on phytoplankton processes along the AWI is to turn off GPP at a certain location and observe the downstream distribution of phytoplankton biomass (B). In this way, we can estimate the *Persistence* of phytoplankton, defined as the time (in days) that a parcel of phytoplankton with B > 0 is transported downstream from the location where GPP = 0. In this experiment, advection and loss processes remain >0. The loss of phytoplankton biomass is then due to the consumption by grazing, respiration, DOC excretion and cell sinking, such that the downstream biomass from where GPP is set to zero is estimated as dB/dt = 0 – Respiration – Sinking – DOC Excretion – Grazing + Advection-IN – Advection-OUT (Figure 2). The extent of phytoplankton biomass loss after GPP was turned off is shown for three locations in Figure 5. When the spatial distribution of phytoplankton Persistence in each model grid cell is mapped, biomass (as %) that remains in the WSC is compared to the location where GPP was cut-off. The contour in each panel shows the distance traveled by 20% of the original biomass or the location where 80% of the initial phytoplankton carbon is lost. Notably, phytoplankton biomass along the AWI reaches longer distances than elsewhere in the study domain. However, there is spatial variability: phytoplankton biomass persists longer (i.e., travels farther) in the AWI waters at the entrance of the BO (~300 km), decreasing to 200 km south of Svalbard and decreasing further to ~150 km at the entrance to the Arctic Ocean, regardless of time between July and August. Such dispersal distances are typical for larval transport of benthic, sessile organisms and a

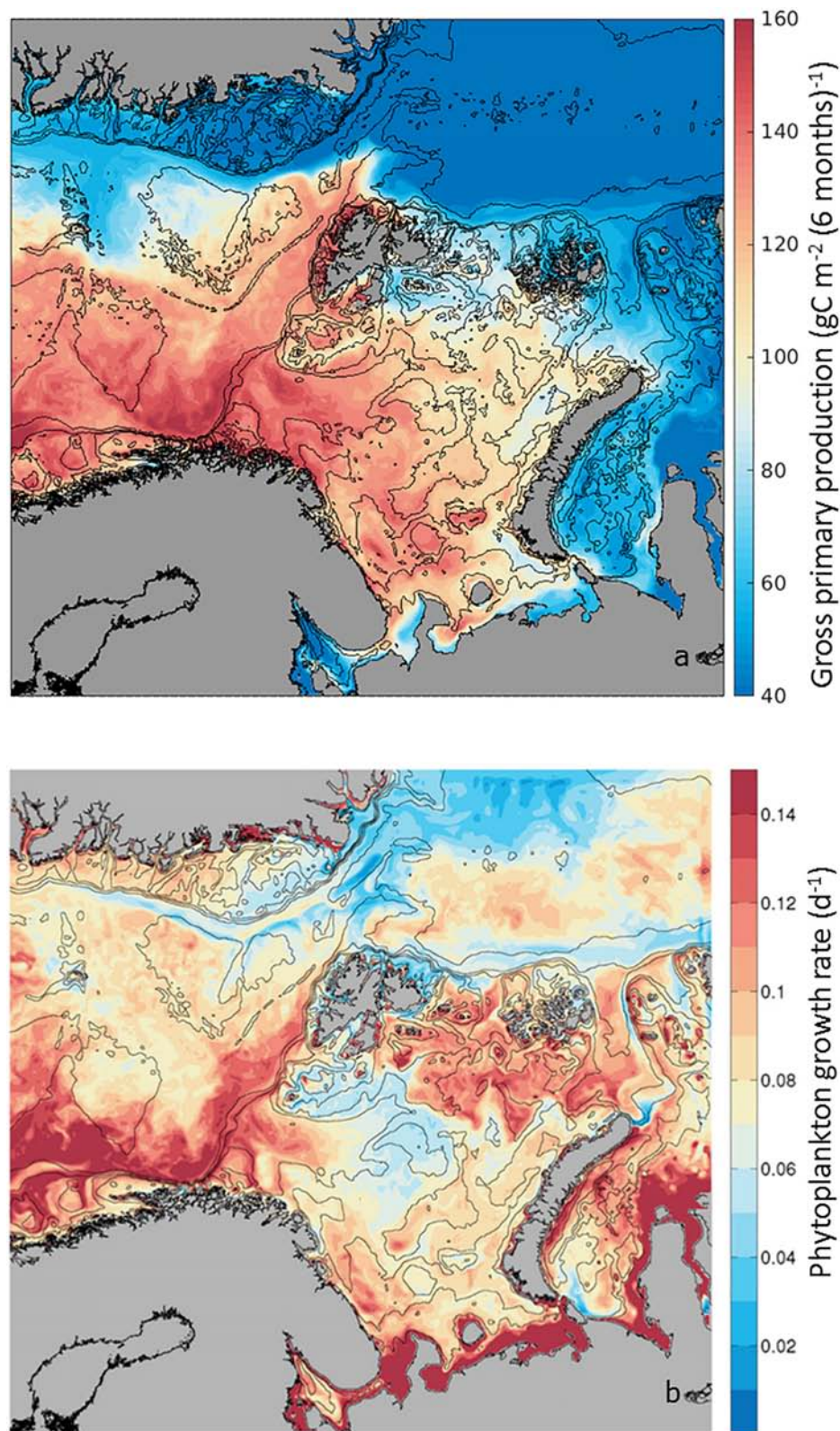


FIGURE 3 | (a) Seasonal phytoplankton Gross Primary Production (GPP) estimated as $\text{gC m}^{-2} \text{ 6mo}^{-1}$ from April to September 2012. Low production (in blue) and high production (in red), from 20 to $200 \text{ gC m}^{-2} \text{ 6mo}^{-1}$ for the study area. **(b)** Phytoplankton growth rate (d^{-1}) calculated in the SINMOD model as Net Primary Production/Biomass. Range of values from 0.02 d^{-1} to 0.14 d^{-1} . Note that in the literature (GPP-Respiration) is also considered phytoplankton primary production, also known as Net PP or NPP (e.g., Matrai et al., 2011).

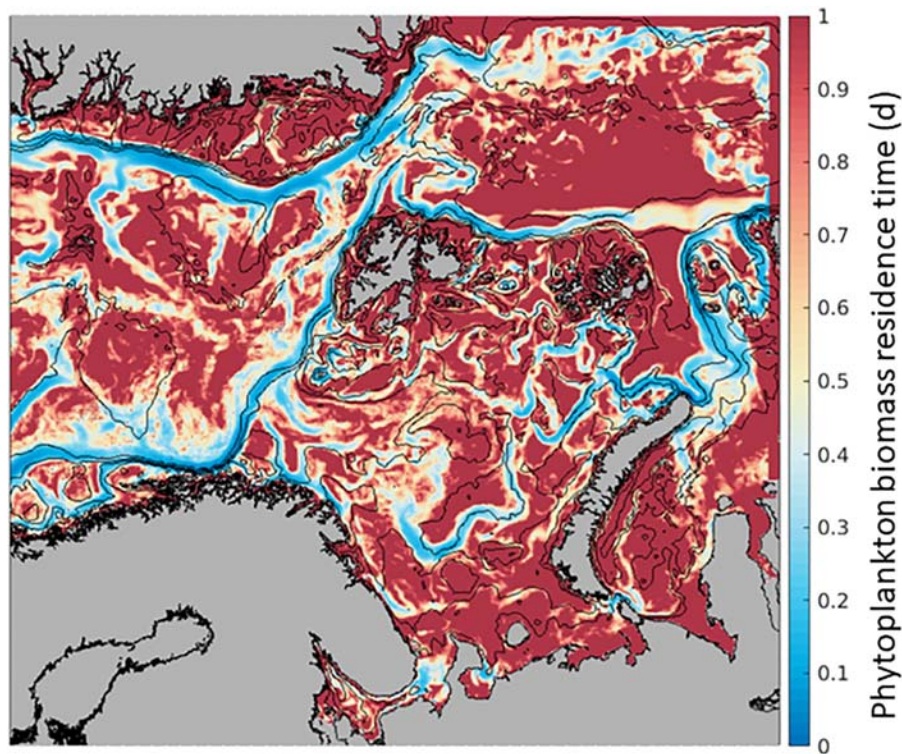


FIGURE 4 | Phytoplankton residence time (mean over 6 months, April–September, 2012) within the 4 km × 4 km × 50 m SINMOD model grid cell where lower values (blue) indicate shorter time of phytoplankton carbon biomass within the cell and higher values (red), a longer time of the phytoplankton carbon biomass within the cell. In units of days, calculated as Biomass within the grid cell/Biomass advected In.

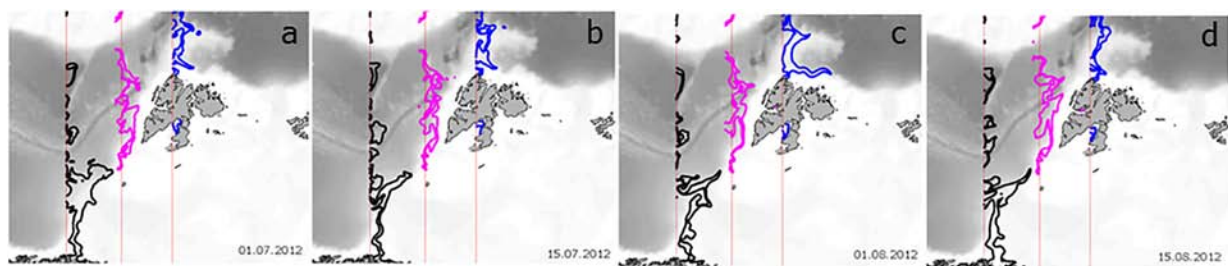


FIGURE 5 | Persistence of summer phytoplankton biomass along the Atlantic Water Inflow after GPP is turned off. The three locations are depicted with the vertical red lines (see also orange transect lines in **Figure 1b**). The thick lines depict the locations where 20% of the initial biomass is retained, after GPP = 0, from the NW Norway (black), Barents Opening (pink) and NW Svalbard (blue) for **(a)** 1 July, **(b)** 15 July, **(c)** 1 August and **(d)** 15 August 2012.

variety of fish (50–150 km) with large ocean currents being major pathways of larval dispersal (Cowen et al., 2006, 2007; Trembl et al., 2008), enriching population abundance, genetic diversity, persistence and resilience.

Importance of Advection to Primary Production

Given that Biomass at any given location can increase by transport from another location or from local processes, we calculated the ratio of phytoplankton advected (into a grid cell) per unit of *in situ* GPP (Advection-IN/GPP, **Figure 2**). This unitless ratio indicates what proportion of the biomass in any given location originated from advection ($\text{mg C m}^{-2} \text{ d}^{-1}$) and

how much from local photosynthesis ($\text{mg C m}^{-2} \text{ d}^{-1}$). When the spatial distribution of the ratio in each model grid cell is mapped, the values are always positive, indicating advection of phytoplankton is greater than, or equal to, *in situ* GPP in our region of interest (**Figure 6**). For the growth season, the ratio, that is the contribution of biomass by advection, is maximum along the currents on average, with ratios of up to 40 indicating a much larger contribution of advected phytoplankton compared to contribution of carbon by *in situ* primary production. This large contribution of biomass by advection of phytoplankton is similar in the NAC, the BO and NSv, although ratios are somewhat lower ($\sim 30\times$) in the WSC. Similarly, the East Greenland Current, west

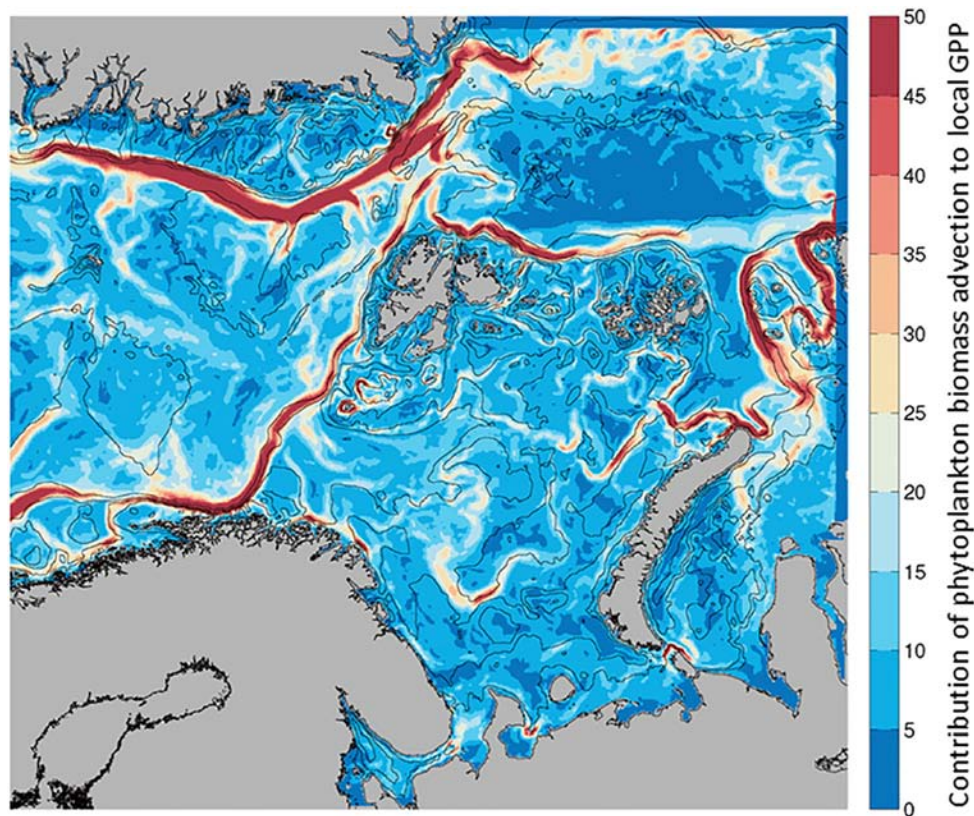


FIGURE 6 | Average contribution of Phytoplankton Biomass Advection to local Gross Primary Production estimated as Biomass advected IN/GPP (no units), from April to September. Low contribution of advection (blue) to high (red) from 0 to 50 times higher Phytoplankton Advection than local GPP.

of the Fram Strait and Greenland Sea, and the Santa Ana Trough region, located north of Nova Zemlya in the Arctic Ocean, exhibit a high contribution of advection to GPP.

The relative balance between advected and locally produced biomass at each location has a strong seasonality (**Supplementary Figure S2**). When GPP is low, as in the beginning and end of the growth season, the ratio is intermediate (10–20), as presumably advected biomass is also low. During the spring bloom (May), when *in situ* production is high, the ratio is lowest (sometimes <5), indicating the local production is closer to the advected biomass, in particular in the WSC. Advection of biomass becomes more important as local productivity lessens later in the summer. In August, the ratio is highest (~50), i.e., advection brings phytoplankton carbon from the productive regions of the south toward the north at a time when GPP is low. In the NSv, the importance of advected biomass is highest also late in the growth season, in August and September.

Phytoplankton Carbon Transported by the Atlantic Flow

If phytoplankton biomass is being advected along the AWI current, how much carbon is being transported at any given location? The transport of phytoplankton carbon biomass and water through sections along the advective pathway was calculated (Advection-OUT for biomass, **Figure 2**) and

integrated for the growth period (from April to September). We defined four sections along the AWI to examine potential changes in transport occurring from south to north (**Figure 1b**). These sections have variable lengths as they were set to be representative of all northward transport that varies along the current due to topography (Hansen et al., 2008). As there is no objective measure of water and carbon flow, these transects are meant to give a semi-quantitative estimate of south-to-north changes in fluxes.

A decrease in phytoplankton biomass transport was observed from the NAC to the NSv that can be considered a net loss of biomass toward the north (**Table 1** and **Supplementary Table S3**). In northern Norway (the southernmost section), the flow carries $2.31 \pm 1.06 \text{ Tg C } 6\text{mo}^{-1}$ of phytoplankton carbon during the growth season. As the current flows northward, $0.97 \text{ Tg C } 6\text{mo}^{-1}$ is advected eastward to the Barents Sea, whereas $1.18 \pm 0.07 \text{ Tg C } 6\text{mo}^{-1}$ is advected northward toward the south of Spitsbergen. Transport of carbon decreases to $0.76 \pm 0.19 \text{ Tg C } 6\text{mo}^{-1}$ over the Yermak Plateau, north of the Svalbard Archipelago at the entrance of the Arctic Ocean and to $0.36 \text{ Tg C } 6\text{mo}^{-1}$ along the NSv. As a result, the AWI entering the Arctic Ocean continental slope transports only a sixth of the phytoplankton biomass advected out of the NAC. Some of the simulated biomass is likely transported toward the Greenland Sea, given that in this area, AW water returns southward south of 80°N , due to the eddy-driven recirculation toward

TABLE 1 | Carbon in Tg C 6mo^{-1} (average $\pm$ standard deviation) and water (Sv) within the upper 50-m of the water column transported northwards by the Atlantic Water Inflow at different locations spanning 11 degrees of latitude from northern Norway to southern Arctic Ocean.

Location	Carbon transport (Tg C 6mo^{-1})	Carbon loss (Tg C 6mo^{-1})	Water transport (upper 50 m) (Sv)
NAC	2.31 ± 1.06	BSO 0.97	1.4
WSC	1.18 ± 0.07		0.7
NSv	0.76 ± 0.19		0.1
NBS	0.36		0.1

NAC, BSO, WSC, NSv, and NBS correspond to the Norwegian Atlantic Current, the Barents Sea Opening, the West Spitsbergen Current, the North of Svalbard and North of Barents Sea, respectively. Location of transects is depicted in Figure 1b, in orange.

the west (e.g., Marnela et al., 2013; Hattermann et al., 2016; Wekerle et al., 2017). Thus, we expect a fraction of phytoplankton carbon to enter this westerly recirculation, in agreement with the decrease of phytoplankton carbon from NW Svalbard to north of Barents Sea, from $0.76 \text{ Tg C } 6\text{mo}^{-1}$ to $0.36 \text{ Tg C } 6\text{mo}^{-1}$ (Table 1). The high seasonal variability in carbon flux in any region is attributed in part to the seasonal variability in water transport within the AWI, with summer water transport half that in winter (0.2 Sv vs. 0.4 Sv, respectively; Beszczynska-Möller et al., 2012). Furthermore, copepod grazing in the NAC is highest at the time of reproduction in early spring, affecting carbon export out of this region.

Ecosystem Carbon Balance Along the Atlantic Water Inflow

Due to the variability of advected and *in situ* production of biomass at any given location (Figure 6 and Supplementary Figure S2), what is the net carbon balance between phytoplankton production and loss rates at each location along the AWI? A positive carbon balance between these processes would indicate a net accumulation of phytoplankton biomass due to *in situ* processes while a negative one relates to net loss. If we define total Net Carbon Production (NCP) as the difference between Phytoplankton production and Phytoplankton losses ($\text{NCP} = \text{GPP} - \text{Respiration} - \text{Sinking} - \text{DOC Excretion} - \text{Grazing}$) for each location (or model grid cell, Figure 2), NCP is >0 in areas and times where *in situ* input terms are higher than the *in situ* losses (and vice versa). Areas of $\text{NCP} >0$ indicate excess carbon production that can be considered “exportable” phytoplankton biomass (Jönsson et al., 2011), either to depth or advected northward/eastward.

Mapping the NCP during the growth season along the AWI, we find phytoplankton biomass accumulation ($\sim 20 \text{ g C m}^{-2} 6\text{mo}^{-1}$) in the BSO and the northern WSC, and a net loss of phytoplankton in the NAC and over the Yarmak Plateau ($\sim -15 \text{ g C m}^{-2} 6\text{mo}^{-1}$; Figure 7 and Supplementary Table S4). A slightly positive biomass accumulation of $\sim 5 \text{ g C m}^{-2} 6\text{mo}^{-1}$ is visible in the NSv area. Looking at a time evolution of NCP from April to September (Supplementary

Figure S3), there is a strong seasonal signal for NCP in NW Svalbard that is dominated by the spring bloom in May. In June, the NAC and the BO are dominated by carbon losses; nonetheless, the WSC remains productive overall. By the end of the summer season, the whole region has become dominated by net carbon losses, indicating higher consumption than production. The overall seasonal signal west of Svalbard (Figure 7) is positive due to the high NCP in May and June that is not compensated by *in situ* losses later in the season.

DISCUSSION

A major question in the Arctic region concerns the changes in the Arctic Seas and their effect on the connectivity with the Central Arctic Ocean. The most active of these connections is the AWI from the North Atlantic to the Nansen Basin, an eastern boundary current well known for bringing heat and nutrients to high latitudes (e.g., Dickson et al., 2008 and refs. therein, Hofmann et al., 2011). Water masses and their biological and chemical constituents advected in eastern boundary currents such as the AWI are subject to transformation along their transit from temperate to polar waters (Saloranta and Haugan, 2004; Longhurst, 2010). We can expect local biological processes to take place at every location, through photosynthesis (bottom-up processes) and the interactions of the food web components (top-down processes). Furthermore, phytoplankton are exposed to ever changing environmental conditions, as light and nutrients change with latitude (Torres-Valdés et al., 2013). The series of experiments performed with the SINMOD model in this study provides insights into the transformation of the phytoplankton biomass from Northern Norway to the entrance to the Arctic Ocean and the role of advection for phytoplankton productivity and ecosystem processes along this pathway.

The year 2012 was ideal to perform the model experiments for two main reasons: first, it was a year of unusually low sea-ice extent in the Arctic Ocean, providing a glimpse of future conditions as sea ice extent continues to decline (Polyakov et al., 2017; Stroeve and Notz, 2018). Second, there is interest in understanding ecological processes in the NSv area, at the entrance of the AWI into the Arctic Ocean, particularly with respect to the potential development of cod fisheries in this region (Haug et al., 2017). Conditions observed in 2012 reflected the open-water fraction of this northern region, particularly during springtime when sea ice drift normally covers the northern Fram Strait (Lind et al., 2018). In this study, we address the central question: how are primary production processes affected by advection of phytoplankton carbon in the AWI and what are the consequences for the pelagic ecosystem? As all variables and processes from the model are in units of phytoplankton carbon, we can infer answers to these questions.

At the entrance of the Arctic Ocean, and in most Arctic Seas, sea ice edge blooms are considered critical to annual productivity (e.g., Sakshaug, 1993; Carmack and Wassmann, 2006; Wassmann and Reigstad, 2011). Sea ice retreat in NSv is predicted to regionally increase GPP (Slagstad et al., 2015), and longer ice-free periods have increased total Arctic productivity by 47%

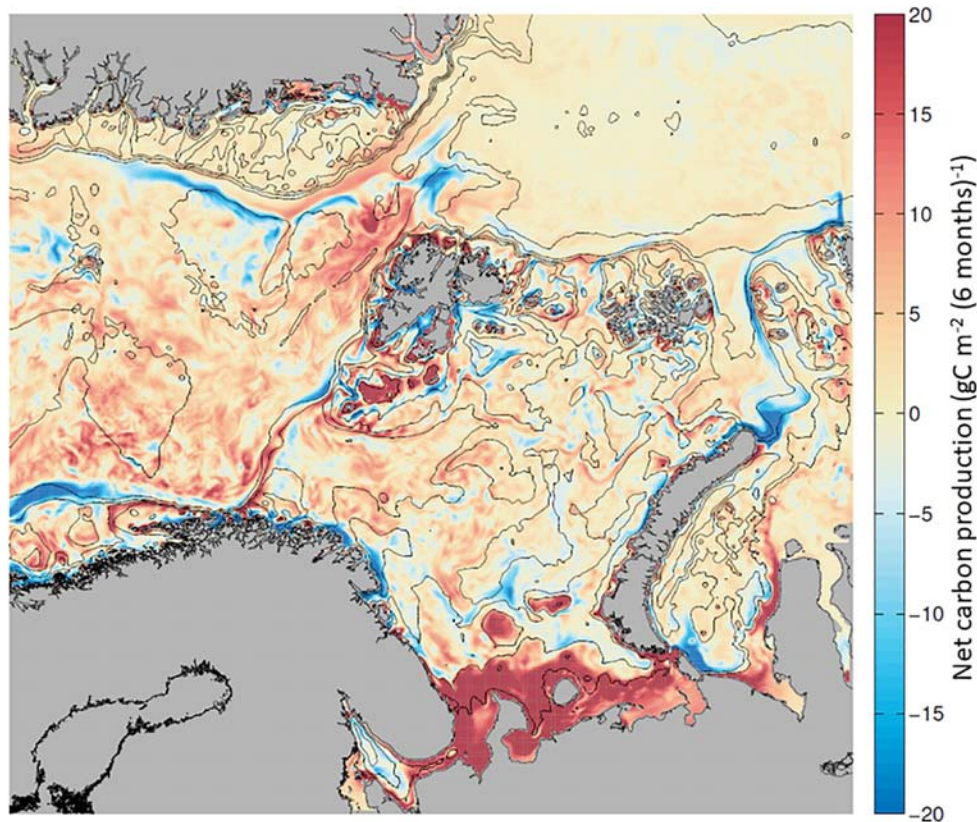


FIGURE 7 | Net carbon production (NCP), calculated as the balance between *in situ* production (GPP) and *in situ* carbon losses (respiration, DOC excretion, sinking and grazing), calculated for each grid cell and mapped. Positive NCP (in red) and net carbon losses (in blue) from +20 to $-20 \text{ g C m}^{-2} \text{ 6mo}^{-1}$, between April and September 2012.

between 1997 and 2015 (estimated from remote sensing and close to $\text{NPP} = \text{GPP} - \text{Respiration}$, as in **Figure 2**; Kahru et al., 2016). Advection of phytoplankton (Carbon Transport, **Table 1**) along the AWI is expected to have a positive effect on GPP rates in ice-free waters. Results from this study suggest a $\sim 100\%$ GPP increase in the WSC. For example, the waters west of Svalbard influenced by the AWI produce $\sim 120 \text{ g C m}^{-2} \text{ yr}^{-1}$ while waters of the Greenland Sea toward the west only produce $\sim 60\text{--}80 \text{ g C m}^{-2} \text{ yr}^{-1}$ (**Figure 3a**). As the transport of phytoplankton arrives to the ice edge in the WSC or NSv, it is expected to enhance the ice-edge blooms as well.

Integrated primary production rates in open waters of the Arctic Ocean, estimated from remote sensing and closer to Net PP (or $\text{GPP} - \text{Respiration}$ in **Figure 2**), are approximately $100 \text{ g C m}^{-2} \text{ yr}^{-1}$ (Arrigo and van Dijken, 2015; IOCCG, 2015), with production supported by winter nitrogen concentrations of $5\text{--}12 \mu\text{M NO}_3$ (Codispoti et al., 2013). Known standing stocks of available nitrogen in the Arctic are not enough to support the annual Arctic Ocean production (Tremblay et al., 2015), meaning additional sources, either from advection or from diffusive processes, are required. Diffusion of nitrate from deep waters through the pycnocline has recently been estimated at $0.2\text{--}2.0 \text{ mmol N m}^{-2} \text{ d}^{-1}$ in the NSv area during the growth season, equivalent to an excess 1.3 nM per day in a

15-m summer mixed layer (Randelhoff et al., 2015, 2018). This diffusive nitrate input is expected to support $31 \text{ g C m}^{-2} \text{ yr}^{-1}$ (Randelhoff et al., 2015). However, deep-sea O_2 demand is higher than can be supported by local GPP (Boetius et al., 2013). This imbalance between supply and demand suggests organic carbon is advected into the Central Arctic Ocean. Similarly, food web modeling concludes that the Central Arctic Ocean is heterotrophic, with organic carbon being imported into the system to meet zooplankton and fish needs (Olli et al., 2007). Compared to $127\text{--}136 \text{ Tg C yr}^{-1}$ photosynthesized each year for the Nordic Seas/Nansen Basin and Barents Sea regions, as defined by Arrigo and van Dijken (2015; but see IOCCG, 2015), the SINMOD simulations suggest an advection via the N. Atlantic into the Arctic Ocean of phytoplankton carbon of $0.76 \text{ Tg C yr}^{-1}$ (**Table 1**). This is a conservative estimate, considering it does not account for winter carbon advection.

South-to-North Phytoplankton Carbon Gradient

Similar to physical and chemical seawater properties, phytoplankton abundance and physiology along the AWI present a gradient from South to North. The waters of the AWI cool and freshen on their transit north. However, due to their

fast movement, they maintain higher heat and salt content than surrounding waters of the Norwegian and Greenland Seas (Lind and Ingvaldsen, 2012). Similarly, nutrients are imported from the North Atlantic and are transported north (Carmack and Wassmann, 2006). It is now known that zooplankton from temperate oceans are also advected northward, specifically the copepod *C. finmarchicus* (Wassmann et al., 2015, 2019). However, phytoplankton and zooplankton carbon have an overall net loss toward the north, albeit with regional variability (**Figure 7** and **Supplementary Figure S3**), indicating that on average, in AWI waters, carbon losses exceed production northwards (**Table 1**, Ellingsen et al., 2008; Weydmann et al., 2014).

A small percentage of the biomass generated in the entire Norwegian Sea, $2.31 \text{ Tg C (6mo)}^{-1}$ (**Table 1**), or 2.4% of the $78 \text{ Tg C (6mo)}^{-1}$ produced (as per SINMOD, data not shown), is free to be advected north. From there, the phytoplankton biomass decreases to the entrance of the Arctic Ocean by 85% to 0.76 Tg C . This decrease can be attributed to two concurrent effects: primary production rates (GPP) diminish northward as irradiance decreases (**Figure 3a**) while grazing by macro- and microzooplankton remains more constant (Banse, 1995; Wassmann et al., 2010). High microzooplankton grazing in the AWI has been measured in NSv where a large portion of local primary production is consumed *in situ* (Lavrentyev et al., 2019). Other loss factors contribute to carbon decrease, such as phytoplankton respiration that increases toward the north, where respiration in the summer, during 24-h light, was found to be 10-fold higher than in the dark (Mesa et al., 2017).

There is an abrupt change in simulated production-related processes in the AWI as it enters the Arctic Ocean into NSv (**Figure 3a**). Although the modified Atlantic water that can be found along the Arctic shelf break maintains higher production than surrounding waters, NSv primary production is 30% lower in relation to the WSC. The decrease in primary productivity at this interface is attributed to higher concentrations of sea ice, decreased light availability and increased stratification by meltwater annually, resulting in less nutrient availability after the spring bloom (Harrison et al., 2013; Tremblay et al., 2015). In contrast, the WSC features deep mixing in winter bringing up nutrients to surface waters (Appen et al., 2016). When these waters are affected by sea ice cover and later by meltwater input, increased stratification limits phytoplankton access to the deep nutrients only after the spring bloom. In the absence of sea ice, the stratification is less pronounced, enhancing access to deep nutrients. Lower stratification can increase diffusion of nutrients through the thermocline by ten-fold, from 0.1 to $2.0 \text{ mmol NO}_3 \text{ m}^{-2} \text{ d}^{-1}$ (Randelhoff et al., 2016, 2017). These processes are similar to the difference in stratification affecting productivity in ice-covered northern versus ice-free southern waters of the Barents Sea (Rey and Loeng, 1985).

Increased GPP in the WSC relative to the Fram Strait approximates trends observed for secondary production (**Supplementary Figure S4a**, Wassmann et al., 2010). This high productivity results in a net positive annual carbon production, or $\sim 15 \text{ g C m}^{-2} \text{ yr}^{-1}$ (or $\sim 12.5\%$), that is available for transport elsewhere in spring and summer (**Figure 7**).

Along with $\sim 2/3$ of the waters from the WSC recycling into the Fram Strait (Hattermann et al., 2016; Wekerle et al., 2017), the remaining phytoplankton carbon ($\sim 5 \text{ g C m}^2 \text{ yr}^{-1}$) is likely transported east, toward the Arctic Ocean, via a branch north of the Yermak Plateau or directly into the slope waters of NSv (**Figure 6**; Beszczynska-Möller et al., 2012). This advective source adds up to $0.76 \text{ Tg C yr}^{-1}$ (**Table 1**) of live phytoplankton cells that can sustain additional GPP. With an efficiency of $\sim 0.5 \text{ mg C (mg chl a}^{-1}) \text{ h}^{-1}$ for the phytoplankton in the euphotic zone (Vernet et al., 1998) and an average seasonal C:chl a ratio of ~ 53 (Wassmann et al., 2006; Vernet et al., 2017; Paulsen et al., 2018), $23.1 \text{ Tg C yr}^{-1}$ are supported by advected phytoplankton in the NSv, i.e., the same order of magnitude of the simulated annual GPP in NSv (60 g C yr^{-1} ; **Figure 3a**) or the 30 g C yr^{-1} estimated from nitrate input through the summer pycnocline (Randelhoff et al., 2015). This estimate underlines the importance of advection to *in situ* production (**Figure 4**). However, any calculation of this type is sensitive to the average parameters extracted from the literature and deserves further study (Lind et al., 2018).

Effect of Advection on Phytoplankton Ecology

The AWI transports phytoplankton biomass from a southern location to a more northern one. Upon arrival, the biomass can synthesize new carbon in response to local conditions of light and nutrient availability (i.e., GPP). If we consider bulk quantities, the transport along the current is such that at least 20% of the biomass is maintained by advection for $75 - 250 \text{ km}$ (**Figure 5**). With a growth rate of 0.1 d^{-1} or a doubling time of 7 days (**Figure 3b**) and a Residence Time of 0.2 days (**Figure 4**), an average phytoplankton cell takes ~ 1 day to travel 20 km (equivalent to five model grid boxes), which translates into a cell division cycle within 140 km (Nelson and Brand, 1979). Hence, the current can disperse phytoplankton beyond its location of growth and move biomass to areas of lower local primary production, increasing productivity toward the north.

Adding to the mechanical advection of cells northward, the AWI provides an environment that enhances phytoplankton growth and physiology. Higher growth rates are observed within the current, in comparison to areas of same latitude toward the west. Growth in the AWI can reach $\sim 0.14 \text{ d}^{-1}$, decreasing to $\sim 0.08 \text{ d}^{-1}$ in the Greenland Sea (**Figure 3b**). Several factors could account for this enhancement. Temperatures in the AWI are higher, increasing metabolism (Eppley, 1972; Huot et al., 2013; Chen, 2015). Enhanced grazing, associated with advected microzooplankton and *C. finmarchicus* (Gluchowska et al., 2017), is also known to benefit phytoplankton growth, through nutrient recycling and mortality of unhealthy cells (Michel et al., 2015).

Enhanced physiology affects the phenology of the primary production. Two main regions along the AWI show that the timing of phytoplankton growth is altered in such a way as to result in a longer productive season: the spring (May) bloom starts earlier in the NAC in comparison to the Norwegian and Greenland Seas where peak productivity is delayed until June

(**Supplementary Figure S1**). In the absence of sea ice, early productivity implies a better use of light within the current, though it is likely that the NAC may replenish its nutrient load sooner due to its shallower nature and proximity to coastal processes (Sætre, 2007; Pacariz et al., 2016; but see Johnson et al., 2013). In addition, advection, by bringing carbon to the north, enables productivity (GPP) in the WSC as late as September, extending the growth season. This results in better use of the seasonally available nutrients contributing to the overall annual GPP.

Carbon Balance Along the Atlantic Water Inflow

Overall, there is no consistency of NCP in space and time along the AWI, suggesting the timing of the different components of the system within is not synchronous. Considering the AWI from western Norway to the Arctic Ocean, we mentioned before that NCP defines three main regions: the NAC extending to the southern BO, the WSC including the northern portion of the BO and the waters in NSv. The decrease in primary productivity toward the north (**Figure 3a**) is likely determined by bottom-up controls of shortening day length and mixed-layer depth dynamics, as mentioned above in section “South-to-North Phytoplankton Carbon Gradient,” as well as by decreasing grazing pressure, as zooplankton biomass experiences losses toward the north (**Supplementary Figure S4**, Ellingsen et al., 2008; see section “Input of Carbon to the Arctic Ocean”). For example, NW of Svalbard, the WSC current features an accumulation of carbon as the phytoplankton input exceeds the loss terms for May and June, resulting in a NCP >0 for the growth season (**Figure 7** and **Supplementary Figure S3**). Similarly, the GPP in the NAC is high ($120 \text{ g C m}^{-2} \text{ yr}^{-1}$, **Figure 3a**), resulting in another region with net harvestable phytoplankton biomass in the system. Seasonally, the NCP shows variability in all the regions; it is most variable in the NAC, with two periods of negative NCP, one in May-beginning of June and one in July-August, following periods of positive NCP (**Figure 8** and **Supplementary Figure S3**). The WSC shows similar dynamics on NCP, with a lag of ~ 1 month. In contrast, NSv switches from a positive NCP in mid-June to negative for the remainder of the growth season.

The NCP, expressed as the carbon balance between GPP and loss terms for each location (Eq.1, **Figure 2**), and mapped in **Figure 7** and **Supplementary Figure S3**, can also be expressed in terms of advection. If $dB/dt = 0$, and if the system is assumed in balance for 1 day, then any excess production will generate phytoplankton biomass that can then be advected out of a given location. In this way, the net advection north, calculated as the difference between import and export of carbon to/from a location, is equal to the NCP. If advection of phytoplankton provides 5–50 times more biomass than local production along the AWI (**Figure 4**), this import is maximum at times of low GPP (see section “South-to-North Phytoplankton Carbon Gradient”). The AWI water flow, in its seasonal variability, decreases by half in summer, at the time of highest GPP (Beszczynska-Möller et al., 2012). In comparison, the seasonal variability of GPP

is 1,000-fold, from an average $<3 \text{ mg C m}^{-2} \text{ d}^{-1}$ in winter to $>1 \text{ g C m}^{-2} \text{ d}^{-1}$ during the spring bloom (Vernet et al., 1998) and is expected to dominate the phytoplankton advection. During early spring and fall, when GPP rates are intermediate, the current flow must have a disproportionate role in moving phytoplankton biomass from the NAC toward the north, not only to feed the zooplankton being advected, but also for birds, benthic filter feeders and fishes (Kwasniewski et al., 2012). Furthermore, advected phytoplankton carbon can provide a more constant supply, reducing any short-term variability of local productivity. In summary, copepod biomass in northern latitudes, such as the NSv and food availability to benthic feeders and fish populations in western and northern waters of the Svalbard Archipelago, are partly maintained by the advection of phytoplankton biomass that can be consumed directly, or by supporting increased *in situ* GPP resulting from this advection of biomass.

Input of Carbon to the Arctic Ocean

Phytoplankton production is dependent on environmental factors and biomass concentration (e.g., light and nutrient availability, sea ice conditions and the amount of chlorophyll *a* available to photosynthesize, Dierssen et al., 2000) while zooplankton abundance and physiology are more dependent on internal population dynamics, such as periods of reproduction and diapause (Basedow et al., 2018). These zooplankton processes, in turn, control grazing pressure on phytoplankton, influencing B and GPP spatial and temporal variability (**Figure 3** and **Supplementary Figure S4**).

Accounting for the dynamics and life history of *C. finmarchicus*, the most abundant grazer in the AWI, can also help explain the variability observed in NCP (**Figure 7**). *C. finmarchicus* is a temperate copepod that can be transported northward from the North Atlantic (Wassmann et al., 2015; Basedow et al., 2018). The southern NAC contains overwintering *C. finmarchicus* that are ready to start grazing at the onset of light in April followed by GPP initiation (Hirche, 1996). The grazing pressure generates a negative NCP (blue in **Supplementary Figure S3**). The larvae and adults are moved north with the current (Wassmann et al., 2019) and maintain a high grazing pressure (**Supplementary Figure S4a**), resulting in negative NCP in NW Norway and southern BO in June (**Supplementary Figure S3**). Along the NAC, grazing pressure from *C. finmarchicus* continues to consume available phytoplankton carbon (**Figure 8** and **Supplementary Figure S3**), despite the negative NCP concurrent with the highest GPP rates in May and June. Spatially, 50% of the simulated zooplankton biomass in the WSC is reported as found in NSv where the cohort from the southern NAC enters diapause 6 months later, in September (Wassmann et al., 2019). Despite this loss, the modified AWI waters arriving to the Arctic shelf break in NSv are shown to have twice the zooplankton biomass than in the Nansen Basin, and hence can exert twice the grazing pressure on GPP, resulting in twice the secondary production (**Supplementary Figure S4b**). The presence of *C. glacialis*, an Arctic copepod, is expected to start

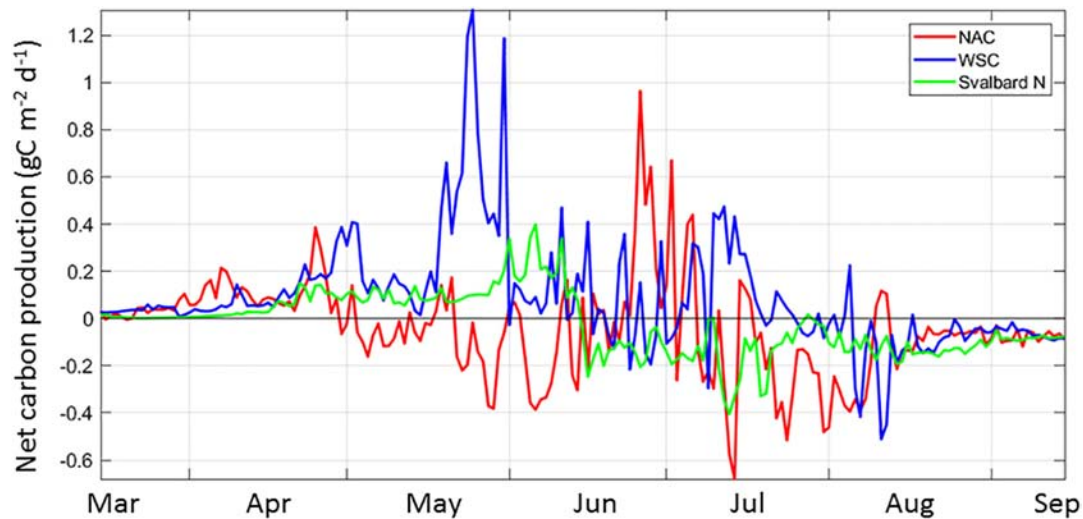


FIGURE 8 | The spatial and temporal variability of Net Carbon Production (NCP) from March to September for three regions along the Atlantic Water Inflow: the Norwegian Atlantic Current (NAC, red), the West Spitsbergen Current (WSC, blue) and North of Svalbard (Svalbard N or NSv, green) for the year 2012. Representative locations for these three regions are indicated in **Figure 1b**.

exerting grazing pressure as the cooler AWI waters reach NSv (Svensen et al., 2019). Similar to *C. finmarchicus*, this species also depends on the spring bloom, now associated to the ice edge, to reproduce and develop (Søreide et al., 2010; Daase et al., 2013).

As already indicated, phytoplankton biomass accumulates when GPP exceeds grazing, establishing a positive NCP, as other loss terms in the model are calculated as percentage of GPP (Banse, 1995; Wassmann et al., 2006). In this way, NCP in NSv waters becomes positive in mid-April, when the spring diatom bloom occurs (**Figure 8**). At this time of the year, microzooplankton are not able to consume all diatoms (Lavrentyev et al., 2019). In June, grazing increases. Grazing by *C. finmarchicus* is 13%, by *C. glacialis* is 2%, and 20% by ciliates (Ellingsen et al., 2008), in agreement with recent field data (Reigstad et al., pers. comm., Paulsen et al., 2018; Lavrentyev et al., 2019; Sanz-Martin et al., 2019; Svensen et al., 2019). Such processes result in an accumulation of phytoplankton biomass in the NSv area until mid-June, when the new copepod cohort arrives. By July, and further into August and September, grazing exceeds GPP and generates a net carbon loss from mid-June to the end of phytoplankton growth season.

Despite their proximity, the AWI waters in northern WSC present a contrasting scenario to the NSv region, for both GPP (**Figure 3a**) and NCP (**Figure 7**), as discussed earlier. As the waters cool in their transit north, we can expect *C. finmarchicus* grazing pressure to decrease in relation to GPP due to a temperature-controlled delay in grazing pressure, combined with the diminishing zooplankton biomass. In northern WSC, the net loss starts in July (**Supplementary Figure S3**), after the arrival of the new *C. finmarchicus* cohort (Kosobokova and Hopcroft, 2010). In this region, *C. glacialis* abundance is still relatively low, estimated at 100-fold lower than *C. finmarchicus*

(Wassmann et al., 2019). This scenario is similar to the decoupling between primary and secondary production observed in advected waters of the Chukchi Sea, where low temperatures delay the peak of secondary production (Grebmeier et al., 2015). A decrease in grazing pressure, allowing for GPP to exceed the loss terms for phytoplankton, may also result from *C. finmarchicus* ingesting microzooplankton, such that photosynthesizing flagellates can bloom, as observed in field and mesocosm experiments (Verity et al., 1999; Irigoien et al., 2005; Löder et al., 2011).

Advective Processes in the Study of Arctic Ocean Primary Production

Most of the estimates of primary production, either from field observations, remote sensing, or estimates from models (e.g., SINMOD **Figure 3**), provide *in situ* rates that translate into new biomass becoming available for consumption or dispersal. These approaches do not differentiate between the carbon produced locally and the carbon brought in by, or lost to, a current, although alternative methods to account for the effect of advection are becoming available (Jönsson et al., 2011; de Verneil and Franks, 2015). By differentiating between biomass advected into a location and the rate of local production, we have shown that the bulk of the simulated production in the AWI is maintained by advection (**Figure 7**). By defining new variables based on model output, we provide first-time evidence that in absence of advection, local production would be decreased by half in this region. The importance of the strength of the AWI cannot be discounted in assessments of sub-Arctic Ocean health and productivity.

The benefit of the AWI flow for primary production in the eastern Fram Strait is expressed over different time scales. GPP

rates are higher in the WSC on annual time scales where, as noted before, the production is higher than in neighboring Greenland Sea (Figure 3) and its importance increases with latitude. However, the enhanced GPP by the AWI flow is more noticeable on (sub-annual) seasonal time scales, with maximum effect in early spring and late summer (see April and August in Supplementary Figure S1), due mainly to advective processes before and after the peak in June productivity (Supplementary Figure S2).

The entrainment of phytoplankton in the AWI facilitates its dispersal and increases its connectivity between sub-Arctic and Arctic regions (or domains, Wassmann et al., 2015; Moore et al., 2018), as shown for larval stages elsewhere (Cowen et al., 2006). Advection is one of the main processes involved in connectivity (Tremblé et al., 2008). Defining ocean connectivity as the probability that water parcels from one location have advected to another site over a given time interval (Mitarai et al., 2009), this study has shown higher connectivity, expressed as shorter residence time, along the AWI than in surrounding waters of the Greenland Sea (Figure 5). The global surface ocean is emerging as highly interconnected with waters from the Atlantic Ocean taking a median time of 6.4 ± 2.2 years to reach the Arctic (Jönsson and Watson, 2016). Along a main oceanic current such as the AWI, the transport time from NAC to NSv is shortened considerably to a few months, as indicated by the consumption of the local NSv productivity by the arrival of the new *C. finmarchicus* cohort in mid-July (Figure 8; Svensen et al., 2019; Wassmann et al., 2019). In this way, this study provides a first glimpse of the degree of interconnectivity from the Norwegian Sea to the Arctic Ocean through the balance between local processes and phytoplankton seasonal evolution driven principally by advection in this sub-Arctic region.

The degree of connectivity can also be assessed in relation to a species growth rate, which can be considered an intrinsic organismal residence time within a population. In the case of the AWI, phytoplankton persistence of up to 250 km (Figure 6), combined with a simulated growth rate of 0.1 d^{-1} (Figure 4), suggests about two cell cycles are necessary to travel that distance (see also section “Effect of Advection on Phytoplankton Ecology”). In the $\sim 2,000$ km from NAC to Svalbard (Wassmann et al., 2019), this translates to approximately ~ 16 cell divisions from April to July. For longer lived organisms, such as *C. finmarchicus*, the cohort reaching NSv in mid-July originated in April in the NAC (Wassmann et al., 2019) and is equivalent to one reproductive cycle. The difference in phytoplankton vs. zooplankton residence times in the AWI suggests that phytoplankton can have an expanded ability to adapt when transported from temperate to Arctic waters, not only as a result of their increased plasticity in relation to zooplankton but also by having more opportunities to evolve, i.e., 16 times more. Thus, we can predict higher resiliency in phytoplankton (Pancic et al., 2015).

Changes in climate are further expected to affect dispersal and connectivity among locations (Lett et al., 2010). For phytoplankton, enhanced current temperature can increase

specific growth rates (Figure 4), shortening the time of dispersal per cell by advection, or a decrease in Persistence (Figure 6); this would result in higher *in situ* GPP in relation to advection (Figure 7). Other factors could compensate, such as the survival of temperate zooplankton species reaching and reproducing in northern latitudes, as seen for the amphipod *Thermistos compressa* (Schröter et al., 2019) and *C. finmarchicus* copepodites (Gluchowska et al., 2017), or increasing zooplankton grazing rate (Lett et al., 2010). Although no trends in zooplankton abundance or biomass are recorded for the surface waters (0–60 m) of the WSC in a 14-year time series (Carstensen et al., 2019), *C. finmarchicus* becomes an increasing proportion of zooplankton biomass reaching the Barents Sea in warmer years (Gluchowska et al., 2017). Expansion of North Atlantic temperate phytoplankton species into the Arctic will be enhanced by the warming AWI flow (Polyakov et al., 2012), as a highway facilitating transport into higher latitudes within seasonal timescales, as observed in 2014 by the presence of unusually abundant *Synechococcus* sp. in NSv during summer (Paulsen et al., 2016).

CONCLUSION

Several interesting conclusions have arisen from this modeling study, indicating advection contributes to phytoplankton biomass and production in the North Svalbard area and to the transport of autotrophic plankton from the northern Norway coastal region to the gateway to the Arctic Ocean, supporting the importance of field studies to parameterize and test modeling predictions in this transition region (Slagstad et al., 2015).

Specifically:

1. Advection of phytoplankton provides 5–50 times more biomass than local production along the Atlantic Water Inflow, suggesting the planktonic foodweb in the area is constantly fed during the growth season.
2. A high phytoplankton growth rate is maintained along the AWI, in comparison to open ocean regions west of the WSC, suggesting that the physical, chemical and biological processes within the current provide an environment for healthy phytoplankton.
3. Overall, there is no consistency of NCP in space and time along the AWI, suggesting the timing of the different components of the system within the current is not synchronous. Variability in zooplankton grazing is the most likely source of variability in NCP.
4. Advection extends phytoplankton biomass further north at the end of the summer, i.e., August and September, likely initiating blooms toward the north, and providing food for local benthic and fish populations in polar and sub-polar ecosystems.
5. The model predicts net import of phytoplankton biomass into the Arctic Ocean as it is produced in the system west of Svalbard. $\sim 15 \text{ g C m}^{-2} (6\text{mo})^{-1}$ (or $\sim 12.5\%$) of GPP can be exported from the WSC annually, either to the Arctic or recirculated.

AUTHOR CONTRIBUTIONS

MV organized the project, participated in experimental design, interpreted the results, and wrote the manuscript. IE was in charge of model results, contributed with experimental design, interpreted the results and revised the manuscript. LS contributed with experimental design, interpreted the results, and revised the manuscript. DS revised model results, contributed with experimental design, and interpreted the results. MC interpreted the results and revised the manuscript. PM interpreted the results, revised and edited the manuscript and figures.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: <https://www.frontiersin.org/articles/10.3389/fmars.2019.00583/full#supplementary-material>

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Microbial Communities in the East and West Fram Strait During Sea Ice Melting Season

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Climate models project that the Arctic Ocean may experience ice-free summers by the second half of this century. This may have severe repercussions on phytoplankton bloom dynamics and the associated cycling of carbon in surface waters. We currently lack baseline knowledge of the seasonal dynamics of Arctic microbial communities, which is needed in order to better estimate the effects of such changes on ecosystem functioning. Here we present a comparative study of polar summer microbial communities in the ice-free (eastern) and ice-covered (western) hydrographic regimes at the LTER HAUSGARTEN in Fram Strait, the main gateway between the Arctic and North Atlantic Oceans. Based on measured and modeled biogeochemical parameters, we tentatively identified two different ecosystem states (i.e., different phytoplankton bloom stages) in the distinct regions. Using Illumina tag-sequencing, we determined the community composition of both free-living and particle-associated bacteria as well as microbial eukaryotes in the photic layer. Despite substantial horizontal mixing by eddies in Fram Strait, pelagic microbial communities showed distinct differences between the two regimes, with a proposed early spring (pre-bloom) community in the ice-covered western regime (with higher representation of SAR11, SAR202, SAR406 and eukaryotic MALVs) and a community indicative of late summer conditions (post-bloom) in the ice-free eastern regime (with higher representation of *Flavobacteria*, *Gammaproteobacteria* and eukaryotic heterotrophs). Co-occurrence networks revealed specific taxon-taxon associations between bacterial and eukaryotic taxa in the two regions. Our results suggest that the predicted changes in sea ice cover and phytoplankton bloom dynamics will have a strong impact on bacterial community dynamics and potentially on biogeochemical cycles in this region.

Keywords: Arctic Ocean, phytoplankton bloom, microbial interactions, bacterioplankton, network analysis

INTRODUCTION

In recent decades, Arctic warming has resulted in remarkable environmental changes in the Arctic Ocean, and the region is warming much faster than the global mean rate (Dobricic et al., 2016; Sun et al., 2016). Arctic sea ice has declined by approximately 50% since the late 1950s, and its extent is shrinking at approximately 10% per decade since the late 1990s (Kwok and Rothrock, 2009;

Peng and Meier, 2017). Current predictions indicate that the Arctic Ocean may experience ice-free summers by the second half of this century (Polyakov et al., 2017). In addition, recent observations suggest increasing temperatures of the Atlantic water inflow (Walczowski et al., 2017). The combination of these environmental changes results in weakened stratification of the water column and increased vertical mixing of the deep Atlantic core water, a process also termed 'Atlantification' (Polyakov et al., 2017). Based on these observations, the general agreement is that the Arctic Ocean is currently in a transitional phase toward warmer conditions (Polyakov et al., 2005, 2017; Dmitrenko et al., 2008).

The 450 km wide Fram Strait is the only deep gateway to the Arctic Ocean, and has two distinct hydrographic regimes. In the eastern part of Fram Strait, the northward flowing West Spitsbergen Current (WSC), transports relatively warm and saline Atlantic water into the Arctic Ocean (Beszczynska-Moller et al., 2012; von Appen et al., 2015). The East Greenland Current (EGC) flows southward along the Greenland shelf, transporting cold polar water and exporting approximately 90% of the Arctic sea ice to the North Atlantic (de Steur et al., 2009). These distinct water masses are separated by the East Greenland Polar Front system (Paquette et al., 1985). However, recent ocean simulation analyses show substantial horizontal mixing and exchange by eddies (Wekerle et al., 2017). Repeated summer sampling in the water column and at the seafloor of the Fram Strait, as part of the Long Term Ecological Research (LTER) site HAUSGARTEN, have revealed major ecological variations associated with anomalies of the Atlantic Water inflow (Soltwedel et al., 2016). Examples for such variations are a slow increase in phytoplankton biomass and shifts species composition which followed the Atlantic Water warming event in 2005–2007 (Nöthig et al., 2015). This included a transition from diatom to flagellate (e.g., *Phaeocystis*) dominated communities during the summer months (Nöthig et al., 2015; Engel et al., 2017). Recent model predictions showed substantial differences in carbon export following diatom- or flagellate- dominated phytoplankton blooms (Vernet et al., 2017; Wollenburg et al., 2018). Depending on timing, flagellate dominated blooms may result in increasing abundance of microzooplankton (e.g., ciliates) and a more active microbial loop, or a more rapid export in connection with ice-formed mineral precipitation. Furthermore, a year round study of physical and biogeochemical hydrography in the WSC suggested that the ongoing 'Atlantification' in the region is leading to increased pelagic primary productivity (Randelhoff et al., 2018).

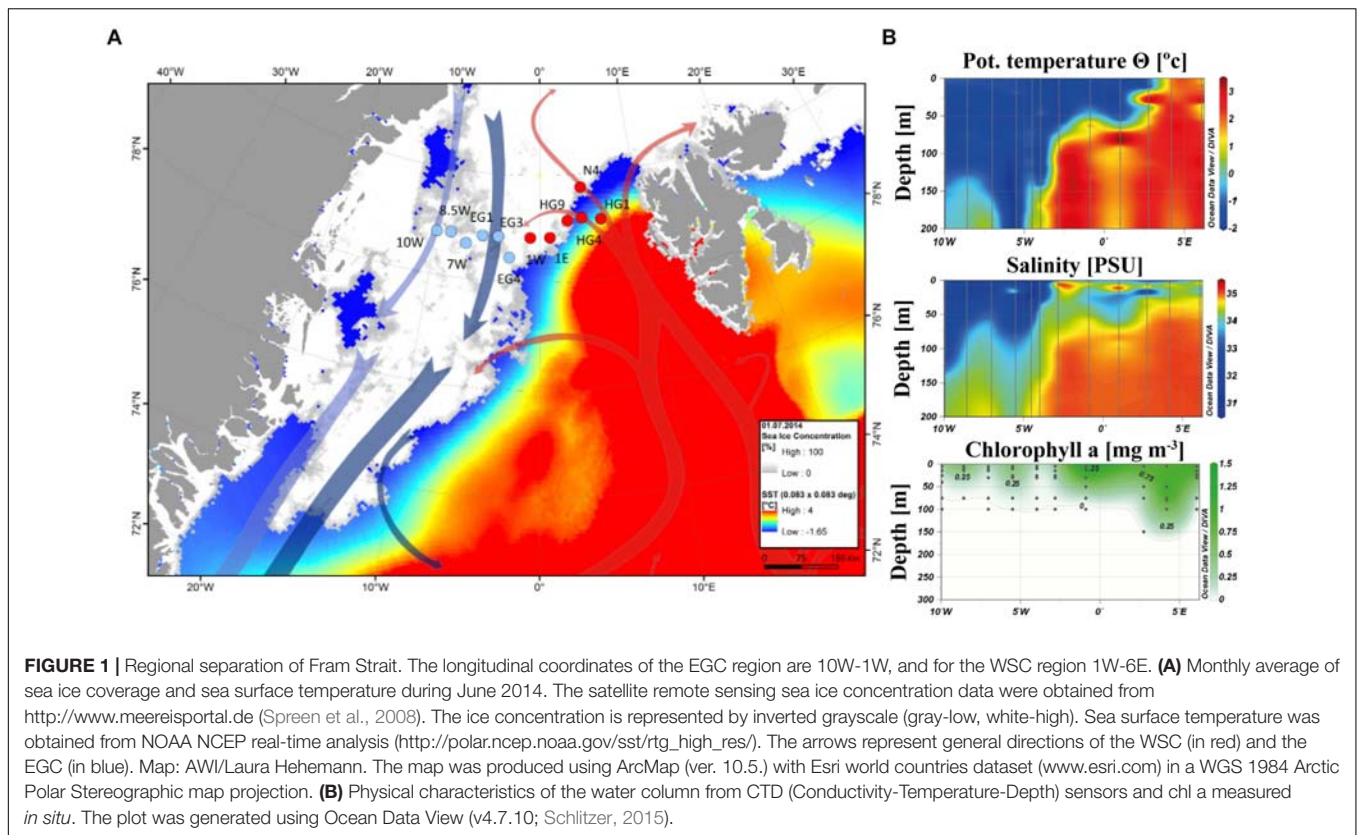
However, the harsh climatic conditions in the open Arctic Ocean during winter typically limit sampling opportunities to the Arctic summer season, so that seasonal dynamics within the pelagic ecosystem, especially in ice-covered parts of the Arctic, remain understudied (Soltwedel et al., 2013; Nöthig et al., 2015). Phytoplankton bloom dynamics may, to some extent, be monitored using remote sensing of chlorophyll *a* (chl *a*) by satellites in ice-free ocean areas, with substantial limits due to Arctic fog and the dark season (Perrette et al., 2011). However, monitoring the dynamics of heterotrophic microorganisms requires physical sampling. Wilson et al. (2017) were the first to describe changes of bacterial community

composition in the eastern Fram Strait throughout a polar year. In accordance with observations from other polar regions (Alonso-Sáez et al., 2008; Iversen and Seuthe, 2011; Ghiglione and Murray, 2012; Williams et al., 2012), their results showed that the extreme seasonality of polar marine ecosystems, with ice-covered dark winter conditions and extended irradiance in summer, leads to pronounced seasonal differences in heterotrophic bacterial communities. Winter-time bacterial communities in the upper water column showed higher phylogenetic and functional diversity compared to the summertime, with increased importance of chemolithotrophic processes (e.g., Alonso-Sáez et al., 2014; Müller et al., 2018). During late spring, the increasing irradiance and decreasing sea ice cover initiate large phytoplankton blooms, which can lead to major shifts in heterotrophic bacterial community composition.

Biological interactions among microbes are important drivers of the dynamics in pelagic microbial communities (Fuhrman et al., 2015). Specific interactions between phytoplankton and heterotrophic bacteria have been documented, many of which are based on the exchange of energy sources and metabolites, including various forms of chemical signaling (Cole, 1982; Grossart et al., 2006; Grossart and Simon, 2007; Ramanan et al., 2016). Analyses of bacterial communities co-occurring with diatoms, using advanced molecular approaches, revealed complex interspecies signaling (Amin et al., 2012). While a full characterization of such interactions requires targeted experiments under laboratory conditions, molecular methods in combination with network analyses allow us to identify potential interactions directly from environmental samples (e.g., Gilbert et al., 2012; Lima-Mendez et al., 2015; Peura et al., 2015; Milici et al., 2016; Chafee et al., 2018).

One such interaction with relevance to the proportion of pelagic recycling versus carbon export is the physical association of bacteria with plankton detritus. Pelagic bacteria have different strategies to tap into the detritus pool, free-living in the water column or associated with particulate matter (Stocker, 2012). Previous studies have revealed strong differences between potential associations of free-living (FL) and particle-associated (PA) bacteria with microbial eukaryotes (Lima-Mendez et al., 2015; Milici et al., 2016). While the FL fraction is often dominated by cosmopolitan oligotrophic bacteria that rely on the availability of organic matter in the dissolved fraction (Morris et al., 2012; Giovannoni et al., 2014), the PA fraction is usually represented by copiotrophic motile bacteria which colonize living or decaying microbial eukaryotes, fecal pellets, gel-like particles or other forms of particulate organic matter (Simon et al., 2002; Herndl and Reinthaler, 2013; Busch et al., 2017).

Microbial studies of the photic layer of Fram Strait have so far focused on eukaryotic plankton (Kilias et al., 2013; Nöthig et al., 2015; Metfies et al., 2016), and biogeochemical recycling of detritus by bacteria (Piontek et al., 2014, 2015). Although bacteria are key players in the biogeochemical cycling of carbon and nutrients in the water column (Azam and Malfatti, 2007; Falkowski et al., 2008), very little is known about the composition and the dynamics of their communities in this region. In order to understand the impact of projected environmental changes on these communities,



it is necessary to establish a fundamental knowledge about the biogeography and variability of microbial communities in the Fram Strait. Using a set of measured and modeled environmental parameters and sequence-based assessments of microbial community composition, the objectives of the study were: (1) to identify differences in bacterial community composition in the two hydrographic regimes of Fram Strait in relation to hydrographical and biogeochemical parameters; (2) to test whether these differences are related to specific productivity phases of the Arctic pelagic ecosystem; (3) to assess whether and to what extent these differences are reflected in specific taxon–taxon associations between bacterial and eukaryotic community members.

RESULTS

Phytoplankton Bloom Dynamics Across the Fram Strait

Based on previously defined physical characteristics of the two main currents of Fram Strait (Rudels et al., 2013), we identified two origins of our sample sets: (1) the eastern Fram Strait with warmer and more saline Atlantic Water of the WSC; (2) the western Fram Strait with colder and less saline Polar Water of the EGC (Figure 1). The two regions had distinct sea ice conditions at the time of sampling, with an ice-covered regime in EGC and an ice-free regime in WSC (Figure 1). Furthermore, measured chl a concentrations showed higher concentrations in the WSC, and

chl a was present down to water depths of more than 100 m in this region (Figure 1B).

In WSC all measured inorganic nutrients (silicate – SiO_3 , nitrate – NO_3 , and phosphate – PO_4) showed lower concentrations near the surface compared to deeper water layers below the pycnocline (roughly below 50 m). Contrary, in EGC there were only small differences in nutrient concentrations throughout all measured depths. In addition, while measurements of SiO_3 and PO_4 concentrations in deeper water layers were similar between the regions, NO_3 concentrations were lower in EGC (Supplementary Figure 1). The depth of the water column pycnocline represents the mixed layer depth during the last winter (Rudels et al., 1996). Generally only the nutrients above the pycnocline within the photic zone (upper ~50 m) are consumed by phytoplankton. Therefore, the calculated differences in nutrient concentrations (Δ) below and above the seasonal pycnocline provide a proxy estimation for phytoplankton productivity in the different regions, since the beginning of the seasonal bloom (Table 1). The estimated productivity based on the stoichiometry of consumed nutrients (see Material and Methods), as well as the integrated chl a and phytoplankton carbon biomass all showed higher values in WSC. Furthermore, based on a ratio 1:1 of $\text{NO}_3:\text{SiO}_3$ we estimated that the contribution of diatoms to the total productivity was roughly 30% in both regions. However, biomass estimates of diatoms showed a much larger fraction of the total phytoplankton biomass in EGC at the time of sampling (Table 1).

TABLE 1 | Comparison of nutrient consumption, phytoplankton biomass and productivity between the EGC and WSC regions.

	EGC	WSC
Nutrient consumption (Δ)		
ΔNO_3 [$\mu\text{mol Liter}^{-1}$]	3.2 ± 1.2 (6)	6.4 ± 0.9 (5)
ΔSiO_3 [$\mu\text{mol Liter}^{-1}$]	1 ± 0.9 (5)	2.4 ± 0.9 (5)
ΔPO_4 [$\mu\text{mol Liter}^{-1}$]	0.07 ± 0.03 (4)	0.3 ± 0.2 (5)
Phytoplankton community		
Integrated chl. a conc. [mg m^{-3}]	8.1 ± 4.8 (6)	43.3 ± 26.4 (5)
Estimated productivity since winter [$\text{g C m}^{-2} \text{yr}^{-1}$]	250 ± 98 (6)	509 ± 73 (5)
Estimated diatom contribution to productivity [%]	32	37
Phytoplankton carbon estimate in chl a max.* [mg m^{-3}]	0.76 (4)	5.6 (3)
Diatom carbon estimate in chl a max.* [mg m^{-3}]	0.28 (4)	0.49 (3)
Estimated diatom contribution to phytoplankton biomass in chl a max.* [%]	36	8

The values represent the mean and the standard deviation for each parameter and the number in parentheses represents the number of stations. Negative values in nutrient consumption were excluded from the mean calculation. *Phytoplankton carbon measurements were calculated from microscopy counts of the different phytoplankton groups and previously published in Engel et al. (2017).

To verify that these differences in biogeochemical parameters represent different ecosystem states, we used surface chl a dynamics of the biogeochemical model FESOM-REcoM2, set to the studied dates, to estimate the phytoplankton bloom stages in the two regions. Because of the lack of chl a remote sensing measurements for the ice-covered regions, we could only use the ice-free region for calibration (Supplementary Figure 9). In the model, a strong relationship between the estimates of chl a and the shifting sea ice edge was observed (Figure 2). In the beginning of June, surface chl a concentrations were elevated in the whole ice-free area of WSC, while remaining very low in the ice-covered EGC (Figures 2A–C). In the second half of June 2014, with the ice thinning and the sea ice edge shifting westward, an increase in surface chl a concentrations was observed also in EGC (Figures 2D–F).

Differences in Microbial Community Composition Between the Eastern and Western Regions of the Fram Strait

Using Illumina 16S rRNA amplicon sequencing of the V3-V4 hypervariable region, we obtained a final dataset of 2,462,994 reads (amplicons) in 63 samples, which were assigned to 7,167 OTUs associated with 406 bacterial taxonomic lineages. The OTUs which were taxonomically assigned to chloroplasts or mitochondria were excluded from further analysis. The rarefaction curves did not reach a plateau in any of the samples, and on overage the samples covered 60% of the bacterial community richness (Supplementary Table 1 and Supplementary Figure 2A). However, coverage-based rarefaction estimations (i.e., Good's estimator), revealed

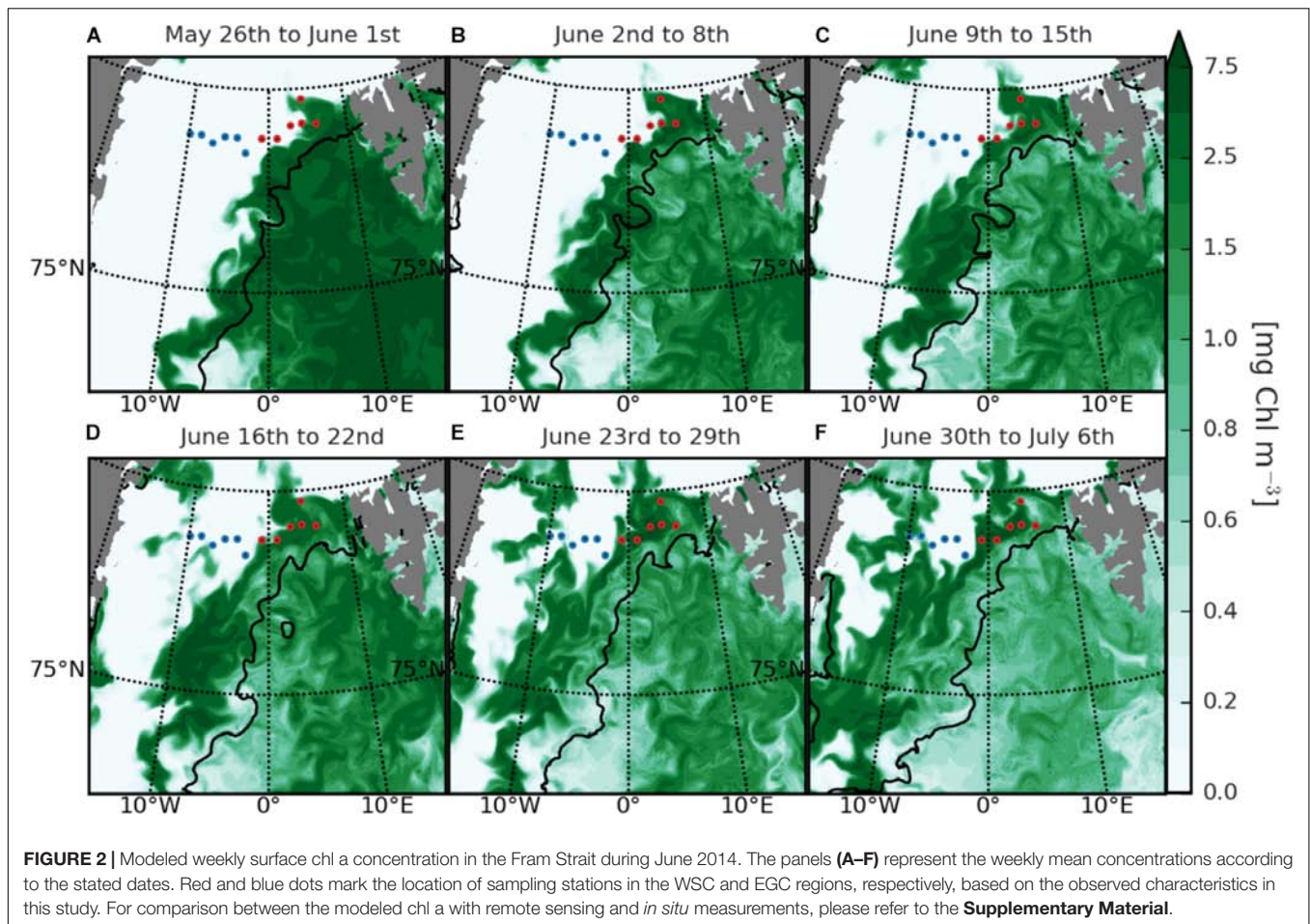
a sample completeness higher than 98% in all samples (Supplementary Figure 2B; Chao and Jost, 2012; Chao et al., 2014). This suggests that although additional OTUs could be expected with additional sequencing, our sequencing depth was satisfactory to represent most of the diversity within the bacterial communities.

Comparison of bacterial community composition between the different regions and fractions was conducted based on the presence/absence of an OTU (Figure 3). A total of 974 OTUs (13% of the total OTUs) were shared throughout the entire dataset, and represented more than 75% of all sequences. Especially the FL communities of both regions were similar (Figure 4). Hence, differences between the bacterial communities mainly resulted from variations in the proportional abundance of these taxa.

In order to further investigate the differences in community composition between the different regions, we performed differential abundance tests for all shared OTUs from both the FL and PA fractions using 'DESeq2'. The OTU which had a fold change of absolute value higher than 1 and an adjusted p -value < 0.05 was defined as 'differentially abundant OTU' – daOTU. Furthermore, using 'GAGE' we tested for the enrichment of bacterial groups at a lower taxonomic resolution, i.e., that of bacterial families. Only bacterial families in which all OTUs were enriched in only one region and showed statistical significance (adjusted p -value < 0.05), were considered to be enriched.

A total of 757 (10% of all OTUs) and 869 (12% of all OTUs) daOTU were identified in the FL and PA fractions, respectively (Supplementary Figure 3). For both fractions, the EGC region was represented by a higher proportion of daOTU compared to the WSC (60 and 65% for FL and PA, respectively), as well as by a higher number of sequence-enriched bacterial families (Figure 5). The WSC was characterized, in both fractions, by few significantly enriched families in various taxonomic groups, such as *Alphaproteobacteria* (*Rhodobacteraceae*) and *Gammaproteobacteria* (*Piscirickettsiaceae*, *Porticoccaceae*). Furthermore, *Flavobacteria* (*Cryomorphaceae*) and *Gammaproteobacteria* (OM182 clade) were significantly enriched in the FL fraction of WSC. Enriched taxa in the EGC were distributed across a broader taxonomic range, with large differences also between the fractions. In the FL fraction the significantly enriched families were associated with the poorly classified *Chloroflexi* (SAR202), *Marinimicrobia* (SAR406) and *Deltaproteobacteria* (SAR324, *Bdellovibrionaceae*), as well as members of *Alphaproteobacteria* (SAR11, *Rhodospirillaceae*) and *Gammaproteobacteria* (*Colwelliaceae*, *Pseudoalteromonadaceae* and JTB255). In the PA fraction significantly enriched families were associated mainly with *Deltaproteobacteria* (*Bdellovibrionaceae*, *Bradymonadales*, *Oligoflexaceae*, NB1-j) and *Gammaproteobacteria* (*Pseudoalteromonadaceae*, *Shewanellaceae* and JTB255).

A similar workflow was applied to investigate microbial eukaryotic communities. Using Illumina 18S rRNA amplicon sequencing of the V4 hypervariable region, we obtained a final dataset of 2,396,433 reads (amplicons) in 33 samples,



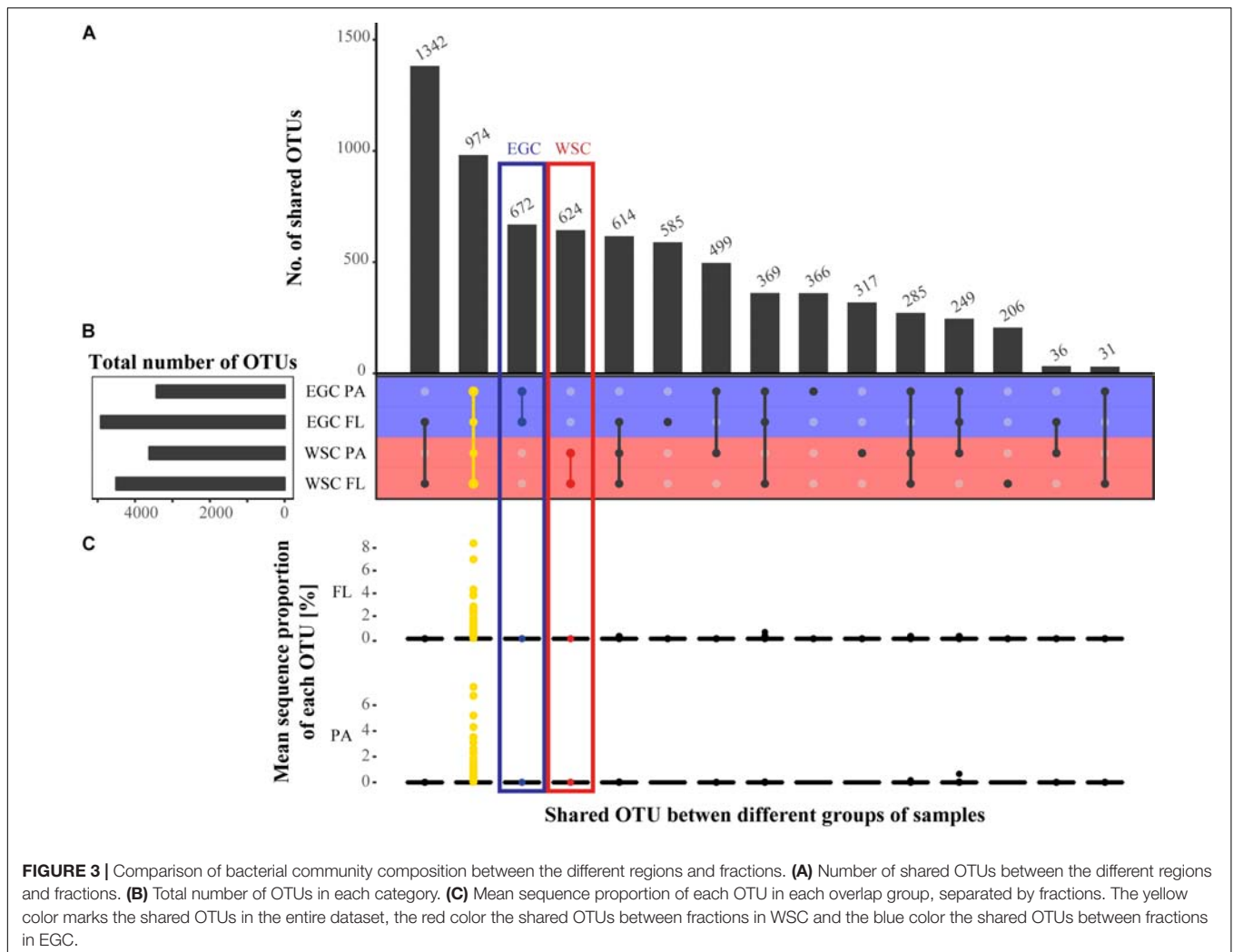
which were assigned to 4,419 OTUs associated with 173 eukaryotic taxonomic lineages. The eukaryotic OTUs which were taxonomically assigned to metazoa were excluded from further analysis. Rarefaction curves did not reach a plateau in any of the samples, and on average the samples covered 75% of the eukaryotic community richness (**Supplementary Table 1** and **Supplementary Figure 2C**). Nevertheless, coverage-based rarefaction estimations (i.e., Good's estimator), revealed a sample completeness higher than 98% in all samples (**Supplementary Figure 2D**; Chao and Jost, 2012; Chao et al., 2014). This suggests that although additional OTUs could be expected with additional sequencing, our sequencing depth was satisfactory to represent most of the diversity within the eukaryotic communities.

A corresponding OTU presence/absence analysis between eukaryotic communities in each region revealed that 2,502 OTUs (56% of the total OTUs) were shared between the regions (**Supplementary Figure 4**), comprising more than 80% of the sequences in all eukaryotic samples (**Figure 6**). Hence, the relatively high proportion of region-specific OTUs showed very low relative sequence abundances. Furthermore, the taxonomic groups *Syndiniales*, *Dinophyceae* (dinoflagellates) and *Diatomea* showed larger number of daOTU in EGC (**Supplementary Figure 5**). In the WSC on the other hand, the largest taxonomic

group (in terms of number of daOTU) was the heterotrophic *Thecofilosea* (*Cercozoa*).

Environmental Drivers of Microbial Communities in the Fram Strait

Bacterial cell densities and production estimates based on leucine incorporation showed statistically significant differences between the two regions (*t*-test, $p < 0.001$; **Figures 7A,B** and **Supplementary Table 2**). The results showed almost one order of magnitude higher bacterial cell densities in WSC compared to EGC, as well as higher ratios between high nucleic acid (HNA) and low nucleic acid (LNA) cells. Total bacterial productivity was higher in the WSC compared to the EGC region, while cell specific productivity (total productivity divided by cell concentration) did not show significant difference between the regions. Moreover, a principal coordinate analysis (PCoA) of bacterial community composition revealed significant differences between samples according to their geographic origin, in addition to clear differences in the community structure of FL and PA fractions (**Figures 7C,D**). Samples from different depths showed no clear clustering. The separation of samples according to their bacterial community structure was confirmed using a permutational multivariate analysis of variance. Similar



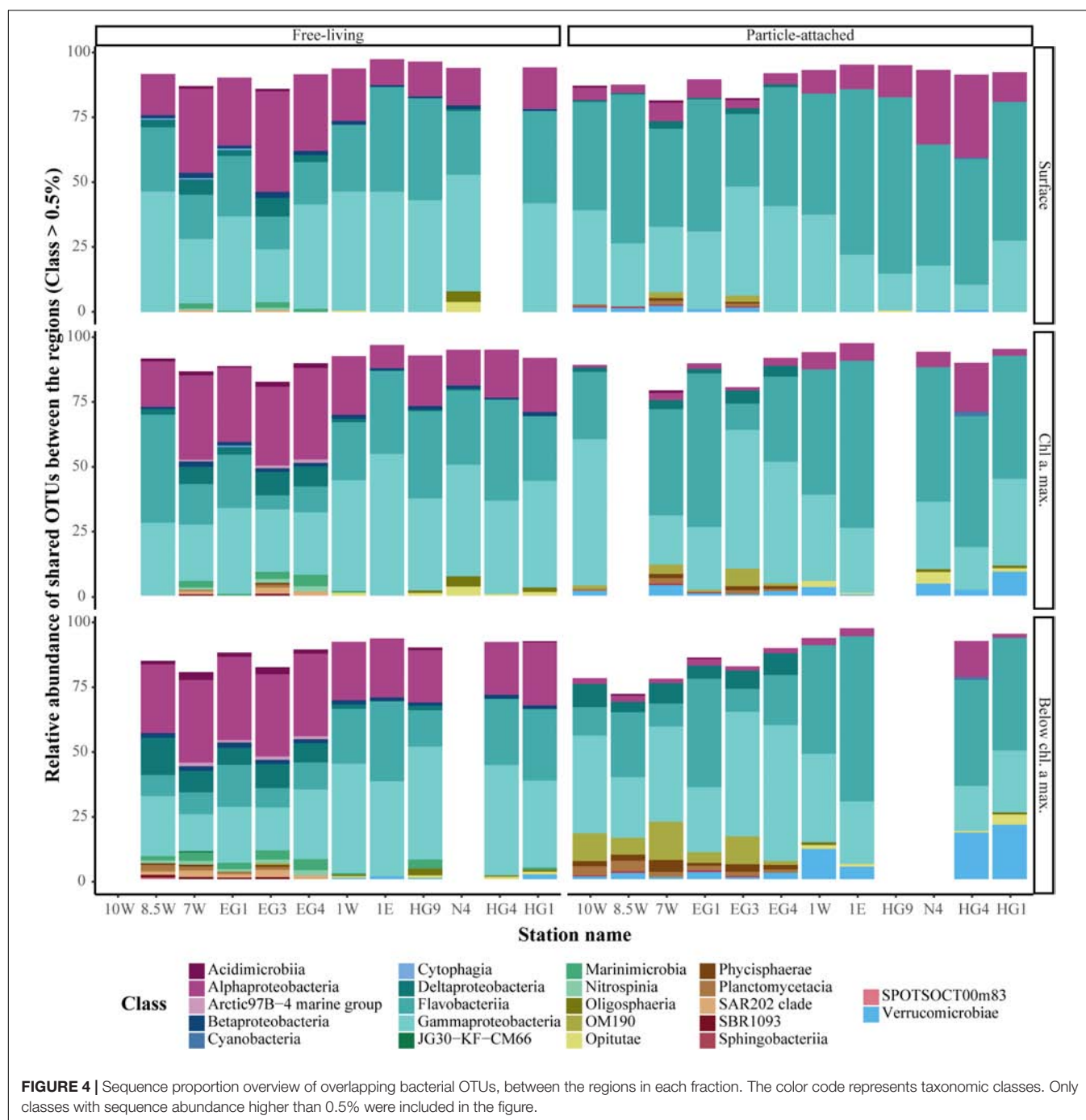
differences between the regions were observed for the microbial eukaryotic community, with higher phytoplankton estimated biomass in the WSC (Table 1), and community composition clustering according to regions, although to a lesser extent than bacterial communities (Supplementary Figures 6A,B).

To compare the explanatory power of a range of environmental variables in structuring bacterial communities, we performed redundancy analysis (RDA) and constrained the ordination by the following environmental parameters: temperature, salinity, chl a, and consumed nutrients (ΔNO_3 , ΔSiO_3 and ΔPO_4). Due to the different environmental conditions in EGC and WSC regions, we selected these parameters to account for the combined effect of the different water masses (temperature and salinity) and different ecosystem states (chl a and nutrients). The analysis was performed separately for FL and PA bacterial communities, as the fractions may be influenced by different environmental factors (Figures 8A,B). In accordance with the PCoA ordination (Figure 7C), both FL and PA fractions exhibited a strong separation of bacterial communities between EGC and WSC (mainly along RDA axis 1, which explained roughly 80% of

the variance). Using a stepwise model selection test ('ordistep' algorithm in 'vegan' package), we identified that temperature, salinity and chl a were the strongest explanatory variables in the FL fraction, explaining 66% of the total variance. Community variation in the PA fraction was mainly explained by temperature, salinity, chl a and consumed nitrate (ΔNO_3), which explained 63% of the total variance. A similar stepwise model selection test for the microbial eukaryotic community revealed that community variation was mainly explained by temperature, salinity, consumed silicate (ΔSiO_3) and nitrate (ΔNO_3), adding up to 38% of the total explained variance (Supplementary Figure 6C).

Associations Between Bacteria and Eukaryotic Microbes – Based on Co-occurrence Networks

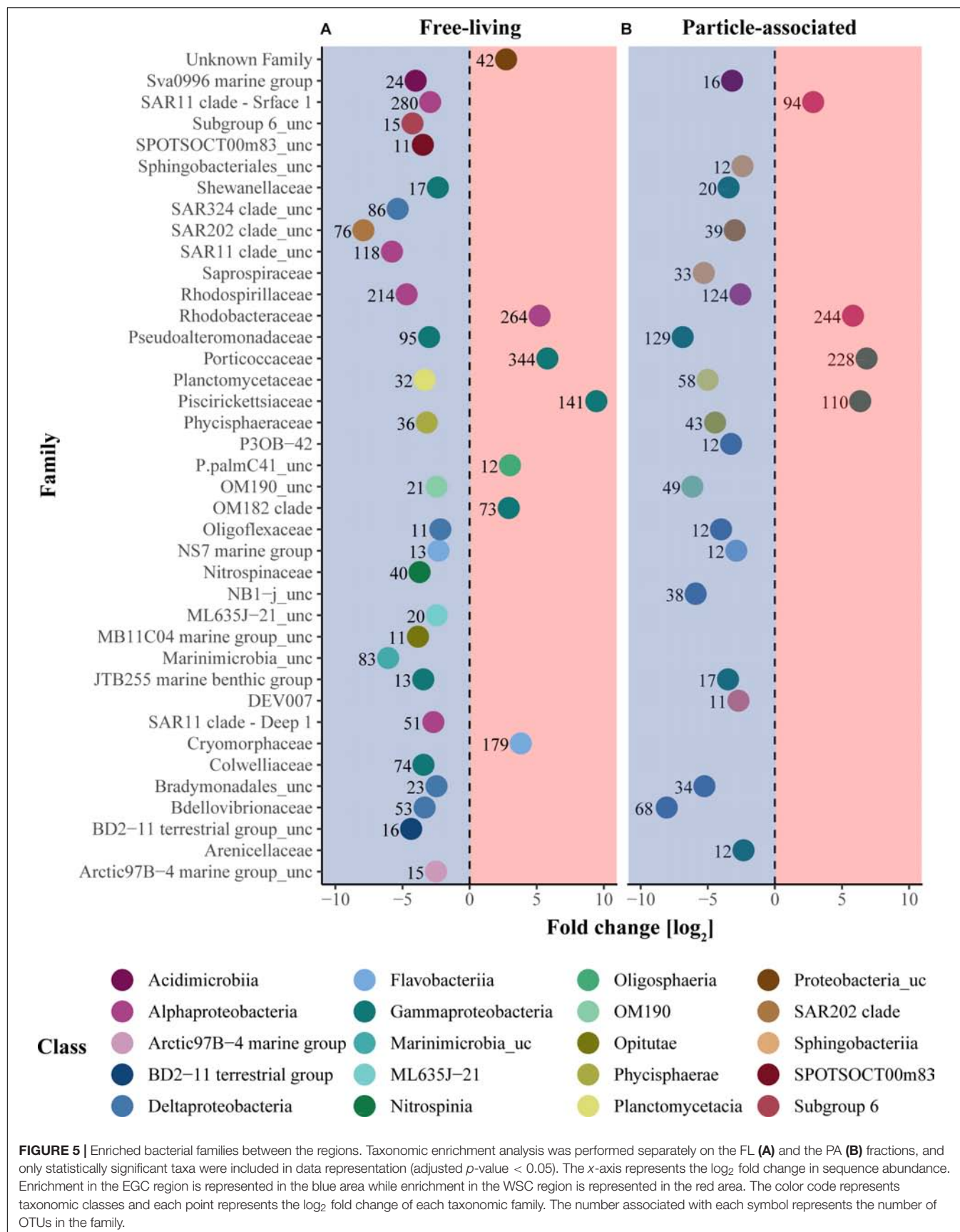
Two separate co-occurrence networks were constructed to examine potential associations between free-living bacteria and microbial eukaryotes ('FL network') and between particle-associated bacteria and microbial eukaryotes ('PA network') at the



chl a max. depth. In the FL network 85% of potential associations were positive, in the sense that sequence-richer taxa of bacteria were associated with sequence-richer taxa of eukaryotes. The PA network consisted of a larger number of total potential associations, but only 71% of them were positive (**Supplementary Table 3**). An overview of both positive and negative associations (**Figure 9**) revealed two taxonomic groups that showed highest numbers of associations in both fractions together, the eukaryotic order *Syndiniales* (*Alveolata*) and the bacterial order *Flavobacteriales* (*Flavobacteriia*). In addition, high number of

potential associations was associated with *Gammaproteobacteria*, such as *Alteromonadales*, and *Oceanospirillales* (**Figures 9A,C**). Among the microbial eukaryotes, two groups showed relatively high numbers of associations: *Diatomea* and *Dinophyceae* (*Dinoflagellata*; **Figures 9B,D**).

In order to identify regionally specific associations of microbial eukaryotes with bacterial taxa, we generated for each fraction a sub-network of positive associations between eukaryotic OTUs and previously identified bacterial daOTU for the EGC and WSC, respectively (**Supplementary Figure 3**).



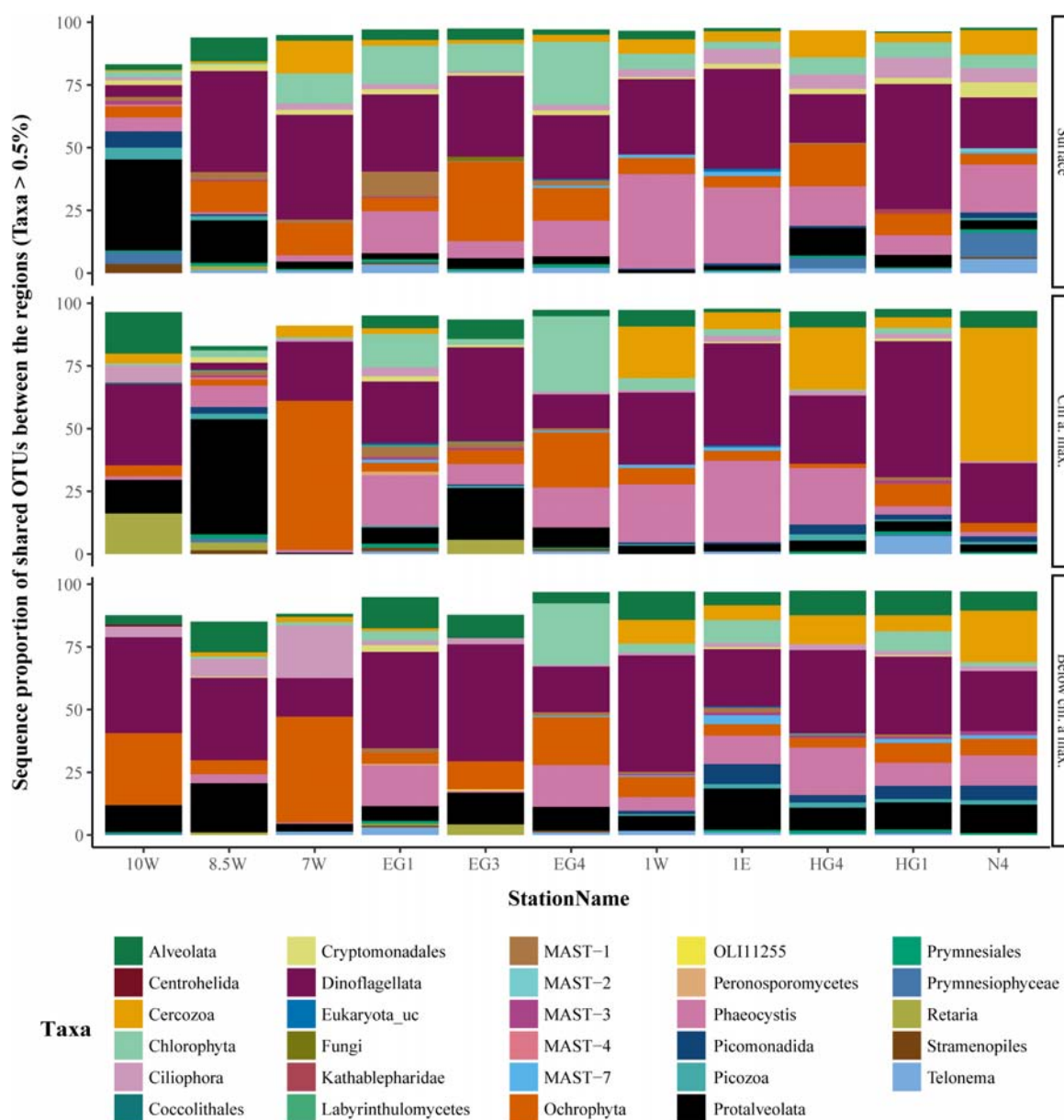


FIGURE 6 | Sequence proportion overview of overlapping microbial eukaryote OTUs, between the regions. The color code represents taxonomic lineages. Only taxa with sequence abundance higher than 0.5% were included in the figure.

The sub-network topologies showed different patterns in the FL and the PA networks. Overall, the FL network consisted of 159 nodes of daOTU, out of a total 363 bacterial OTUs in the network (81 daOTU in EGC and 78 in WSC). In the PA network there were 226 nodes of daOTU, out of a total 363 bacterial OTUs in the network (197 daOTU in EGC and 30 daOTU in WSC). Subsequently, the sub-networks were clustered into metanodes, each incorporating OTUs of a specific taxonomic group (Figure 10). The clustered sub-networks of both fractions revealed strong differences between the regions, with larger number of taxon-taxon associations in the EGC. The strongest associations, based on the number of connecting edges, in all

sub-networks, were related to co-occurrences of *Syndiniales* (*Alveolata*) with various bacterial orders such as *Flavobacteriales* and *Oceanospirillales*.

DISCUSSION

Pelagic Ecosystem State – *in situ* and *in silico* Observations

In our study we investigated the summer dynamics of pelagic bacterial communities from the photic zone of Fram Strait (top 60 m). Using measurements of physical and biogeochemical

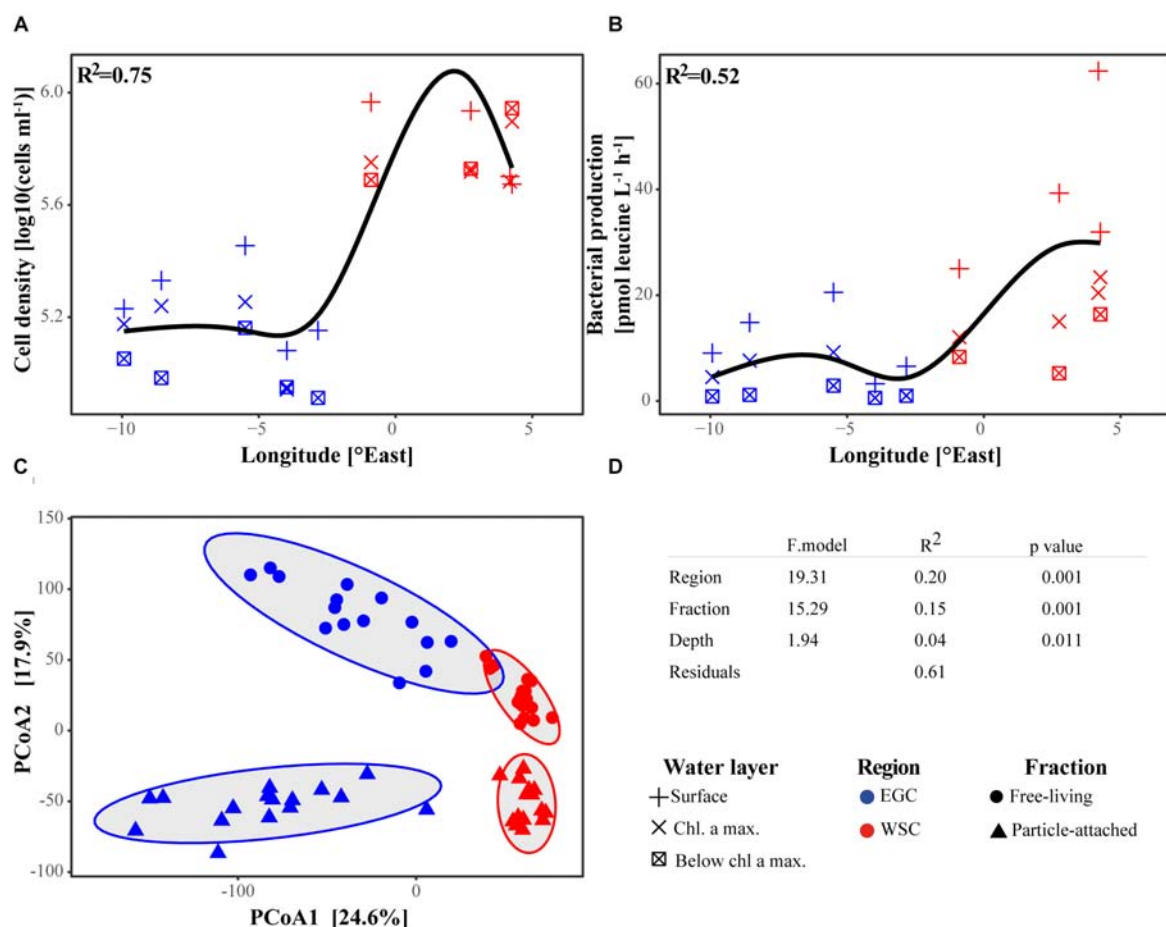
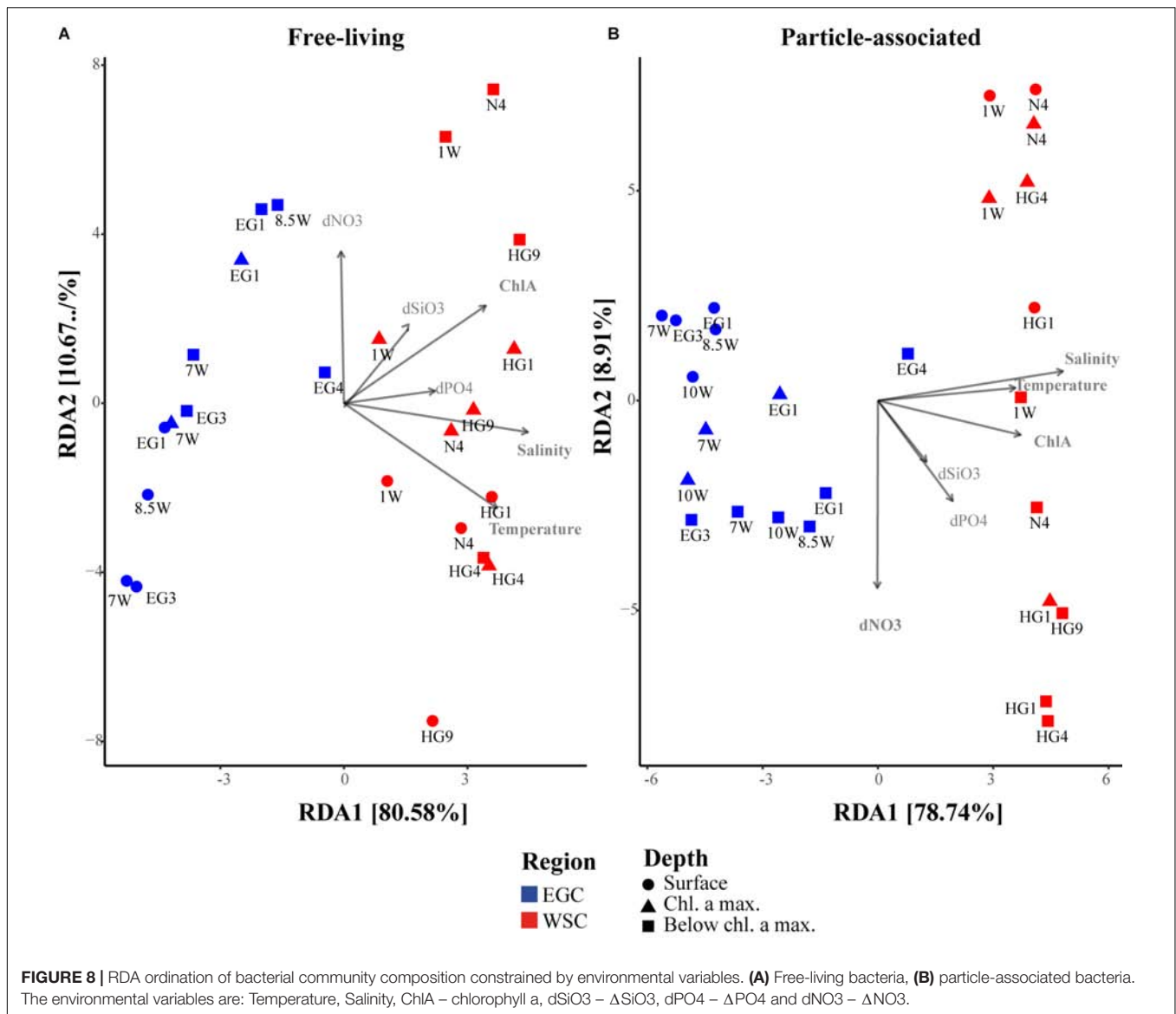


FIGURE 7 | Bacterial community characteristics across the Fram Strait. **(A,B)** Bacterial cell density and production in three water layers: surface (5–10 m), chl a maximum (10–30 m) and below chl a maximum (30–60 m). By applying a generalized additive model with cubic spline we observed a longitudinal trend between the different regions (p -value < 0.05, adjusted $r^2 > 0.75$). **(C)** PCoA of bacterial community composition in FL and PA fractions in all three water layers based on a Euclidean similarity matrix. The ellipses encompass each of the groups with normal confidence of 0.95. The percentages on both axes represent the explained variance of the axis. **(D)** Permutational multivariate analysis of variance between the groups of samples ('ADONIS' in R package 'vegan').

parameters, combined with sea ice coverage, we separated the Strait into two main pelagic ecosystem regions (**Figure 1**). These different regions were directly related to the distinct current systems in the Strait; one transporting Atlantic Water to the Arctic Ocean (WSC) and the other one exporting Polar Water and sea ice (EGC; Beszczynska-Möller et al., 2011). These distinct current systems differed not only in physical characteristics of the water (temperature and salinity) but also in their nutrient concentrations (**Table 1** and **Supplementary Figure 1**). The different geochemical and sea ice conditions potentially affect biological processes in these distinct regions (e.g., nutrient and light limitation of the phytoplankton bloom). We thus used a combination of measured and modeled biogeochemical variables to further investigate the ecosystem states in the two regions.

The high phytoplankton biomass and production estimates (**Table 1**), as well as elevated bacterial cell densities in the WSC compared to the EGC (**Figures 7A,B**), are likely related to the decaying phytoplankton bloom (Pinhassi and Hagström, 2000; Riemann et al., 2000; Alonso-Sáez et al., 2008; Buchan

et al., 2014). Further evidence for such a relationship has been detected by a previous study in Fram Strait, which showed correlations of bacterial activity with concentrations of amino acids and carbohydrates in the water (Piontek et al., 2014). In the WSC region maximum integrated chl a values during seasonal blooms reach up to 100 mg/m³ (Nöthig et al., 2015). Thus based on the chl a concentrations, the fully depleted nutrients above the pycnocline and the low pCO₂ (**Table 1** and **Supplementary Figure 7**), we conclude that we had sampled a post-phytoplankton bloom situation. In the EGC, the low nutrient depletion in surface waters, the low chl a concentration and the high pCO₂ rather suggest a pre-phytoplankton bloom stage. Moreover, the stoichiometry-based estimate of new production in both regions was in a comparable range to previous estimates of Nöthig et al. (2015) in Fram Strait as well as to estimates in other regions of the Arctic Ocean (Arrigo et al., 2008; Wassmann et al., 2010; Boetius et al., 2013). The generally high ratio between NO₃ and PO₄ concentrations in the EGC indicate a Pacific origin of the sampled Polar Water (Wilson and



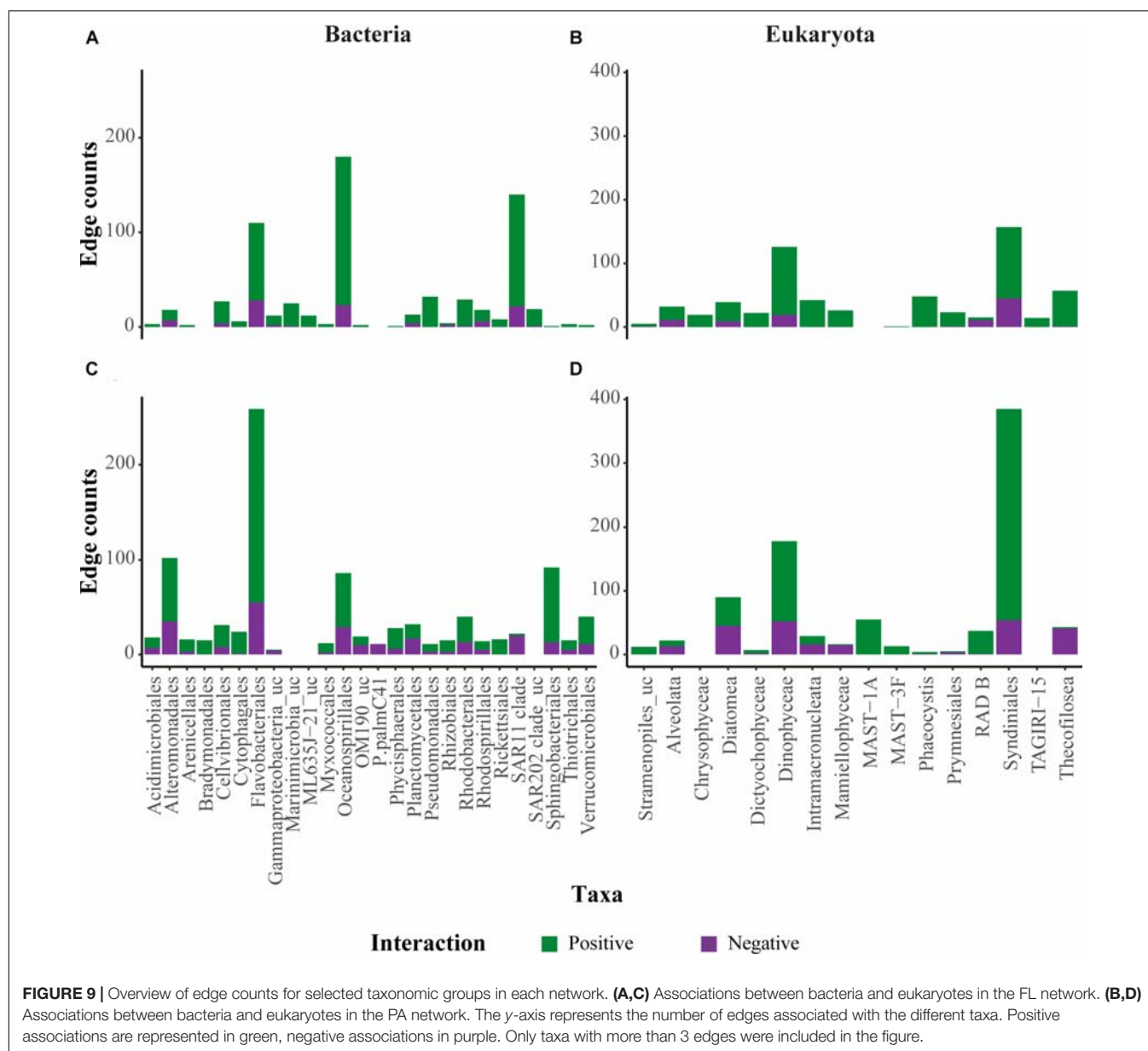
Wallace, 1990), and PO₄ may be one of the limiting factors for the development of a phytoplankton bloom in this region, at the time of the sampling (Taylor et al., 1992).

In order to test whether the biogeochemical differences between the sampled regimes represent different ecosystem states, or simply represent hydrographical differences between Polar Water and Atlantic Water, we used surface chlorophyll a dynamics obtained from the coupled FESOM-REcoM2 model (Figure 2 and Supplementary Material; Schourup-Kristensen et al., 2014). In June 2014, when the sea ice cover, hydrographical and nutrient conditions fit well with observations (Supplementary Figures 8, 9), the annual dynamics produced by the model showed an increase in surface chl a concentration in EGC in the second half of June, associated with the seasonal thinning of the sea ice in the region (Leu et al., 2011; Nöthig et al., 2015). Moreover, in the WSC the model showed a decline in surface chl a concentration throughout the month. In summary,

our observations and the model results support the hypothesis that during the time of sampling early phytoplankton bloom conditions prevailed in the ice-covered EGC (first half of June), and that the phytoplankton bloom of the ice-free WSC was already in decline (second half of June).

Functional and Regional Differences in Microbial Communities Across the Fram Strait

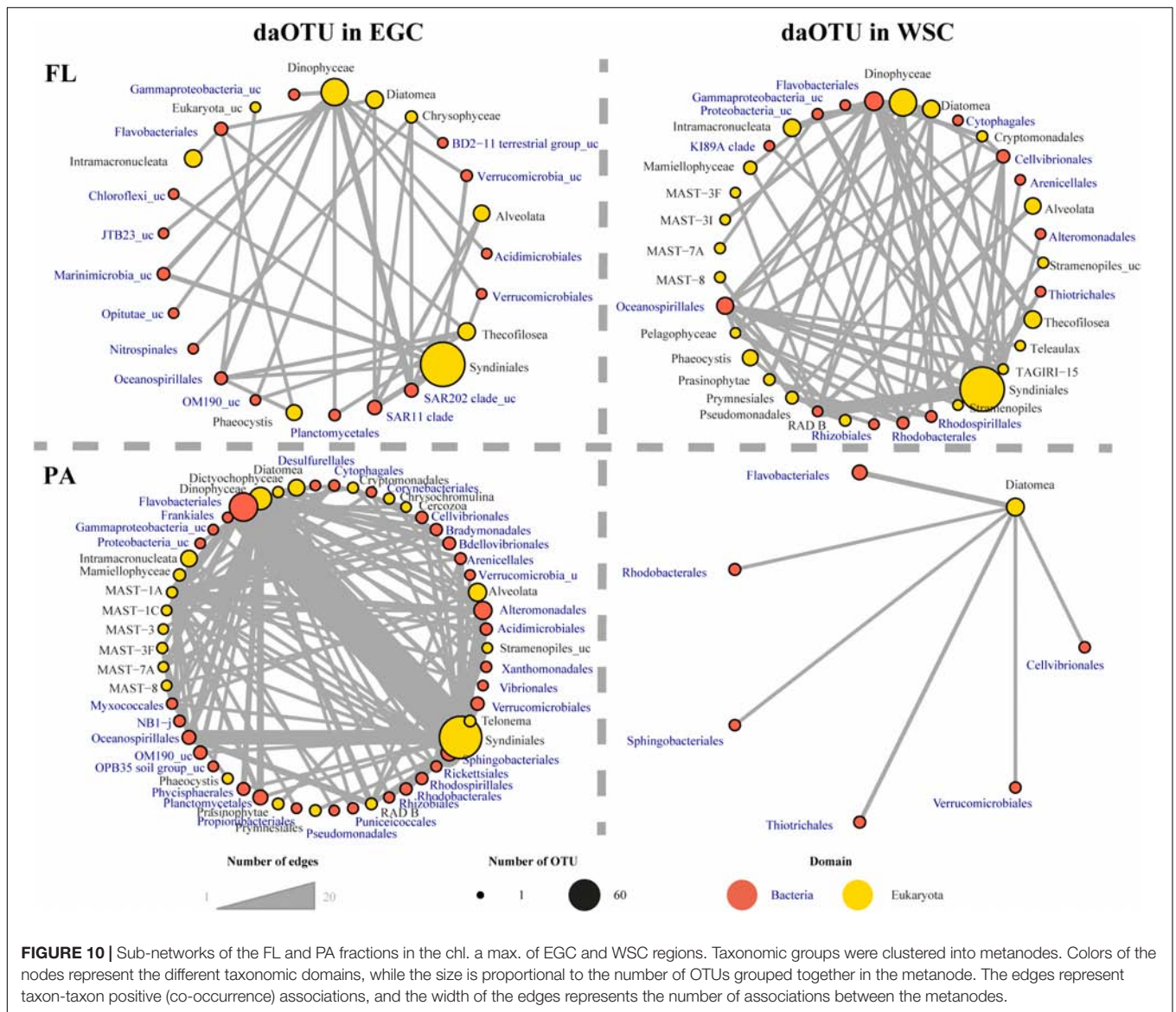
Both WSC and EGC regions exhibited a large number of OTUs, which were unique to one of the regions (Figure 3). However, these OTUs represented only a small proportion of the total sequence abundance of the bacterial community, and consisted of taxa, which were previously identified as rare bacterial community members in the Arctic Ocean (Galand et al., 2009). The vast majority of the sequence proportion was related to



OTUs which were shared between the regions and fractions (Figure 4). Moreover, bacterial community variations in the FL and PA fractions were explained by the same environmental parameters, suggesting that both fractions are subject to similar environmental drivers (Hanson et al., 2012). Hence, we hypothesized that community variation was mostly driven by environmental factors such as bloom stage, selecting for different sequence proportions of shared OTUs. It is important to note that size-fractionated filtration may lead to different observations compared to bulk filtration (Padilla et al., 2015). In this study we did not observe a clogging of filters, but cannot exclude effects on FL and PA fractions.

In order to investigate differences in the relative contributions of the shared OTUs to the communities in WSC and EGC, we identified differentially abundant OTUs (daOTU) in both the

FL and PA fractions (Supplementary Figure 3). *Flavobacteria* and *Gammaproteobacteria* were the two main heterotrophic bacterial taxa which showed high numbers of daOTU and numerous enriched taxa in both fractions (Figure 5 and Supplementary Figure 3). For both fractions combined, the WSC consisted of almost twice the number of flavobacterial daOTU compared to EGC (176 and 107 daOTU, respectively), suggesting an enrichment of this taxonomic group by post-bloom conditions in this region. *Flavobacteria* specialize on targeting complex organic biopolymers and were previously described to respond to phytoplankton blooms in high latitudes (Simon et al., 1999; Teeling et al., 2012; Williams et al., 2013; Chafee et al., 2018). Moreover, *Cryomorphaceae*, a significantly enriched flavobacterial family in the FL fraction of WSC (Figure 5), was previously identified as one of the main taxa responding to



a flagellate bloom in mesocosm experiments (Pinhassi et al., 2004).

Additionally, in both fractions, there was a large number of daOTU and several significantly enriched families related to *Gammaproteobacteria* (Figure 5 and Supplementary Figure 3). These opportunistic copiotrophs, which have previously been described from both FL and PA fractions, are highly diverse and specialized in adapting to a wide range of carbon sources, also responding to different stages of phytoplankton blooms (Alonso-Sáez et al., 2008; Teeling et al., 2012; Nikrad et al., 2014). Interestingly, the genus *Balneatrix* (*Oceanospirillales*) which was previously identified to strongly correlate with phytoplankton bloom presence in the North Sea (Wemheuer et al., 2014), accounted for 30 daOTU in the WSC and only 5 daOTU in the EGC, which may be linked to the different phytoplankton bloom conditions in the region. Furthermore, the order *Pseudoalteromonadales* which consisted of several significantly

enriched families in both fractions in EGC (Figure 5), contains several psychrophilic genera which were previously found in sea ice (Bowman et al., 1997; Brown, 2001; Brinkmeyer et al., 2003; Eric Collins et al., 2010; Yu et al., 2015), and their enrichment in the EGC may thus be partly a result of their release from ice-associated communities. An interesting observation was provided by two outlier samples. Although they originated from the WSC, the proximity of station 1W and HG9 to the sea ice edge (Figure 1), potentially resulted in bacterial communities more similar to stations from the EGC (Figure 7C). This may indicate that the effect of the seasonal phytoplankton bloom extends into the zone where both water masses mix, e.g., by eddies (Wekerle et al., 2017).

Several cryptic taxonomic groups, such as *Chloroflexi* (SAR202), *Marinimicrobia* (SAR406) and various members of *Deltaproteobacteria*, were significantly enriched in EGC (Figure 5), and also consisted of a large number of unique OTUs

in this region. These enriched taxonomic groups in the ice-covered EGC were previously reported from surface waters in the western Svalbard region (WSC) during the Arctic winter (Wilson et al., 2017). Therefore, our results support and strengthen the hypothesis of Wilson et al. (2017) that bacterial community dynamics in Fram Strait are to a large extent affected by seasonal variability (e.g., availability of light under changing sea ice conditions), rather than hydrographic differences between water masses.

Enriched eukaryotic taxa differed strongly between the EGC and WSC regions (**Supplementary Figure 5**), with the taxonomic groups being consistent with previously reported seasonal dynamics in the Arctic Ocean (Lovejoy, 2014). In the EGC region all enriched taxa were related to previously identified, dominant members of pelagic Arctic winter communities (e.g., *Syndiniales*; Guillou et al., 2008; Jephcott et al., 2016; Marquardt et al., 2016). Two different taxonomic groups of phytoplankton were enriched in the WSC: the class of green algae *Prasinophytae* abundant photosynthetic organisms in late summer-autumn seasons in the Arctic (Lovejoy et al., 2007; Vader et al., 2015; Marquardt et al., 2016; Metfies et al., 2016; Joli et al., 2017). Furthermore, several heterotrophic eukaryotic taxa (e.g., *Thecofilosea*) were enriched in the WSC. These organisms are mainly grazers and depend on the presence of phytoplankton and bacteria (Monier et al., 2013); their higher representation may thus be linked to the declining phytoplankton bloom in the WSC. Microbial eukaryotic community composition clearly differed between the two regions (**Supplementary Figure 6C**). Interestingly, stations 10 and 8.5 W showed some similarity to the WSC region, which may be related to a coastal phytoplankton bloom east of Greenland (**Supplementary Figure 8**). However, overall our observations of the microbial eukaryotic community further support our classification of early bloom conditions in the EGC and late bloom conditions in WSC.

Co-occurrence Networks Reveal Potential Candidates for Cross-Domain Interactions

Numerous studies have described shifts in bacterial community composition during phytoplankton blooms (Teeling et al., 2012; Wemheuer et al., 2014; Chafee et al., 2018), but very little is known about specific biotic interactions between bacteria and phytoplankton during blooms (Töpper et al., 2010; Amin et al., 2012; Hartmann et al., 2013; Lima-Mendez et al., 2015). Our results revealed an enrichment of specific bacterial taxa in the different regions, which we suggest to be related to the seasonal development of the phytoplankton bloom. Using network co-occurrence analyses (Faust and Raes, 2012), we therefore tested whether these enriched taxa exhibit potential associations with eukaryotic microbes in the chl *a* max. communities.

Both FL and PA networks consisted of a large number of edges (**Figure 9** and **Supplementary Table 3**), which may indicate potential ecological interactions between taxa. Among the bacterial taxa in the FL network, a large number of associations was related to the typically free-living SAR11 clade (Giovannoni, 2017). In the PA network, on the other hand, large

number of associations were related to typical particle-associated *Gammaproteobacteria*, such as *Alteromonadales* (Crespo et al., 2013; Fontanez et al., 2015). In both fractions, *Flavobacteria* and *Syndiniales* outnumbered all other taxonomic orders in terms of the number of associations. These observations are in line with a previous report from the global plankton interactome study conducted as part of the global Tara Oceans expedition (Lima-Mendez et al., 2015), which did, however, not cover the Arctic Ocean.

Roughly 30–40% of bacterial nodes in the networks consisted of daOTU associated with one or more eukaryotic taxa. Interestingly, “regional” (WSC vs. EGC) sub-networks displayed strong differences between both regimes in the PA fraction, with a much higher number of associations in the EGC (**Figure 10**). Little is known about the lifestyle and physiology of many of the organisms identified in the networks, especially for the bacterial fraction, and the translation of observed associations into biological traits is thus extremely limited (Ramanan et al., 2016). Furthermore, in many cases the association may represent a common response of taxonomic groups to environmental conditions, rather than direct interaction between them (Weiss et al., 2016). Nevertheless, the observed cross-domain associations showed clear differences between the regions with different phytoplankton bloom conditions, resulting in the enrichment of specific bacterial taxa and the development of distinct ecological networks. It has been previously proposed that shifts in the timing and composition of phytoplankton blooms, as well as temporal mismatches with grazers resulting in an altered food web, are among the main impacts of climate change in the Arctic (Soltwedel et al., 2016; Engel et al., 2017). Our observations of specific associations between eukaryotes and bacteria in the plankton suggest that such ecological shifts may be accompanied by substantial changes in the microbial community structure.

CONCLUSION

Our study revealed strong differences in pelagic microbial community activity and structure in the photic layers of the ice-free eastern (WSC) and ice-covered western (EGC) Fram Strait during summer 2014. Measured and modeled biogeochemical parameters suggested distinct ecosystem states in the two regions, namely different stages of the summer phytoplankton bloom, as a result of differences in sea ice cover and irradiance. Although it is challenging to conclusively decouple effects of water masses, seasonally driven biogeochemistry and biotic associations, our study shows that differences in bacterial communities between the regions could be explained by environmental parameters associated with phytoplankton bloom dynamics. This includes a strong increase in bacterial cell densities and activity in response to a declining phytoplankton bloom in the WSC, with an enrichment of phytoplankton bloom associated bacterial taxa commonly known to degrade phytoplankton products, such as *Flavobacteria*. In contrast, the EGC region showed high relative sequence proportions of bacterial taxa that have been associated with Arctic winter conditions (e.g., SAR202 clade, *Marinimicrobia* and *Deltaproteobacteria*).

Moreover, co-occurrence networks provided evidence for a high variety of potential interactions between bacteria and microbial eukaryotes in the early bloom conditions, and their possible specialization with the advancement of the phytoplankton bloom. In times of a rapidly changing Arctic Ocean, our results highlight the potential impact of future ice-free summers on the structure and function of Arctic Ocean pelagic microbial communities. Additional sampling throughout the year will help to better resolve seasonally driven microbial community dynamics and contrast them to long-term shifts.

MATERIALS AND METHODS

Field Sampling

Samples were collected in Fram Strait during the Polarstern expedition PS85 (June 6th – July 3rd 2014) from the eastern Greenland shelf to the west coast of Spitsbergen (**Supplementary Table 1** and **Figure 1**). Sampling was carried out with 12 L Niskin bottles mounted on a CTD rosette (Sea-Bird Electronics Inc. SBE 911 plus probe) equipped with double temperature and conductivity sensors, a pressure sensor, altimeter, chlorophyll fluorometer, and transmissometer. The chlorophyll maximum depth (chl a max) was determined based on chl a fluorescence during the downcast, while the water samples were collected during the upcast. Along the transect samples were collected from surface water (5–10 m), the chl a max (10–30 m) and below the chl a max (30–60 m, **Supplementary Table 1**). Hydrographic data of the seawater including temperature and salinity were retrieved from the PANGAEA database (Rabe et al., 2014). Water masses were identified based on their hydrographic characteristics, according to Rudels et al. (2013).

Sampling for Bacterial Communities

For assessing bacterial community composition, 2 L of water were filtered through successive membrane filters of 3 μm (Whatman Nucleopore, 47 mm polycarbonate), and 0.22 μm (Millipore Sterivex filters) using a peristaltic pump (Masterflex; Cole Parmer). All samples were stored at -20°C until DNA isolation.

Sampling for Eukaryotic Microbial Communities

For assessing eukaryotic community composition, 2 L subsamples were taken in PVC bottles from the Niskin water samplers. Eukaryotic microbial cells were collected by sequential filtration using a Millipore Sterifil filtration system (Millipore, United States). Each water sample was filtered through three different mesh sizes (10, 3, and 0.4 μm) on 45 mm diameter Isopore Membrane Filters at 200 mbar. All samples were stored at -20°C until DNA isolation.

DNA Isolation and Amplicon Sequencing

Bacteria

Genomic bacterial DNA was isolated from the 3 μm and the 0.22 μm filter membranes to analyze the particle-associated (PA) and the free-living (FL) community, respectively, in

a combined chemical and mechanical procedure using the PowerWater DNA Isolation Kit (MO BIO Laboratories, Inc., Carlsbad, CA, United States). Prior to DNA isolation the sterivex cartridges of the 0.22 μm membranes were cracked open in order to place the filters in the kit-supplied bead beating tubes. The isolation was continued according to the manufacturer's instructions, and DNA was stored at -20°C . Library preparation was performed according to the standard instructions of the 16S Metagenomic Sequencing Library Preparation protocol (Illumina, Inc., San Diego, CA, United States). The hypervariable V3–V4 region of the bacterial 16S rRNA gene was amplified using bacterial primers S-D-Bact-0341-b-S-17 (5'-CCTACGGGNGGCWGCAG-3') and S-D-Bact-0785-a-A-21 (5'-GACTACHVGGGTATCTAATCC-3'; Klindworth et al., 2013). Sequences were obtained on the Illumina MiSeq platform in a 2×300 bp paired-end run (CeBiTec Bielefeld, Germany), following the standard instructions of the 16S Metagenomic Sequencing Library Preparation protocol (Illumina, Inc., San Diego, CA, United States).

Eukaryotic Microbes

Genomic eukaryotic DNA was isolated from the 10, 3, and 0.4 μm filter membranes using the NucleoSpin Plant Kit (Machery-Nagel, Germany), following the manufacturer protocol. The resulting DNA-extracts were stored at -20°C . DNA concentrations were determined using the Quantus Fluorometer (Promega, United States) according to the manufacturer's protocol, and equal volumes of the isolated genomic DNA from the three different filter fractions were pulled together. Library preparation was performed according to the standard instructions of the 16S Metagenomic Sequencing Library Preparation protocol (Illumina, Inc., San Diego, CA, United States). The hypervariable V4 region of the eukaryotic 18S rRNA gene was amplified using 528iF (5'-GCGGTAATTCCAGCTCCAA-3') and 964iR (5'-ACTTTCGTTCTTGATYRR-3') primers. All PCRs had a final volume of 25 μL and contained 12.5 μL of KAPA HIFI Mix (Kapa Biosystems, Roche, Germany), 5 μL of each primer 1 $\mu\text{mol L}^{-1}$ and 2.5 μL DNA-template ~ 5 ng. The DNA-template was a mix of equal volumes of genomic DNA isolated from the three different filter fractions, i.e., 10, 3, and 0.4 μm . PCR amplification was performed in a thermal cycler (Eppendorf, Germany) with an initial denaturation (95°C , 3 min) followed by 25 cycles of denaturation (95°C , 30 s), annealing (55°C , 30 s), and extension (72°C , 30 s) with a single final extension (72°C , 5 min). The PCR products were purified from an agarose gel 1% w/v with the AMPure XP PCR purification kit (Beckman Coulter, Inc., United States) according to the manufacturer's protocol. Subsequent to purification DNA concentrations in the samples were determined using the Quantus Fluorometer (Promega, United States). Subsequently, indices and sequencing adapters of the Nextera XT Index Kit (Illumina, United States) were attached in the course of the Index PCR. All PCRs had a final volume of 50 μL and contained 25 μL of KAPA HIFI Mix (Kapa Biosystems, Roche, Germany), 5 μL of each Nextera XT Index Primer 1 $\mu\text{mol L}^{-1}$, 5 μL DNA-template ~ 5 ng and 10 μL PCR grade water. PCR amplification was performed in a thermal cycler (Eppendorf,

Germany) with an initial denaturation (95°C, 3 min) followed by 8 cycles of denaturation (95°C, 30 s), annealing (55°C, 30 s), and extension (72°C, 30 s) with a single final extension (72°C, 5 min). Prior to quantification of the amplification products with the Quantus Fluorometer (Promega, United States) for sequencing the final library was cleaned up using the AMPure XP PCR purification kit (Beckman Coulter, Inc., United States). Sequences were obtained on the Illumina MiSeq platform in a 2 × 300 bp paired-end run (AWI Bremerhaven, Germany), following the standard instructions of the 16S Metagenomic Sequencing Library Preparation protocol (Illumina, Inc., San Diego, CA, United States).

Bioinformatics and Statistical Analyses

Both bacterial and eukaryotic libraries were subject to similar bioinformatic pipelines. The raw paired-end reads were primer-trimmed using 'cutadapt' (Martin, 2011), quality trimmed using 'trimmomatic' with a sliding window of four bases and a minimum average quality of 15 (v0.32; Bolger et al., 2014). The reads were merged using PEAR (v0.9.5; Zhang et al., 2014), and all merged reads below 350 bp or above 450 bp were removed from the dataset. Clustering into OTUs was done with the 'swarm' algorithm using default parameters (v2.0; Mahé et al., 2015). Chimeric sequences were identified and removed using 'uchime' function in VSEARCH (v1.9.7; Rognes et al., 2016). One representative sequence per OTU was taxonomically classified using 'SINA' (SILVA Incremental Aligner; v1.2.11; Silva reference database release 128; Quast et al., 2013) at a minimum alignment similarity of 0.9, and a last common ancestor consensus of 0.7 (Pruesse et al., 2012). The OTUs which were not taxonomically assigned to Bacteria/Eukarya or occurred with only a single sequence in the whole dataset ('singletons') were excluded from further analysis. Furthermore, OTUs in the bacterial dataset which were taxonomically assigned to chloroplast or mitochondria were excluded from further analysis, and OTUs in the eukaryotic dataset which were taxonomically assigned to metazoa were excluded as well.

All statistical analyses were conducted using R (v3.4.1)¹ in RStudio (v1.0.153; RStudio Team, 2015). Sample data matrices were managed using the R package 'phyloseq' (v1.20.0; McMurdie and Holmes, 2013) and plots were generated using the R package 'ggplot2' (v2.2.1; Gómez-Rubio, 2017). A prevalence threshold (i.e., in how many samples did a taxon appear at least once) of 5% was applied to the OTU table prior to downstream analysis following (Callahan et al., 2016). All alpha diversity parameters and curves were obtained using R package 'iNEXT' (v2.0.12; Hsieh et al., 2018). The rarefaction curves for each sample were generated based on 40 equally spaced rarefied sample sizes with 100 iterations.

Principal coordinate analysis was conducted on variance stabilized OTU abundance matrices (McMurdie and Holmes, 2014). The significance of the clustering was tested using the 'ADONIS' function in the R package 'vegan' (v2.4-5; Oksanen, 2017). To determine which environmental variables were significantly correlated with the community composition,

a stepwise ordination significance test was performed using the 'ordistep' function in the R package 'vegan' (v2.4-5; Oksanen, 2017). The fold-change in abundance of each OTU between the regions was calculated using the R package 'DESeq2' (v1.16.1; Love et al., 2014). The method applies a generalized exact binomial test on variance stabilized OTU abundance. The taxonomic enrichment test was performed using the generally applicable gene-set enrichment method in the R package 'GAGE' (v2.26.3; Luo et al., 2009). The results were filtered by significance, after correction for multiple-testing according to Benjamini and Hochberg (1995) with an adjusted *p*-value < 0.05. The shared OTUs calculations and visualization were conducted using R packages 'UpSetR' (v1.3.3; Conway et al., 2017) and 'VennDiagram' (v1.6.18; Chen and Boutros, 2011).

Co-occurrence Network Analysis

The network analysis was conducted separately using the chl a max. FL and PA bacterial communities. The cross-domain co-occurrence networks between bacteria and eukaryotes were constructed using CoNet (v1.1.1beta; Faust and Raes, 2016), as described in Lima-Mendez et al. (2015). The measure-specific *p*-values were merged using Brown's method (Brown, 1975) and correction for multiple-testing was performed according to Benjamini and Hochberg (1995). Edges with an adjusted *p*-value above 0.05 were discarded. The constructed networks were further analyzed and visualized using the R package 'igraph' (v1.1.2; Csardi and Nepusz, 2006).

Calculation of Consumed Inorganic Nutrients

The raw nutrient concentration measurements were retrieved from PANGAEA (Graeve and Ludwichowski, 2017). The nutrient consumption (Δ) at each station was calculated by subtracting the mean value of all collected measurements above 50 m from the mean value of all collected measurements between 50 and 100 m (below the seasonal pycnocline). The integrated chlorophyll a and inorganic nutrient values were calculated according to (Boss and Behrenfeld, 2010). The productivity estimates were calculated using the Redfield ratio 106 C: 16 N: 1 P, and for diatom contribution the ratio of 1:1 N:Si was assumed (see **Supplementary Material**).

Bacterial Abundance and Productivity

Bacterial abundance was determined by flow cytometry (FACSCalibur, Becton Dickinson). Samples were fixed with glutaraldehyde at 1% final concentration and stored at -20°C. Prior to analysis, samples were stained with the fluorescent dye SybrGreen I (Invitrogen) that binds to DNA. Bacterial cell numbers were estimated after visual inspection and manual gating of the bacterial population in the cytogram of side scatter vs. green fluorescence. Fluorescent latex beads (Polyscience, Becton Dickinson) were used to normalize the counted events to volume (Gasol and Del Giorgio, 2000).

The incorporation of 3H-leucine (specific activity 100 Ci mmol⁻¹) was determined to estimate bacterial production (BP).

¹<http://www.Rproject.org/>

The radiotracer was added at a saturating final concentration of 20 nmol L⁻¹ before three replicate samples were incubated for 4–6 h in the dark close to *in situ* temperature at 0–2°C. Incubations were stopped by the addition of trichloroacetic acid (TCA) at a final concentration of 5%. Samples were then processed by the centrifugation method according to Smith and Azam (1992). Briefly, samples were centrifuged at 14,000 × *g* to obtain a cell pellet that was washed twice with 5% TCA. Incorporation into the TCA-insoluble fraction was measured by liquid scintillation counting after resuspension of the cell pellet in scintillation cocktail (Ultima Gold AB, Perkin Elmer).

Chlorophyll a Measurements

The concentration of chl *a* was determined from 0.5 to 2 L of seawater filtered onto glass fiber filters (Whatman GF/F) under low vacuum pressure (<200 mbar); the filters were stored at –20°C before analysis. Pigments were extracted with 10 ml of 90% acetone. The filters were treated with an ultrasonic device in an ice bath for less than a minute, and then further extracted in the refrigerator for 2 h. Subsequently they were centrifuged for 10 min at 5000 rpm at 4°C prior to measurement. The concentration was determined fluorometrically (Turner Designs), together with total phaeophytin concentration after acidification (HCl, 0.1 N) based on methods described in Edler (1979) and Evans (1980), respectively. The standard deviation of replicate test samples was <10%.

The Biogeochemical Model FESOM-REcoM2

To estimate biological productivity in areas and time periods that were not covered by sampling, we used the biogeochemical model REcoM2 coupled to the Finite Element sea ice Ocean Model (FESOM; Schourup-Kristensen et al., 2014). The model runs in a global setup and describes the ocean, sea ice and marine biogeochemistry, thus making it possible for us to estimate the phytoplankton bloom development stage in both the western, ice-covered part of Fram Strait and the eastern ice-free part (see **Supplementary Information**).

Data Accession Numbers and Analyses Repository

Data are accessible via the Data Publisher for Earth & Environmental Science PANGAEA (www.pangaea.de): chlorophyll *a* measurements - doi: 10.1594/PANGAEA.887840; bacterial counts and productivity - doi: 10.1594/PANGAEA.887881. Raw paired-end sequence, primer-trimmed reads were deposited in the European Nucleotide Archive (ENA; Silvester et al., 2018) under an umbrella project number PRJEB28027,

or PRJEB26163 for Bacteria and PRJEB26288 for Microbial eukaryotes. The data were archived using the brokerage service of the German Federation for Biological Data (GFBio; Diepenbroek et al., 2014). Scripts for processing data can be accessed at <https://github.com/edfadeev/Bact-comm-PS85>.

AUTHOR CONTRIBUTIONS

EF, CB, IS, and AB designed and conducted the study. IS and KM provided sequence data for the study. AE and JP provided the cell counts and bacterial productivity data. E-MN conducted the biogeochemical measurements. VS-K provided the modeled chl *a* estimates. EF analyzed the data and wrote the manuscript with guidance from CB, AB, and IS. All authors contributed to the final version of the manuscript.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: <https://www.frontiersin.org/articles/10.3389/fmars.2018.00429/full#supplementary-material>

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Pelagic Ecosystem Characteristics Across the Atlantic Water Boundary Current From Rijpfjorden, Svalbard, to the Arctic Ocean During Summer (2010–2014)

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The northern coast of Svalbard contains high-arctic fjords, such as Rijpfjorden (80°N 22°30'E). This area has experienced higher sea and air temperatures and less sea ice in recent years, and models predict increasing temperatures in this region. Part of the West Spitsbergen Current (WSC), which transports relatively warm Atlantic water along the continental slope west of Svalbard, bypasses these fjords on its route in the Arctic Ocean. In this setting, it is of interest to study the structure of water masses and plankton in the Atlantic Water Boundary Current. This study describes physical and biological conditions during summer (July–August, 2010–2014) from Rijpfjorden across the shelf and continental slope to the Arctic Ocean. Atlantic water (AW) resides over the upper continental slope and occasionally protrudes onto the shelf area. The interplay between the intrusion of AW and meltwater affected the chemical balance of the region by making the carbonate chemistry variable depending on season, depth and distance along the gradient. The pH (aragonite saturation) varied from 7.96 (0.99) to 8.58 (2.92). Highest values were observed in surface waters due to biological CO₂ uptake, except in 2013, when meltwater decreased aragonite saturation to <1 in surface waters on the shelf. All years were characterized by post-bloom situations with very low nutrient concentrations in Polar Surface Water and subsurface chlorophyll *a* maxima. In such circumstances, phytoplankton optimized growth near the limit of the euphotic depth, where the algae still had access to nutrients. In terms of biomass, the protist community was dominated by nanoplankton (2–20 μm), in particular dinoflagellates and ciliates. The prymnesiophyte *Phaeocystis pouchetii* and diatoms often prevailed at subsurface depths associated with the chlorophyll *a* maximum. The boreal *Calanus finmarchicus* and *Oithona similis*

dominated AW over the slope and outer shelf, whereas *Calanus glacialis* and neritic zooplankton (*Pseudocalanus*, *Parasagitta elegans*, and meroplankton) dominated cold water masses inside Rijpfjorden. Continued climate warming is expected to increase the contribution of boreal species and pelagic production in the Arctic Ocean.

Keywords: Arctic ecosystem, carbonate system, nutrient limitation, protists, zooplankton, climate change, Svalbard, Arctic Ocean

INTRODUCTION

Svalbard is located in a transition between boreal and Arctic biogeographic zones. This is most pronounced along the west coast of Svalbard, where the West Spitsbergen Current (WSC) transports Atlantic water (AW) northwards and where its influence is well documented on both protists (Piwosz et al., 2009, 2014; Hegseth et al., 2019) and zooplankton communities (Hop et al., 2006, 2019; Svensen et al., 2011; Vogedes et al., 2014; Soltwedel et al., 2016; Gluchowska et al., 2017b; Ormanczyk et al., 2017). North of Svalbard the Atlantic influence remains substantial as the AW Boundary Current turns eastwards, passing the Yermak Plateau, supplying AW, heat, nutrients and carbon along the upper continental slope en route to the Nansen Basin of the Arctic Ocean (Cokelet et al., 2008; Renner et al., 2018). However, due to the wider and shallow shelf north of Svalbard, the contact between fjords and the core of the Atlantic water is less direct than along the west coast. Fjords along the north coast therefore maintain a more Arctic signature. The northern coast of Svalbard is lined with high-Arctic fjords, such as Rijpfjorden (80°N 22°30'E) that face the Arctic Ocean. Rijpfjorden is a cold system influenced by Arctic Water (ArW) for most parts of the year (January–July), and covered by sea ice for 6–8 months. The pelagic ecosystem of the fjord varies seasonally (Leu et al., 2011; Weydmann et al., 2013), not only because of the seasonal variation in local radiation, but also due to occasional inflow of Atlantic-origin water during summer to late autumn (Wallace et al., 2010).

Continued climate warming with increased “Atlantification” is expected to advance the loss of sea ice in the Eurasian Basin (Polyakov et al., 2017). It will also influence the rate of change in the marine ecosystem on a seasonal basis as the part of the year with ice-covered ocean shortens and open water with associated processes (e.g., wind-driven mixing, air-sea exchanges) will become a more dominant feature of the Arctic Ocean, particularly along the shelves and ice edges and during summer and autumn. Increased heat and volume transport from northward flowing currents affect the phenology and development rates of plankton (Søreide et al., 2010). Water temperature strongly influences the geographical, vertical and seasonal distributions of plankton and can be particularly important for species at the edge of their thermal optimum range (Greene et al., 2003).

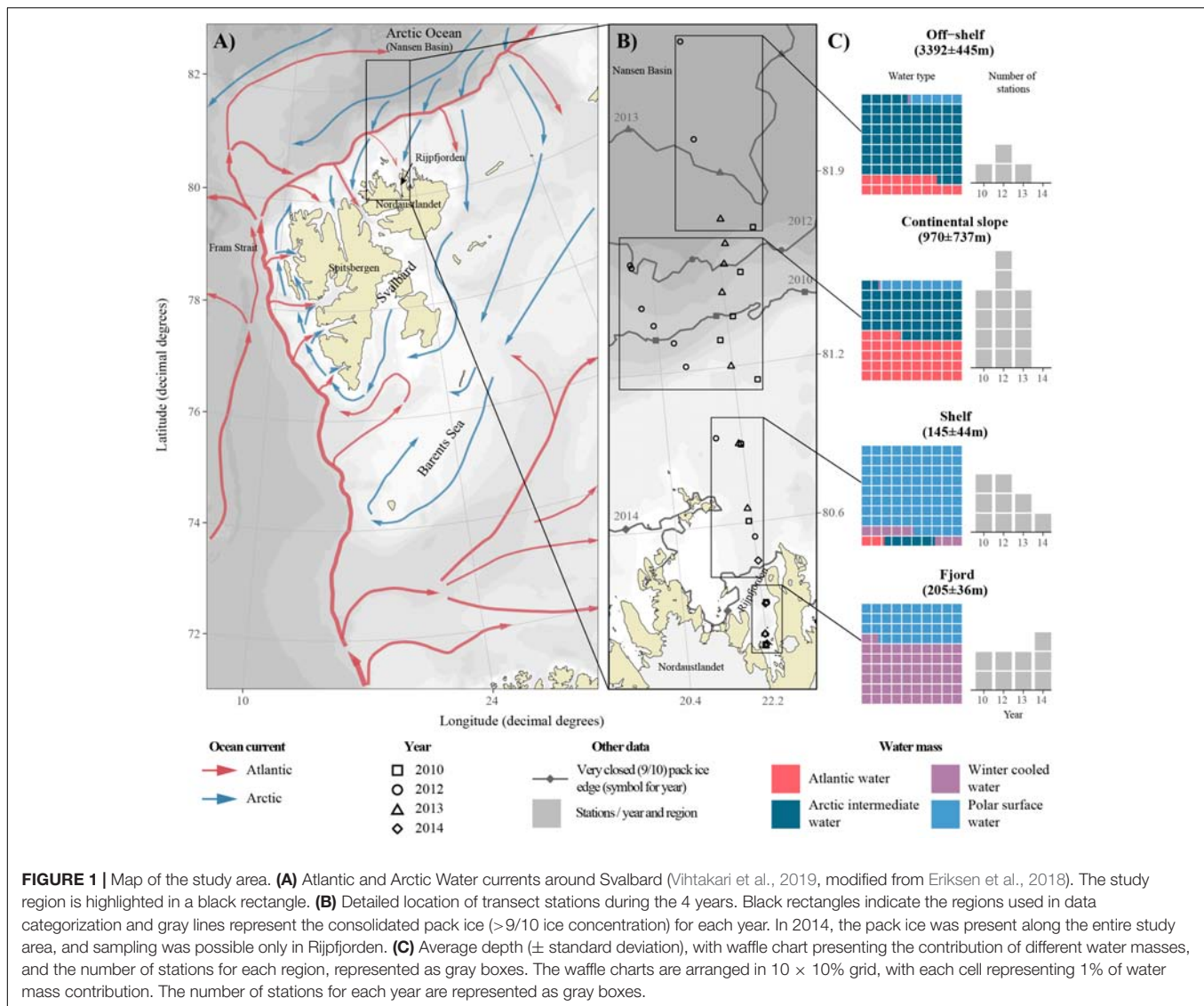
The AW Boundary Current affects not only the Arctic Ocean thermal conditions and sea ice cover (Beszczynska-Möller et al., 2012; Onarheim et al., 2014), but also the stocks and structures of biotic communities from primary producers to higher trophic level consumers, through the supply of nutrients and drifting

organisms (Kosobokova and Hirche, 2009; Bluhm et al., 2015; Wassmann et al., 2015). High biomass of both boreal and Arctic zooplankton is transported along this route (Kosobokova and Hirche, 2009; Wassmann et al., 2015; Gluchowska et al., 2017a; Basedow et al., 2018). Models and temperature records from moorings suggest that the area north of Svalbard will be particularly affected by ocean warming due to increased advection of heat within the WSC, and because of atmospheric warming (Slagstad et al., 2011, 2015; Polyakov et al., 2017). This will also influence the position of the southern extent of the pack ice and its seasonal retreat off the shelf (Onarheim et al., 2014; Polyakov et al., 2017), and will add to the observed loss in sea ice extent and thickness for the Arctic Ocean (Barber et al., 2015). In this setting, it is of particular interest to study the transition of water masses, nutrients, ocean acidification (OA) state and plankton from the fjord, via the shelf and continental slope into the deep Arctic Ocean. As part of the ICE-project (NPI) we extended an established transect in Rijpfjorden northwards across the Atlantic and ArW masses on the shelf and continental slope to 3000 m depth in the Nansen Basin. The crossing of the pelagic zone of the AW Boundary Current is based on summer data along the Rijpfjorden-Arctic Ocean transects from 2010 to 2014 (**Figure 1**). Thus, we here provide baseline conditions for the pelagic system in this part of the Arctic Ocean, which are crucial for identifying and interpreting future changes in the area north of Svalbard. This transect was the most northern and eastern crossing of the AW Current as part of the Carbon Bridge project, and our study is the first to present physical, chemical and biological data along a transect from a fjord to the Arctic Ocean. Because of challenging ice conditions, no repeated transect studies have been carried out previously from fjords at 80°N. Based on our knowledge, we expected to find a post-bloom situation with nutrient limitations in the upper part of the water column during our summer sampling campaigns, and predominance of Arctic zooplankton in ArW masses (e.g., inside cold Rijpfjorden) and boreal zooplankton in the AW Boundary Current.

MATERIALS AND METHODS

Sampling

Physical, chemical and biological data including hydrography (temperature and salinity), nutrient concentrations, carbonate chemistry, and chlorophyll *a* (Chl *a*), as well as protist and zooplankton composition and abundance were collected during annual summer cruises to Rijpfjorden and the adjacent Nansen Basin of the



Arctic Ocean with R/V *Lance* on 17–29 August in 2010, 16 July–3 August 2012, 26–30 July 2013, and 27–29 July 2014 (Table 1). Chlorophyll *a*, nutrients and protist abundance and biomass were determined for the depths of 0, 10, 25, 50, 100 m, and Chl *a* maximum when it differed ($\pm$ 5 m) from the standard depths. Occasionally, samples were collected from depths differing from those listed above. Dissolved inorganic carbon (DIC), pH and total alkalinity (AT) were determined, for carbonate chemistry, during 2012–2014. In 2014, sampling was limited to four stations in Rijpfjorden and inner shelf, because of heavy ice further out on the shelf. Stations along the sampled transects were categorized into four regions: fjord, shelf, continental slope, and off-shelf (Figure 1), each of the regions representing a different environmental setting.

Ice Cover

The location of dense, consolidated (9/10) sea ice north of Rijpfjorden was estimated from vectorized ice maps from the

Norwegian Meteorological Institute (MET Norway¹), for a time close to mid-date of each sampling campaign (Figure 1).

MET Norway ice maps are interpreted manually from Synthetic Aperture Radar data from several available earth observing satellites².

Hydrography

Oceanographic measurements and water samples were collected using a ship-board CTD probe attached to a Rosette-sampler with 12 Niskin bottles (SBE911 plus, Sea Bird Electronics, Bellevue, WA, United States). The CTD is calibrated by Sea Bird Electronics annually before each sampling season. Photosynthetically Active Radiation (PAR, 400–700 nm) was measured with planar sensors (Biospherical Instruments Inc.), one mounted on the CTD Rosette for underwater PAR

¹<http://polarview.met.no/>

²<http://polarview.met.no/documentation.html>

TABLE 1 | Overview of water chemistry parameters.

Region and year	Water depth (m)	Temp (°C)	Sal	pH	DIC ($\mu\text{mol kg}^{-1}$)	AT ($\mu\text{mol kg}^{-1}$)	fCO ₂ (μatm)	Ω_{Ar}	NO _x (mmol m^{-3})	PO ₄ (mmol m^{-3})	Si(OH) ₄ (mmol m^{-3})	Chl <i>a</i> (mg m^{-3})
Fjord and shelf												
2010	≤50	2.7 ± 1.4	33.2 ± 1.0						1.1 ± 2.1	0.2 ± 0.2	1.4 ± 1.0	0.3 ± 0.2
2010	>50	−0.1 ± 1.7	34.5 ± 0.2						0.5 ± 0.7	0.2 ± 0.1	1.7 ± 0.8	0.2 ± 0.3
2012	≤50	0.9 ± 1.2	33.9 ± 0.9	8.3 ± 0.1	2050 ± 49	2268 ± 41	211 ± 35	2.3 ± 0.2	1.0 ± 1.2	0.2 ± 0.2	0.7 ± 0.4	1.4 ± 2.5
2012	>50	−0.3 ± 1.0	34.7 ± 0.1	8.2 ± 0.1	2142 ± 34	2304 ± 9	286 ± 58	1.7 ± 0.3	5.5 ± 3.8	0.8 ± 0.4	2.1 ± 1.5	4.6 ± 5.8
2013	≤50	−0.2 ± 0.7	33.5 ± 1.0	8.2 ± 0.1	2039 ± 104	2206 ± 105	273 ± 100	1.8 ± 0.5	0.6 ± 1.3	0.1 ± 0.1	0.7 ± 0.6	0.6 ± 0.8
2013	>50	−0.6 ± 1.2	34.7 ± 0.2	8.2 ± 0.1	2152 ± 32	2312 ± 15	290 ± 44	1.7 ± 0.2	3.2 ± 2.4	0.4 ± 0.2	1.5 ± 1.2	0.1 ± 0.0
2014	≤50	−0.8 ± 0.5	33.3 ± 1.7	8.3 ± 0.1	1915 ± 258	2123 ± 256	177 ± 73	2.2 ± 0.4	2.6 ± 3.4	0.3 ± 0.3	1.2 ± 1.4	3.2 ± 4.9
2014	>50	−1.5 ± 0.2	34.6 ± 0.2	8.1 ± 0.0	2150 ± 23	2294 ± 13	297 ± 22	1.6 ± 0.1	8.9 ± 1.3	0.7 ± 0.1	4.2 ± 0.7	0.3 ± 0.2
Cont. slope and off-shelf												
2010	≤50	0.8 ± 1.7	33.5 ± 1.3						2.0 ± 1.9	0.2 ± 0.1	1.1 ± 0.7	0.2 ± 0.2
2010	>50	0.9 ± 1.6	34.9 ± 0.1									
2012	≤50	0.5 ± 1.4	33.7 ± 1.1						1.8 ± 2.1	0.2 ± 0.2	1.6 ± 1.0	0.6 ± 0.6
2012	>50	0.6 ± 1.6	34.9 ± 0.1						10.3 ± 2.2	0.9 ± 0.2	6.0 ± 2.5	0.2 ± 0.1
2013	≤50	−0.1 ± 1.2	33.8 ± 1.0	8.2 ± 0.1	2025 ± 113	2205 ± 92	242 ± 99	1.9 ± 0.4	1.8 ± 2.9	0.2 ± 0.2	1.3 ± 1.2	0.7 ± 0.7
2013	>50	0.3 ± 1.3	34.9 ± 0.1	8.1 ± 0.0	2169 ± 10	2310 ± 8	347 ± 23	1.4 ± 0.2	7.0 ± 2.6	0.7 ± 0.1	3.6 ± 1.8	1.0 ± 1.2

Region (see **Figure 1**), year and water depth-aggregated mean values (+ standard deviation) for temperature (Temp), salinity (Sal), and other parameters explained in text. The depth limit of 50 m was chosen as an approximation of the euphotic depth.

measurements (2012–2014) and one mounted on the front deck of RV *Lance* for reference measurements of incoming PAR (2014). Euphotic depth was defined as the depth with PAR closest to $0.48 \mu\text{mol photons m}^{-2} \text{ s}^{-1}$. The threshold value was an average of 0.1% surface PAR (sPAR) for the four CTD casts with sPAR information in 2014. The depth of maximum stratification was defined as the depth of maximum squared buoyancy frequency (N^2), which was calculated with the oce package (Kelley and Richards, 2018).

Four different water masses were identified based on a modified classification from Pérez-Hernández et al. (2017): Atlantic Water (AW) was defined using the temperature threshold $>1^\circ\text{C}$ and salinity >34.87 ; Arctic Intermediate Water (AIW) was defined using the same salinity threshold and temperature range of $[-1, 1]$; Winter Cooled Water (WCW) was defined following Cottier et al. (2005) with a temperature threshold of $< -0.5^\circ\text{C}$ and salinity threshold of >34.4 (excluding the AIW data points); Remaining salinity and temperature values were assigned to Polar Surface Water (PSW, **Figure 2**).

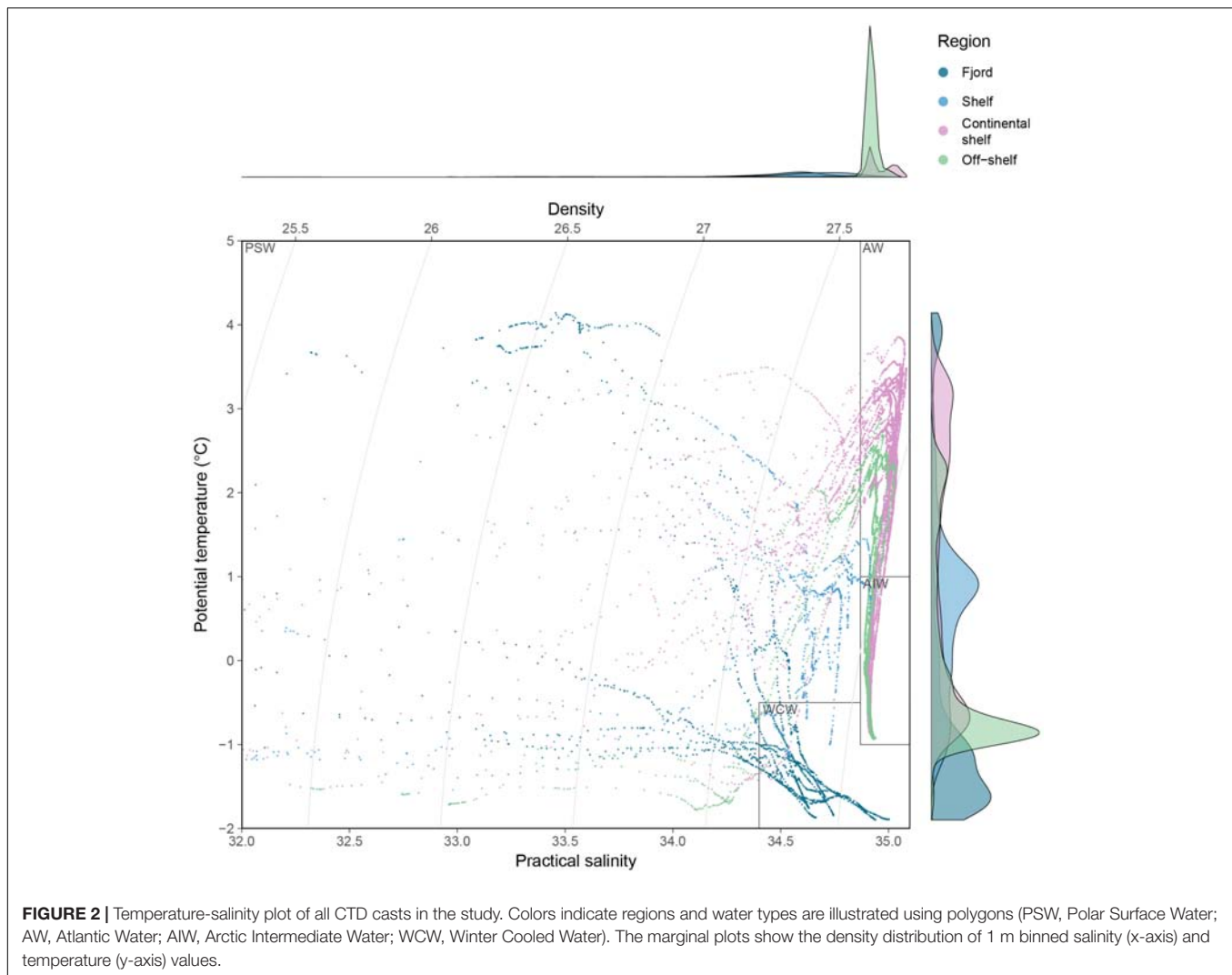
Carbonate Chemistry and Ocean Acidification State

Carbonate chemistry parameters were calculated from DIC and total alkalinity (AT) values that were analyzed after the cruises at the Institute of Marine Research (IMR Tromsø, Norway) following the method described in Dickson et al. (2007). DIC was determined using gas extraction of acidified samples followed by coulometric titration and photometric detection using a Versatile Instrument for the Determination of Titration carbonate (VINDTA 3C, Marianda, Germany). The AT was determined by potentiometric titration with 0.1 N hydrochloric acid using a Versatile Instrument for the

Determination of Titration Alkalinity (VINDTA 3D, Marianda, Germany). Routine analyses of Certified Reference Materials (CRM, provided by A. G. Dickson, Scripps Institution of Oceanography, United States) ensured the accuracy of the measurements, which was better than $\pm 1 \mu\text{mol kg}^{-1}$ and $\pm 2 \mu\text{mol kg}^{-1}$ for DIC and AT, respectively. We used DIC, AT and nutrient concentrations as input parameters in a CO₂-chemical speciation model (CO2SYS program; Pierrot et al., 2006) to calculate other variables in the carbonate chemistry, such as pH, fugacity of CO₂ ($f\text{CO}_2$), saturation state of aragonite (Ω_{Ar}) and calcite (Ω_{Ca}). The calculations are based on the carbonate system dissociation constants (K^*_1 and K^*_2) estimated by Mehrbach et al. (1973), modified by Dickson and Millero (1987), and the HSO_4^- dissociation constant from Dickson (1990).

Inorganic Nutrients, Chlorophyll *a*, and Protist Community Composition

Inorganic nutrient samples (2010–2014) were frozen and later analyzed at UiT The Arctic University of Norway by standard seawater methods using a Flow Solution IV analyzer (O.I. Analytical, United States). The analyzer was calibrated using reference seawater from Ocean Scientific International Ltd., United Kingdom. Detection limits were $0.02 \mu\text{mol L}^{-1}$ for nitrate+nitrite (NO_x), $0.01 \mu\text{mol L}^{-1}$ for phosphate and $0.07 \mu\text{mol L}^{-1}$ for silicic acid. The set of samples from the inner fjord from 2012 was analyzed at IMR. These samples were collected in 20 mL scintillation vials, fixed with 0.2 mL chloroform and stored refrigerated until sample analysis approximately 3 months later. Nitrite, nitrate, phosphate and silicic acid were measured spectrophotometrically at 540, 540, 810, and 810 nm, respectively, on a modified Scalar autoanalyzer.



The measurement uncertainty for nitrite was $0.06 \mu\text{mol L}^{-1}$ and 10% or less for nitrate, phosphate and silicic acid.

To estimate Chl *a* concentrations, seawater samples of 100–500 mL were filtered through 25 mm GF/F filters (Whatman), extracted in 100% methanol for 12 h at 5°C on board the ship and measured fluorometrically with an AU10 Turner Fluorometer (Turner Design, Inc.) according to the method by Parsons et al. (1984).

Seawater subsamples for protist enumeration were settled in 50 mL Utermöhl sedimentation chambers (Hydro-Bios, Kiel, Germany) for 48 h. Protists in the subsamples were identified and enumerated at 100–600 $\times$ magnification using an inverted Nikon Ti-S light microscope. The organisms were identified to the lowest taxonomic level possible and grouped into size-classes. In cases when detailed identification was not possible, specimens were assigned to higher-rank taxa, incertae sedis (i.e., protists, but not determined to higher rank) or three size classes (3, 3–7, and $>7 \mu\text{m}$) in case of unidentified flagellates (Flagellates indet.). Counts of the dominant organisms in each sample were always well above the recommended number of 50 counts per

sample. Protist abundance per liter was calculated considering the area of the investigated chamber surface, chamber volume and proportion of total chamber surface area to the ocular field of view area. When possible, dominant taxa were measured and the mean cell size was used to calculate the biovolumes from equivalent geometrical shapes (Hillebrand et al., 1999). When detailed measurements were not possible, mean biovolumes were taken from HELCOM database or from <http://nordicmicroalgae.org>. The biovolume was converted to cellular carbon content in $\mu\text{g C cell}^{-1}$ using published carbon conversion factors (Menden-Deuer and Lessard, 2000).

Mesozooplankton Community Composition

Stratified vertical net hauls to collect zooplankton samples were performed with a multiple plankton net (MultiNet, Hydro-Bios, Kiel, Germany) consisting of five nets with 0.25 m^2 opening and $200 \mu\text{m}$ mesh size. The depth strata sampled were: 0–20, 20–50, 50–100, 100–200, and 200 m–bottom, or 0–20, 20–50, 50–200, 200–600, and 600 m–bottom in deeper water. The

lower limit of the deepest layer sampled was set at 20 m above the bottom. Samples were preserved in 4% final concentration hexamethylenetetramine-buffered seawater formaldehyde solution immediately after collection. The organisms were identified and counted under a stereomicroscope equipped with an ocular micrometer, following sample examination procedures recommended by Postel (2000). Each sample was first scanned for macrozooplankton (organisms with total length >5 mm), which were picked out, identified and counted for the entire sample. The remaining mesozooplankton size fraction (<5 mm) was suspended in a fixed volume of water, from which 2 mL subsamples were taken using a large-volume automatic pipette with tip cut to make 5 mm opening (an equivalent of Stempel pipette). At least three subsamples were examined thoroughly under a stereomicroscope during this part of sample examination, and the total number of individuals recorded, identified and enumerated was never less than 500. The rest of the sample was searched in order to identify and enumerate numerically less important taxa. Zooplankters were identified to species or the lowest taxonomic level possible, including identification of the developmental stages whenever feasible. *Calanus* spp. were identified to species for each developmental stage based on morphology and size according to the criteria from Kwasniewski et al. (2003).

Original zooplankton data represent abundance values of zooplankters per unit volume (ind. m⁻³) for each sampled depth strata (see above). Abundance values were converted to biomass estimates (mg dry mass m⁻³) using species-specific dry mass values gathered from published sources or measured by the authors (see Hop et al., 2019 for details). The biomass for each organism in each layer was summed up and converted to depth-averaged biomass at a station using the following equation:

$$\frac{\sum_{i=1}^n a_i d_i}{\sum_{i=1}^n d_i}$$

where a_i is the biomass of species a at depth stratum i , d_i is the sampled distance for depth stratum i in meters, and n is the number of depth strata in net haul at a station. Dry mass was converted to carbon using conversion factors of 0.5 for crustaceans and chordates, 0.3 for meroplankton, and 0.1 for gelatinous taxa (Table 3).

The Shannon-Wiener diversity index and evenness as well as abundance-biomass ratios, were calculated for zooplankton from each of the four regions (Figure 1) and for the two main water masses – Atlantic Water and ArW (including all sub-types listed in Figures 1, 2). All identified zooplankton taxa were considered for these calculations. Regarding the four regions, abundance data were vertically integrated using the above equation for each station and sampling instance, and then averaged over all the stations included in each of the four regions. Calculations were then performed on the averaged data. The abundance of taxa in each water mass was computed from the product of the total abundance of a given taxa in a sample and the fraction of each water mass in the water sample. These calculations were done over all the available samples leading to average abundance of each taxa per water mass weighted by the two main water mass

fractions. Abundance data were used to compute the Shannon-Wiener diversity index, based on natural logarithm and natural digits, nats. ind⁻¹ as measurement unit, and evenness. Biomass data were averaged following the same method as for abundance data, allowing the calculation of abundance-biomass ratios.

RESULTS

Ice Cover

The sea ice extent varied considerably between summers (Figure 1B). In 2010 and 2012, the ice edge was situated over the continental slope while in 2013 it had retreated further northwards over the deep basin. The summer 2014 was distinctively different. Sea ice covered the entire shelf down to the coast of Nordaustlandet with only parts of Rijpfjorden being ice-free.

Water Mass Distribution

The study area is influenced by relatively warm AW transported in the Svalbard branch of the WSC, flowing at subsurface depths along the continental slope into the Arctic Ocean, as the AW Boundary Current, and by colder and fresher Arctic surface waters transported with the Transpolar Drift and Arctic coastal waters (Figure 1A). The relative contribution of the four different water masses identified in this study varied depending on region (Figure 1C). Polar Surface Water and WCW were present along the entire transect. WCW was the dominant water mass inside the fjord, occupying the deeper part of the fjord basin (Figure 3), but its relative contribution declined toward the shelf with only minor contribution to continental slope waters. Polar Surface Water was generally restricted to the upper 100 m of the water column, and the presence of this water mass lead to a stratified water column from the fjord system out to the continental slope (Figure 3). The temperature of the PSW was the coldest in the last 2 years of the time series. In 2013, the water in the upper 50 m was generally colder and fresher than in July 2012, and PSW was coldest in 2014, the year with most extensive ice cover. In contrast, in 2010, sampling along the transect was conducted later in the season than in the other years, thus, the PSW had received the largest surface insolation, which had warmed the water up to nearly 4°C. Penetration of AW onto the shelf was evident in 2010–2013, but made a relatively minor contribution to the water mass budget. The main core of AW was located over the upper continental slope (typically between the 500 and 1000 m isobath) with temperature reaching 3°C and salinity >35.0. The extent of AW differed among years, as can be appreciated from the varying positions of the T = 1°C, S = 34.87 isolines (Figure 3). Atlantic Water remained a prominent water mass off-shelf, where AIW dominated. Distribution of AIW showed an opposite trend to WCW; it declined toward the continental slope and shelf and was absent inside the fjord (Figure 1).

Carbonate Chemistry and Ocean Acidification State

The pH-values and the aragonite and calcite saturation states (Ω_{Ar} , Ω_{Ca}) showed large spatial variability (Figure 4). In 2013,

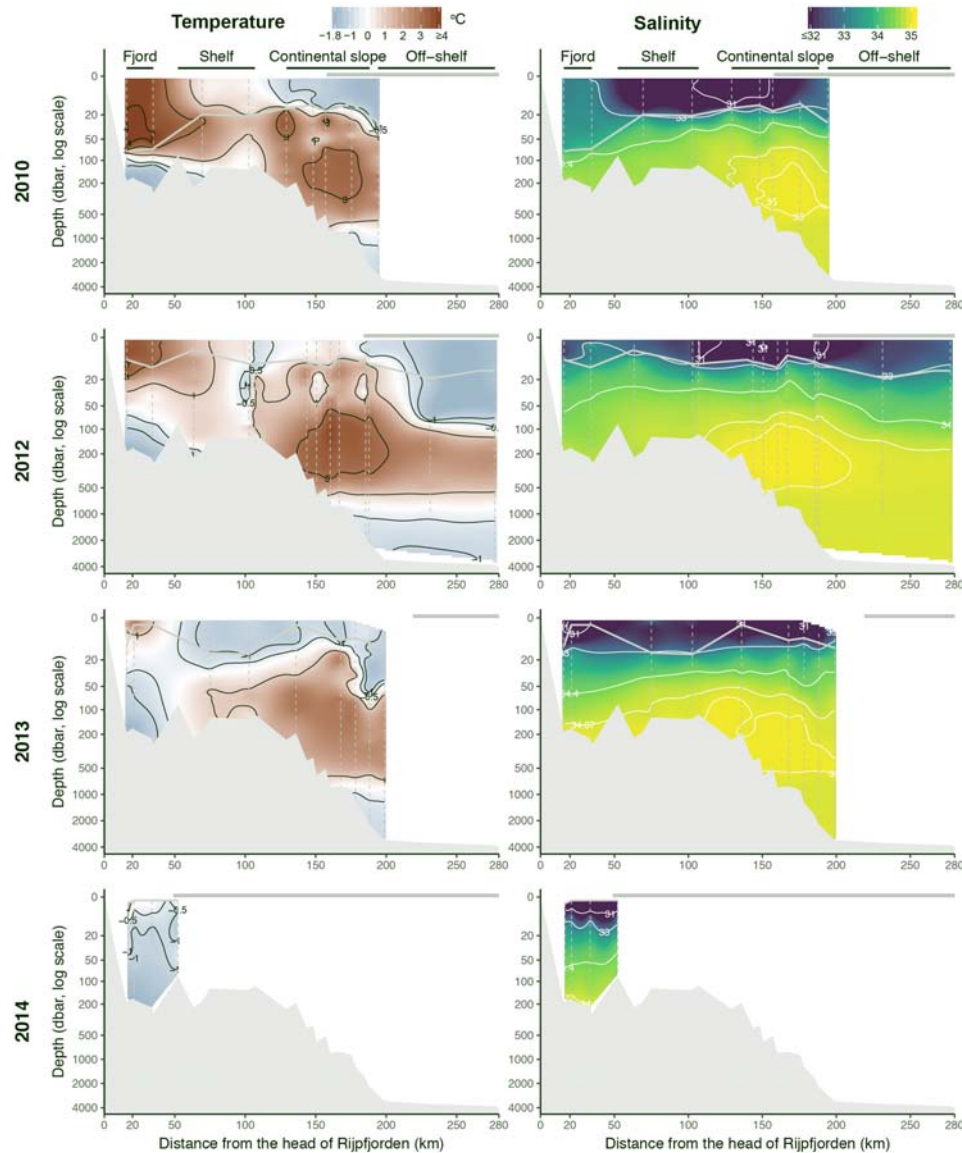


FIGURE 3 | Temperature and salinity along transects from inner Rijpfjorden to the deep Arctic Ocean, in July–August 2010, 2012, 2013, and 2014. Gray horizontal line at 0 m indicates the extent of consolidated pack ice, and they gray line on top of the gridded values is the depth of maximum stratification. The section from 2014 was limited to Rijpfjorden because of heavy sea ice. Vertical dashed lines indicate individual CTD casts.

pH and Ω_{Ar} were relatively high in the surface water along the transect from inside the fjord to shelf slope and off slope, compared to further down in the water column. The variables most relevant for ocean acidification, pH and Ω_{Ar} (Ω_{Ca}) varied between 7.96 and 8.58, and 0.99 (1.53) and 2.92 (4.68), respectively (**Figure 4**). The highest pH and Ω_{Ar} were found at the surface and local spots coinciding with depleted nitrate and phosphate concentrations for all years. The lowest Ω_{Ar} of about 0.99 was observed in the bottom water off the slope in 2013 and was close to 1 (near undersaturation) in the upper 10 m on the shelf. The Ω_{Ar} horizon, where $\Omega_{Ar} < 1$, was located at 2000 m depth in the off-slope area. The highest pH (8.58) and Ω_{Ar} (2.92) were observed in the fjord in the upper 20 m in 2014.

The pH and Ω_{Ar} values varied between years in the upper 200 m along the Rijpfjorden transect (**Figure 4**). Generally, Ω_{Ar} values were higher at the surface decreasing toward the bottom, except for in the fjord and shelf in 2013.

Nutrients and Chlorophyll a Concentration

Nitrate and nitrite (NO_x) concentrations were low or at detection limit in the upper 25–50 m of the water column in all years and increased below 50 m depth (**Figure 5**). NO_x was strongly correlated with PO_4 and $Si(OH)_4$ with Pearson's correlation coefficients of 0.93 and 0.90, respectively. The nutrient status,

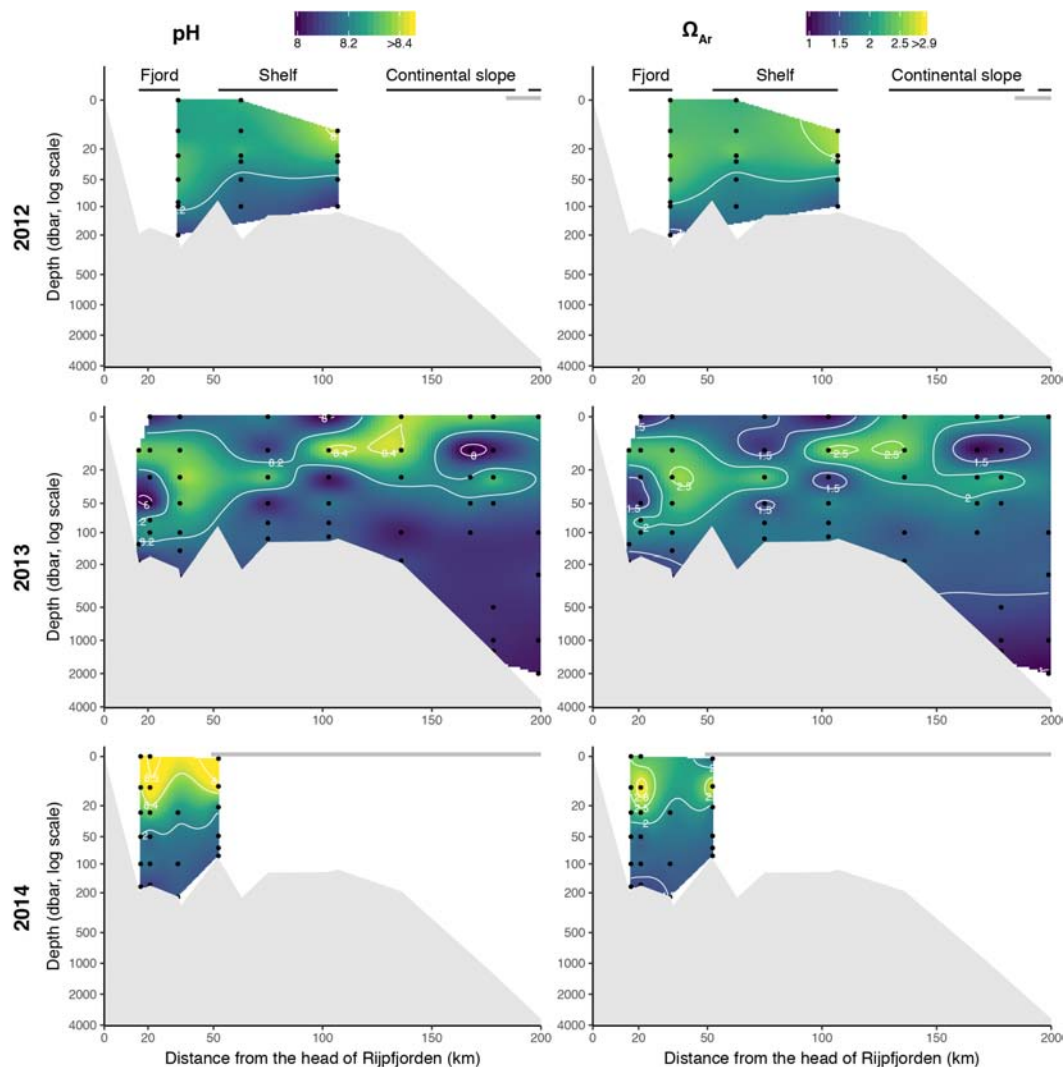


FIGURE 4 | pH and aragonite saturation (Ω_{Ar}) along the Rijpfjorden transect, July–August 2012–2014. Gray horizontal line at 0 m indicates the extent of consolidated pack ice.

as indicated by the $\text{NO}_x:\text{PO}_4$ ratio, was related to water masses (Figure 6). Polar Surface Water showed the lowest $\text{NO}_x:\text{PO}_4$ ratio, well below Redfield ($\text{N}:\text{P} = 16:1$), indicating nitrogen as the putative limiting nutrient and an increase in nitrogen limitation toward the fjord. Shoaling of the nutricline was observed at the upper slope in 2010, 2012 and 2013 with elevated NO_x concentrations at 25 m depth. In 2010 and 2012, elevated surface NO_x concentrations were observed at the northernmost ice-covered stations.

Chlorophyll *a* concentrations were generally $< 1 \text{ mg m}^{-3}$ in surface waters and showed distinct subsurface maxima coinciding with the bottom of the euphotic zone (Figure 5). The depth of maximum stratification was always shallower than the euphotic zone (no PAR data available for 2010) indicating that phytoplankton growth was not light-limited. In 2014, there was a marked sub-surface bloom, with deep Chl *a* max at 30–40 m depth, in the outer part of the fjord while the situation further

out is unknown due to the lack of measurements in that year. Depth-integrated (0–50 m) Chl *a* standing stocks ranged from 9 to 233 mg m^{-2} (Supplementary Figure S1). The subsurface bloom in 2014 is reflected in the high Chl *a* standing stocks of 209 and 233 mg m^{-2} inside the fjord and the inner shelf, respectively, while the range in the other years was much more confined ($9\text{--}48 \text{ mg Chl } a \text{ m}^{-2}$).

Protist Abundance, Biomass, and Composition

Overall, 321 taxa were identified with 141 to species, 121 to genus and 59 to class. The number of taxa varied between years. In 2010, the highest number of 166 taxa was observed: 76 inside the fjord, 86 on the shelf, 135 over the continental slope and 66 off-shelf. In 2012, nearly as many taxa were observed (164). In that year, the fjord also had fewer taxa than

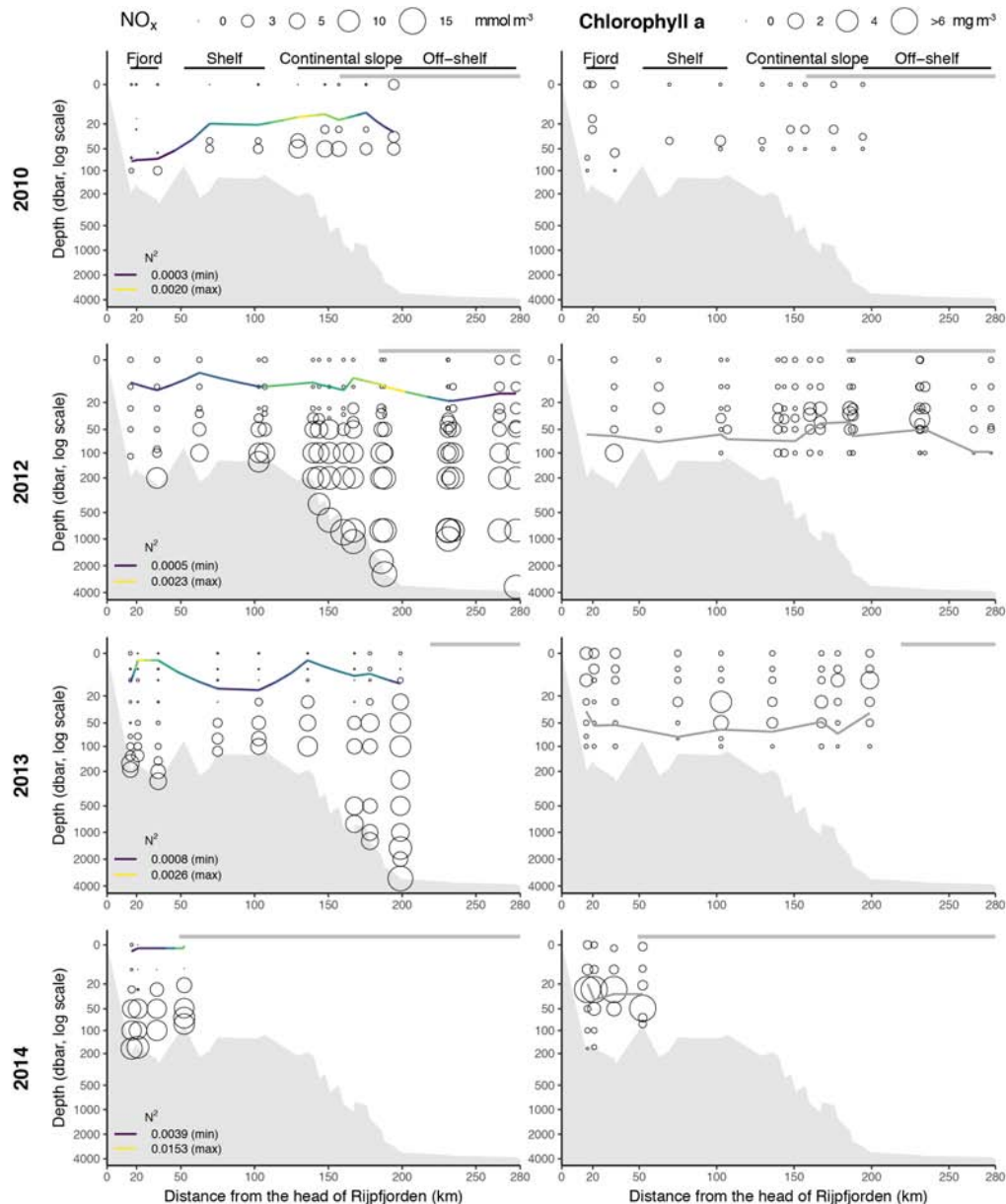


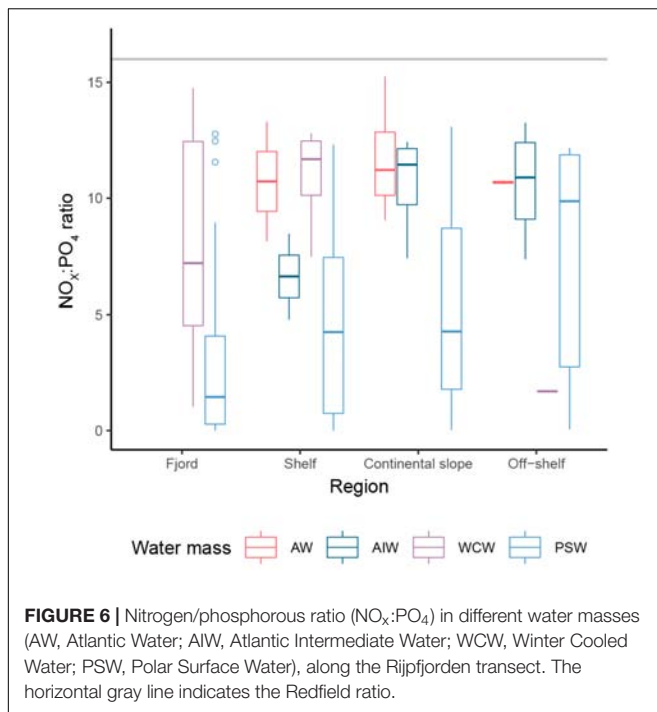
FIGURE 5 | Nitrate and nitrite (NO_x) (left panels) and Chlorophyll *a* (right panels) concentrations along the Rijpfjorden transect. Size of bubbles relates to concentration (mmol m^{-3} and mg m^{-3} , respectively). Thin line in left panels indicates depth of maximum stratification with minimum and maximum levels specified (colors and numbers). Thin gray line in right panels indicates euphotic zone depth (i.e., CTD depth with PAR value $0.47 \mu\text{mol photons m}^{-2} \text{s}^{-1}$, which is 0.1% of surface radiance value for the CTD with surface irradiance measurement). The thick gray horizontal line indicates the extent of consolidated pack ice.

shelf waters, whereas off-shelf waters hosted higher number of protists than the continental slope (145 versus 67). In 2013, the lowest protists richness was recorded (94). In spite of heavy ice conditions in 2014, as much as 129 taxa were observed that year, surpassing the number of taxa observed in this part of the transect the previous years.

The most frequently occurring taxa ($F > 90\%$, sizes $< 30 \mu\text{m}$) were; choanoflagellates (*Monosiga* sp.), flagellates of unknown taxonomic affiliation and nutritional mode (flagellates indet.), dinoflagellates (*Gymnodinium galeatum*,

Gymnodinium sp., $5\text{--}10 \mu\text{m}$ and $10\text{--}20 \mu\text{m}$, respectively), the heterotrophic cryptophyte *Eucryptos marina* and the ciliate *Lochmaniella oviformis*.

Protist abundance and biomass ranged from 2.21×10^2 to $1.39 \times 10^7 \text{ cells L}^{-1}$ and $0.1\text{--}633 \mu\text{g C L}^{-1}$ depending on depth and year (**Supplementary Tables S1, S2**). The biovolume of the observed cells (μm^3) ranged from 1 to $827 \times 10^3 \mu\text{m}^3$ (mean $2.1 \times 10^3 \mu\text{m}^3$). In terms of abundance, species within the nanoplankton size range ($2\text{--}20 \mu\text{m}$) dominated the protistan assemblage, with most prominent taxa being prymnesiophytes



(15.9–60.3%), flagellates indet. (10.6–33.0%), chrysophytes (4.3–13.2%) and cryptophytes (1.3–13.7%), the latter two combined under “other” (**Supplementary Figure S2**). In total, their pooled share ranged from 70.7–82.6%. The common and important members of protistan plankton – dinoflagellates and diatoms – contributed with only 1.7–3.7 and 1.4–12.6% to overall abundance, respectively. However, in terms of biomass, dinoflagellates were the dominant component of protist biomass and standing stocks (0–50 m) in all years (**Figures 7, 8**). Athecate (naked) dinoflagellates belonging to the Gymnodiniales were particularly prominent. Ciliates also contributed a significant share of protist biomass and were represented by both aloricate (in particular *Lohmanniella oviformis*, *Leegaardiella sol*, *Laboea strobila*, and *Mesodinium rubrum*) and loricate (in particular *Parafavella obtusangula*, *Ptychocylis acuta*, and *Acanthostomella norvegica*) ciliate species. Prymnesiophytes, mainly represented by *Phaeocystis pouchetii*, and diatoms were often predominant at subsurface depths (**Figure 7**). Diatoms contributed only significantly to protist biomass in the subsurface bloom on the inner shelf station in 2014 (**Figures 7, 8**). The dominant species in the subsurface bloom were *Fragilariopsis oceanica* and *Shionodiscus bioculatus* (formerly *Thalassiosira bioculata*).

Protist standing stocks in the upper 50 m exceeded zooplankton standing stocks in 2010 and 2014 on all sampled regions, and on the continental slope and off-shelf in 2012 and 2013, while zooplankton standing stocks exceeded protist standing stocks inside the fjord and on the shelf in those years (**Figure 8**).

Mesozooplankton

In general, zooplankton was more abundant in the fjord and on the shelf than on the continental slope and off-shelf regions,

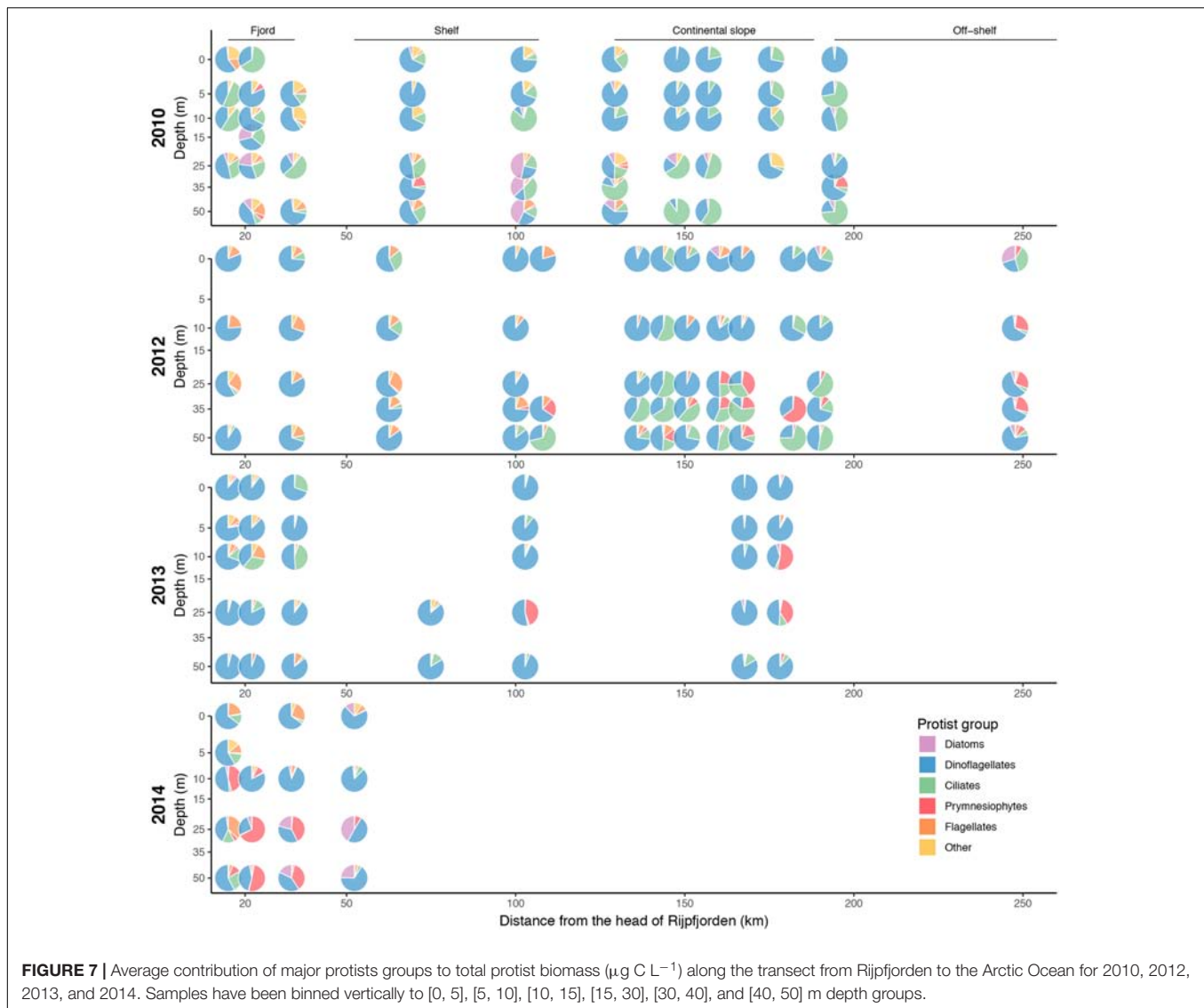
for both meroplankton (Cirripedia nauplii, Echinodermata larvae, Bivalvia veligers) and holoplankton (**Table 2**). Copepods dominated the zooplankton community in terms of abundance, with *Calanus glacialis* being the most common copepod in 2012–2014 and *Oithona similis* dominating in 2010 (**Figure 9**). Among non-copepods, meroplanktic taxa dominated in terms of abundance in 2012–2014, whereas *Fritillaria borealis* tended to overrun the community in 2010. Among pelagic predators, chaetognaths were most common, with *Parasagitta elegans* dominating in the fjord and *Eukrohnia hamata* in the open water.

There were significantly negative relationships between the abundance (log transformed) of *C. finmarchicus*, *C. glacialis*, *C. hyperboreus*, *Pseudocalanus* spp., *O. similis*, copepod nauplii, *P. elegans*, meroplankton, *Oikopleura* sp., and *Limacina helicina* and the distance to the head of Rijpfjorden, i.e., the abundance of these species decreased toward the open water (**Supplementary Figure S3**). In reverse, the abundance of *Microcalanus* spp., *Metridia longa*, Ostracods, *E. hamata*, *Triconia borealis*, and *Themisto abyssorum* increased toward open water. The abundance of *Oithona atlantica*, *F. borealis*, *Aglantha digitale*, and *Themisto libellula* showed no significant trend in distribution along the transect, but in case of the last two species firm conclusions cannot be made because of typically low species abundance.

A comparison of distribution of water masses and zooplankton shows that *C. glacialis*, *P. elegans*, and *Mertensia ovum* occurred in higher numbers in WCW inside the fjord, than outside in association with open ocean water masses (**Table 2**). The AW along the slope had high abundance of boreal *C. finmarchicus*, *O. similis*, and *T. abyssorum* as well as other oceanic species such as *E. hamata* and *Microcalanus* spp.

Zooplankton biomass per unit volume ($\text{mg dry mass m}^{-3}$) was highest inside Rijpfjorden and on the shelf, but dropped at the shelf break (**Figure 10A**). Outside the fjord, the deeper strata had the largest zooplankton biomass. Zooplankton carbon standing stocks (0–50 m) were dominated by *Calanus* spp. across all regions and years (**Figure 8**). Only inside the fjord and on the continental slope in 2010 was the contribution of *O. similis* comparable to that of *Calanus* spp. (**Figure 8**). Among the *Calanus* species, *C. glacialis* contributed the most to the total biomass of mesozooplankton in the fjord and on the shelf (**Figures 10B, 11A**), while its contribution to total zooplankton biomass decreased at the shelf break and further into the deep Arctic Ocean. *Calanus finmarchicus* contributed 19% of the total *Calanus* biomass inside the fjord, but in the core of the AW at shelf and intermediate depth of the continental slope, *C. finmarchicus* and *C. glacialis* contributed in similar amounts to the *Calanus* biomass (30–40%; **Figure 11B**). *Calanus hyperboreus* contributed generally less to the *Calanus* biomass in the fjord and on the shelf (~10%), but contributed substantially off the shelf (70%) (**Table 3** and **Figure 11C**).

The Shannon-Wiener diversity indexes for fjord, shelf, slope and off-shelf regions were 2.04, 2.14, 2.05, and 2.36 nats ind.^{-1} , respectively, whereas corresponding evenness values were 0.49, 0.53, 0.45, and 0.52. The number of taxa for those four regions were: 64, 57, 96, and 95. Thus, higher diversity, was found toward the open ocean and this was reflected in higher diversity index



for AW (2.20) than ArW (2.07). Abundance-biomass ratios for the distinguished regions were: 134, 145, 110, and 114 ind. mg^{-1} . This indicates that the average size of zooplankton taxa was smaller in the fjord and shelf than over the slope and open ocean, which likely reflected the substantial contribution of small-sized *Oithona similis* and meroplankton closer to the coast.

DISCUSSION

Variations in Atlantic Water Boundary Current

The AW Boundary Current has been shown to vary considerably on small temporal and geographical scales, both when comparing nearby transects from the same cruise (Pérez-Hernández et al., 2017) and from mooring time series (Renner et al., 2018). Short-term variability due to meandering (Pérez-Hernández et al., 2017) as well as eddies (Våge et al., 2016; Crews et al., 2017)

affect the position and extent of the AW core. It is therefore difficult to diagnose variability in e.g., advected volume of AW to the region based on single transects occupied in different years; the only published time-series from moorings in the boundary current are from summer 2012–2013 (Renner et al., 2018), hence covering only part of the period between the 2012 and 2014 cruises presented in this study.

The results of the Regional Arctic System Model (RASM), a fully-coupled sea ice-ocean model for the Arctic (Cassano et al., 2017), indicate that the sea ice concentration and volume during the 8 months preceding the survey were the highest in 2014 and 2010 and the lowest in 2013, compared to the average during 1997–2016. On the other hand, anomalies in net heat transport, calculated for a fragment of the study section from the edge of the shelf to the 1000 m isobaths, for the 100–600 m layer, were the highest in 2012 and the lowest in 2014. This suggests that the amount of Atlantic water transported eastward into the Arctic Ocean was the largest in 2012 and the least in 2014.

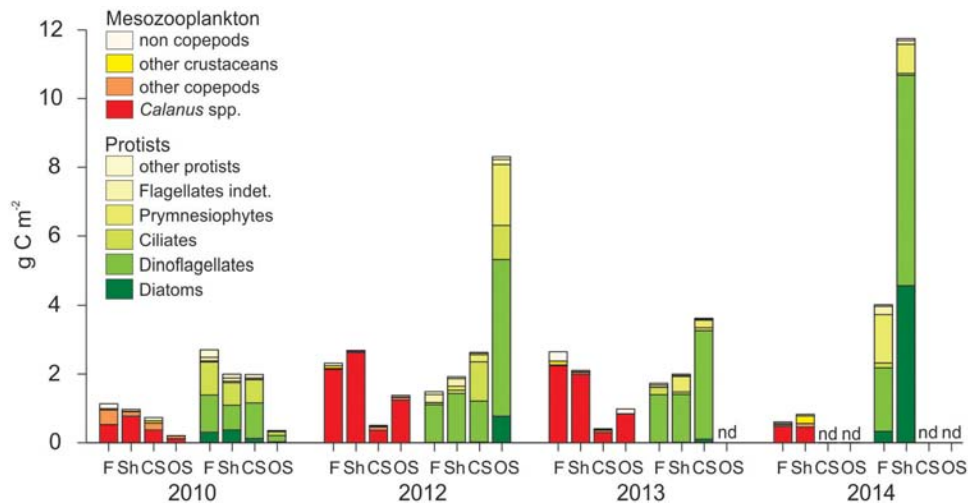


FIGURE 8 | Depth-integrated (0–50 m) protists and mesozooplankton carbon standing stock (g C m^{-2}) in the four regions (F, fjord; Sh, shelf; CS, continental slope; OS, off-shelf) along the transect from Rijpfjorden to the Arctic Ocean in 2010, 2012, 2013, and 2014.

Sea ice cover and the position of the Marginal Ice Zone (MIZ) are strongly dependent on the position and depth of the AW Boundary Current as well as wind conditions in case of the MIZ position. Warming of the AW and heat loss to the atmosphere are the major drivers of sea ice reduction in this area, whereas local winds showed no significant temporal trends (Onarheim et al., 2014). Regional sea ice cover does have a profound impact on surface layer temperatures, melt water volume and hence onset of the spring bloom and consumption of nutrients (Søreide et al., 2010). In this respect, summer 2014 stands out as very different from the preceding years in that the sea ice cover persisted until late summer in the region. Over other parts of the Arctic, sea surface temperatures were not particularly unique in 2014, except for cooler-than-average conditions in the northern Barents and Kara seas where the ice remained extensive compared to recent summers³.

Physical-Chemical Setting

The PSW layer was characterized by low salinity due to sea ice melt and, potentially, glacier run-off inside the fjord, and extended across the entire study area. Nutrients and Chl *a* levels were low and pH and Ω_{Ar} values were high in PSW indicative of the summer post-bloom situation and the Chl *a* maximum was situated at the bottom of the euphotic zone coinciding with the nutricline. This indicates that phytoplankton optimized growth near the limit of the euphotic depth, where the algae still had access to nutrients. The subsurface Chl *a* maximum is a prominent feature in the Arctic Ocean during summer (Arrigo et al., 2011; Ardyna et al., 2013).

Doming of the isopycnals associated with the AW inflow at the shelf break and over the upper slope resulted in elevated NO_x concentrations toward the surface (Randelhoff et al., 2015) reflected in elevated subsurface Chl *a* levels, relative to the other

stations in 2010 and 2013. The low $\text{NO}_x:\text{PO}_4$ ratio in PSW, well below the 16:1 Redfield ratio, indicates that nitrogen was the limiting nutrient in summer, which is in accordance with nitrogen being the main limiting nutrient of primary production during summer in the Arctic Ocean at large (Codispoti et al., 2013; Vancoppenolle et al., 2013). Nutrient versus salinity plots (Supplementary Figure S4) suggest that the fjord, shelf and continental slope are biogeochemical sinks for NO_x and silicic acid in PSW, which was the water mass with the lowest $\text{NO}_x:\text{PO}_4$ molecular ratios. The sharp increase in nutrients in PSW for salinities >33 shows that higher salinity water types are the main nutrient source for this region and not freshwater drainage from land or from glaciers; higher salinity waters were found near the lower boundary of the PSW layer.

Variations in Chl *a* Biomass and Protist Community Composition

The low surface Chl *a* concentrations and a protist community dominated by nanoplanktonic dinoflagellates (gymnodiniales), ciliates and prymnesiophytes are typical for the late summer post-bloom situation in the high-Arctic (Owrid et al., 2000; Piososz et al., 2009, 2014; Kubiszyn et al., 2017). During these oligotrophic conditions, the protist plankton is characterized by a regenerating community that efficiently recycles nutrients between small autotrophs and their protozoan grazers. Inter-annual differences in Chl *a* levels can largely be attributed to differences in the length of the open water season. Year 2010 in our data was characterized by the lowest surface nutrient and Chl *a* concentrations as sampling this year was latest in the season (mid to end of August), which was also reflected in elevated surface temperatures. In contrast, the high Chl *a* concentrations at the outer fjord and inner shelf in the coldest year 2014 were associated with large amounts of pack ice in the neighboring Arctic Ocean and proximity to the ice edge. Interestingly, the two dominant diatoms *Fragilariopsis*

³<http://nsidc.org/arcticseaicenews/2014/09/>

TABLE 2 | Mean zooplankton abundance (ind. m⁻³) and standard deviation of major taxonomical groups and 16 most abundant taxa across the four areas of the study.

Species	Fjord	Shelf	Cont. slope	Off-shelf
Copepoda	1635.0 ± 1662.0	1647.2 ± 474.8	473.4 ± 494.5	136.2 ± 64.1
<i>Oithona similis</i>	729.0 ± 1255.2	471.9 ± 355.3	200.3 ± 312.4	29.9 ± 31.9
<i>Calanus glacialis</i>	454.8 ± 471.5	348.0 ± 263.0	21.9 ± 22.9	3.5 ± 2.7
<i>Calanus finmarchicus</i>	150.7 ± 102.3	301.5 ± 164.5	85.2 ± 88.2	9.4 ± 6.3
<i>Pseudocalanus</i> spp. (CI-CV)	125.1 ± 146.2	283.2 ± 281.0	35.4 ± 60.5	2.6 ± 1.6
<i>Pseudocalanus acuspes</i> (AF)	24.5 ± 41.0	4.9 ± 9.3	0.7 ± 0.7	0.0 ± 0.0
Copepoda nauplii	108.2 ± 145.3	188.0 ± 170.0	42.1 ± 32.9	9.2 ± 12.0
<i>Microcalanus</i> spp.	3.0 ± 1.9	8.3 ± 8.8	28.5 ± 14.5	24.7 ± 12.0
<i>Calanus hyperboreus</i>	20.9 ± 24.8	14.5 ± 12.5	5.9 ± 3.7	4.9 ± 0.8
<i>Triconia borealis</i>	3.6 ± 1.3	6.9 ± 8.7	15.8 ± 12.1	13.6 ± 17.4
<i>Oithona atlantica</i>	2.1 ± 3.3	12.9 ± 13.5	9.4 ± 11.8	1.1 ± 0.8
<i>Metridia longa</i>	3.6 ± 3.4	4.0 ± 3.4	12.2 ± 7.6	10.0 ± 1.7
Amphipoda	1.2 ± 1.1	0.6 ± 0.5	2.5 ± 1.1	2.6 ± 0.8
Euphausiacea	4.1 ± 6.8	1.7 ± 1.6	1.1 ± 0.8	1.5 ± 0.8
Decapoda	0.1 ± 0.2	0.3 ± 0.3	0.2 ± 0.3	0.4 ± 0.4
Isopoda (manca larvae)	1.3 ± 1.4	0.8 ± 1.1	1.2 ± 0.5	1.2 ± 0.7
Ostracoda	0.6 ± 0.8	0.1 ± 0.2	2.6 ± 1.7	3.8 ± 1.1
Cirripedia	59.0 ± 51.0	61.0 ± 176.6	0.1 ± 0.1	0.1 ± 0.1
Cnidaria	1.0 ± 1.2	1.1 ± 0.9	2.0 ± 1.4	2.4 ± 0.6
Ctenophora	2.6 ± 3.0	0.9 ± 0.6	0.2 ± 0.2	0.5 ± 0.5
Chaetognatha				
<i>Eukrohnia hamata</i>	1.4 ± 1.2	2.0 ± 1.0	4.5 ± 1.3	4.1 ± 0.7
<i>Parasagitta elegans</i>	3.8 ± 4.3	2.3 ± 1.1	0.3 ± 0.5	0.0 ± 0.0
<i>Pseudosagitta maxima</i>			0.2 ± 0.3	0.5 ± 0.3
Polychaeta	9.4 ± 11.6	9.0 ± 7.1	3.1 ± 1.5	2.7 ± 0.5
Nemertea		0.5 ± 0.8	0.0 ± 0.0	
Bryozoa (cyphonautes larvae)	0.0 ± 0.1		0.1 ± 0.2	
Mollusca	38.3 ± 68.8	19.1 ± 23.9	3.9 ± 6.6	0.7 ± 0.8
Bivalvia veliger	19.0 ± 47.9	8.7 ± 13.0	1.9 ± 4.2	0.1 ± 0.1
<i>Limacina helicina</i>	17.5 ± 28.0	9.4 ± 12.0	1.7 ± 2.4	0.2 ± 0.3
Echinodermata	105.5 ± 129.5	364.8 ± 374.7	20.7 ± 39.4	0.8 ± 1.1
Chordata	145.1 ± 275.6	101.2 ± 151.1	28.4 ± 44.5	4.9 ± 2.8
<i>Fritillaria borealis</i>	141.1 ± 276.3	91.9 ± 139.8	26.4 ± 44.5	2.8 ± 2.4
<i>Oikopleura</i> spp.	4.0 ± 2.8	9.3 ± 11.7	2.0 ± 1.0	2.2 ± 1.8

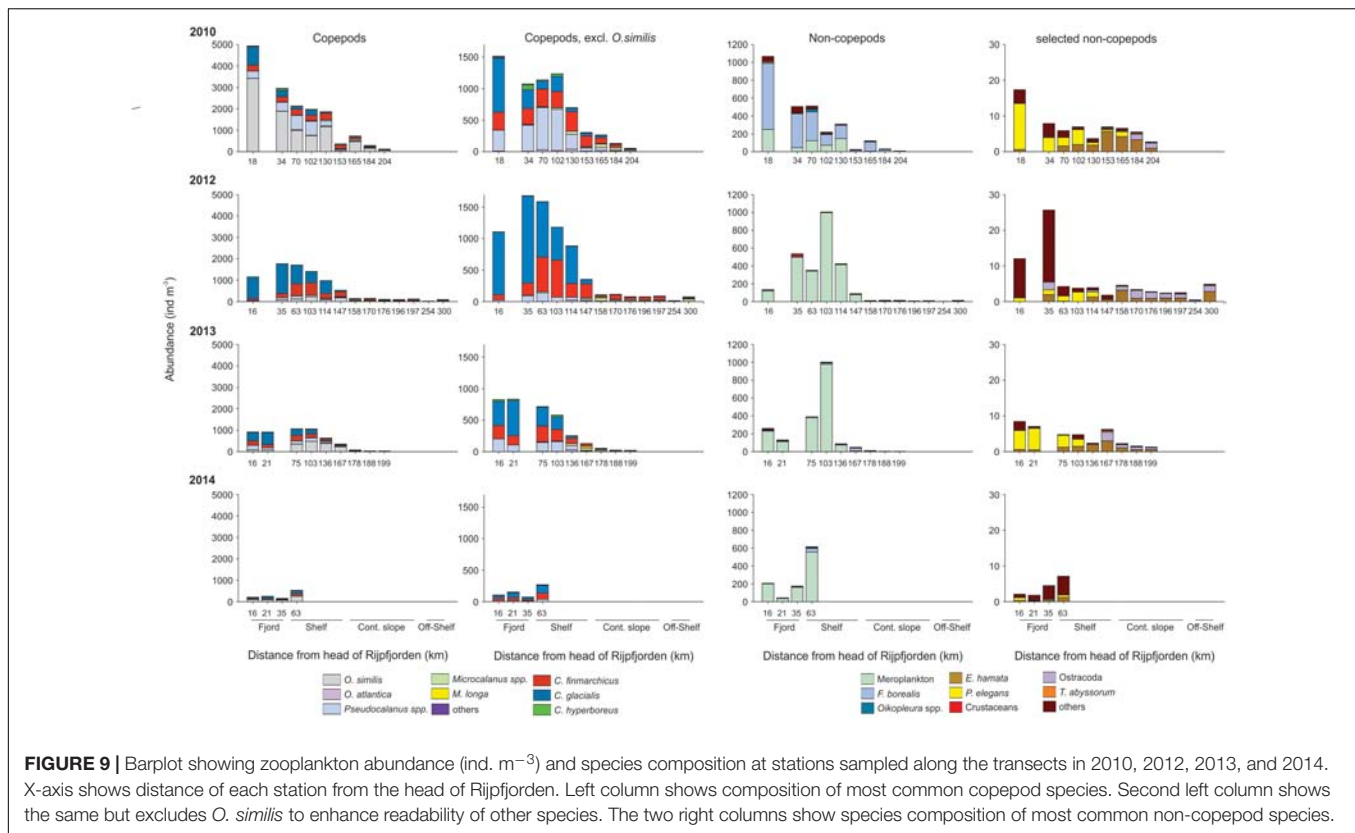
Empty cells indicate that the taxon was missing from the particular area. Values of 0.0 ind. m⁻³ indicate that the taxon was present but with less than 0.05 ind. m⁻³. Stages (CI-CV) and adult females (AF) are indicated when observations were limited to those. For more details, see **Supplementary Table S3**.

oceanica and *Shionodiscus bioculatus* in the subsurface blooms in 2014 are both cryo-pelagic species (Syvertsen, 1991; von Quillfeldt, 2000; Fernández-Méndez et al., 2018) indicating that they might have originated from sea ice. However, the fact that the Chl *a* maxima were found at subsurface depths with surface nutrients already largely depleted indicate a late bloom situation. Prymnesiophytes (in particular *Phaeocystis pouchetii*) and diatoms often had a higher biomass-share at subsurface depths. Access to elevated nutrient concentrations associated with the nutricline is the most likely explanation for the distributional patterns of these two taxa. The post-bloom *P. pouchetii* dominance has also been reported from other areas, such as waters adjacent to west Spitsbergen (Smoła et al., 2017).

Variations in Zooplankton

The zooplankton community in northern Svalbard waters consists of a mixture of boreal, boreo-Arctic, Arctic and ubiquitous species (Daase and Eiane, 2007; Blachowiak-Samolyk et al., 2008), and the community composition along the transect did not deviate from this pattern. Shannon-Wiener diversity and number of taxa were higher toward the continental slope and Arctic Ocean than on the shelf and inside Rijpfjorden. This partly reflected higher values of Shannon-Wiener diversity in Atlantic water, where one tends to find higher diversity of boreal species as well as the presence of Arctic species. The ubiquitous copepod *O. similis* dominated in terms of numbers, while biomass was dominated by *Calanus* spp., with the Arctic shelf species *C. glacialis* dominating inside Rijpfjorden where PSW and WCW prevailed. The Atlantic *C. finmarchicus*, which is advected into Rijpfjorden along with AW waters (Falk-Petersen et al., 2008), constituted a similar biomass to *C. glacialis* on the shelf and over the continental slope, in association with the AW Boundary Current. The biomass of *C. glacialis* on the continental slope was comparable to that of *C. finmarchicus*, which was not as expected since its contribution in terms of abundance was relatively low (**Table 2**). The smaller boreal species was about 4 times more abundant than *C. glacialis* over the continental slope. However, because the biomass of *C. glacialis* is on average 3.2 times the biomass of *C. finmarchicus*, as for older life stages CIV-AF (Falk-Petersen et al., 2009), its low abundance results in relatively high biomass (**Table 2**). North-east of Svalbard, *C. finmarchicus* may still contribute 40% to the total mesozooplankton biomass (Kosobokova, 2012) before its biomass diminishes rapidly en route to the Nansen Basin, to approximately 10%. There, the contribution by *C. glacialis* is higher, about 19% (Kosobokova and Hirche, 2009).

Seasonal changes in Rijpfjorden have been described with regard to zooplankton abundance (Leu et al., 2011; Weydmann et al., 2013). *Calanus glacialis* dominates inside the fjord and at the shelf during all seasons, whereas *C. finmarchicus* increases toward the shelf break, with the highest numbers found in the core of the AW at the shelf break during autumn (Weydmann et al., 2013; NPI unpubl. data). Small copepods (*O. similis*, *O. atlantica*, *Microcalanus* spp., *Pseudocalanus* spp., and *T. borealis/Oncaea* spp.) make up a large fraction of the



relative abundance during all seasons, especially in autumn and winter, but contribute little to the total biomass. During winter, the zooplankton community in the fjord is dominated by smaller copepods such as *Pseudocalanus* spp., and *Calanus* species, with *C. glacialis* making up 40% of the biomass (Weydmann et al., 2013). The occurrence of *C. finmarchicus* in Rijpfjorden is likely dependent on replenishment, in summer and autumn, by inflowing Atlantic water and less on local production. Weydmann et al. (2013) observed late developmental stages in September-October, indicating that this boreal species most likely overwinters in Rijpfjorden. There have also been observations showing high abundance of *C. finmarchicus* in January (Daase et al., 2014, 2018). This is most likely associated with stronger advection of Atlantic waters in autumn and winter (Basedow et al., 2018; Renner et al., 2018). However, the winter mortality of *Calanus* spp., can be high (e.g., Daase et al., 2014), and abundance of *C. finmarchicus* has been found to be very low in spring and early summer (Leu et al., 2011; Weydmann et al., 2013). Physical conditions in Rijpfjorden, such as sub-zero temperatures and a seasonal ice cover causing algal blooms and reproductive events for zooplankton to occur later in the season (Leu et al., 2011; Daase et al., 2013), likely put constraints on this boreal species.

The zooplankton composition showed variability among years. High abundances of *O. similis* and *F. borealis* occurred in 2010. The high abundance of *O. similis* indicates that conditions may have been favorable for omnivorous grazers in summer of 2010 compared to the other years. One likely explanation

is that sampling was conducted relatively late in 2010 (mid-August), thus the zooplankton community was in a different state of its annual cycle and many of the larger *Calanus* species might have already started their seasonal descent to greater depths. Furthermore, *O. similis* is known to preferentially feed on motile prey such as ciliates and dinoflagellates (Svensen and Kjørboe, 2000), which dominated protist standing stocks in 2010. *Fritillaria borealis* often appears in pulses, which has been related to its high fecundity and growth rates resulting in short generation time (Hopcroft and Roff, 1995). Populations of larvaceans have also been reported to increase rapidly in response to bacterio- and nanophytoplankton blooms (King, 1982). Sampling in 2010 likely coincided with such a larvacean “bloom.” If this is a common occurrence in Rijpfjorden, and was just missed in the other years, is unknown.

The abundances of zooplankton in Rijpfjorden were generally low in 2014 compared with the other years. Low temperature and late ice break up likely led to less favorable conditions for growth and development. The abundance of *C. glacialis* has been shown to vary with the timing of ice break up, with cold years potentially leading to a mismatch between recruitment and spring bloom with reduced reproductive success and survival (Søreide et al., 2010; Leu et al., 2011). This would also negatively affect boreal species, such as *C. finmarchicus*. However, this did not seem to affect the recruitment of the benthic community, as meroplankton abundance was quite similar between 2012, 2013, and 2014. The lowest meroplankton abundance was observed in 2010, but sampling that year was conducted later in the season

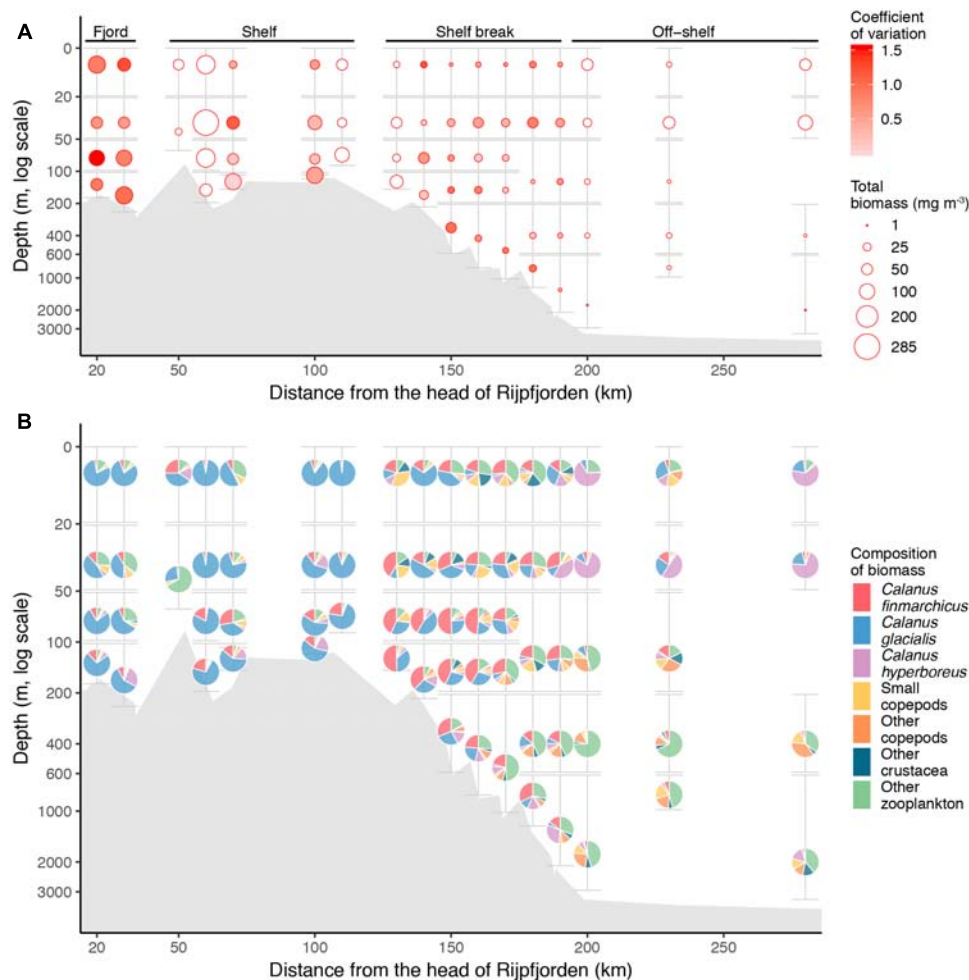


FIGURE 10 | Zooplankton distribution for data from all years combined. **(A)** Mean total mesozooplankton biomass (mg m^{-3}) and **(B)** average composition of main groups along the section from Rijpfjorden to the Arctic Ocean. The data are binned using a 10 km horizontal grid and the maximum and minimum vertical range of binned MultiNet samples. The radius of the dots in A is scaled to average biomass (mg m^{-3} , legend giving the range of averages) and the fill is scaled to coefficient of variation. White fill indicates only one sample from a given location. The height of error bars indicate the maximum and minimum vertical range of binned MultiNet samples, while the width of the error bars indicates the width of horizontal binning. Empty space indicates that sample from that stratum was lost.

when the development of benthic larvae had most probably advanced beyond pelagic life stages.

The zooplankton community in Svalbard waters and the Arctic Ocean can be considerably influenced by Atlantic expatriates (Wassmann et al., 2015). Time series data from the core of WSC in Fram Strait indicate that an increase in warming will likely lead to an increase in Atlantic and ubiquitous species such as *C. finmarchicus* and *O. similis*, respectively (Weydmann et al., 2014; Gluchowska et al., 2017a). During a warm event in 2011, there were more young copepodids of *C. finmarchicus* in the WSC (Gluchowska et al., 2017a). Basedow et al. (2018) estimated that approximately 500,000 tons C y^{-1} in form of *C. finmarchicus* are transported through Fram Strait into the Arctic. A considerable part of this biomass is transported along the continental margin north of Svalbard, with some redistribution onto the shelf including Rijpfjorden. The abundance of *C. finmarchicus* in the upper 600 m in the

off-shelf region varied between 10,600 ind. m^{-2} in 2013, 13,800 ind. m^{-2} in 2010 and 39,400 ind. m^{-2} in 2012. These values are lower than what Basedow et al. (2018) observed in August 2014 in the core of the WSC west of Svalbard (28,000–118,000 ind. m^{-2}), although the 2012 values fall into the lower range of those observations. The transport time from Fram Strait to the western Nansen Basin is about 3 weeks (Hattermann et al., 2016). Based on our lowest and Basedow et al. (2018) highest estimates we can assume that minimum 10% of the *C. finmarchicus* abundance transported along the west coast reaches the area north of Rijpfjorden, but based on mean values for our observations and the range reported in Basedow et al. (2018) it could be higher, likely around 30%. A decrease in abundance between the west and north coast is to be expected as the WSC is splitting into different branches north of Svalbard and some of these recirculate into Fram Strait (Hattermann et al., 2016; von Appen et al., 2016). Part of this loss can also be

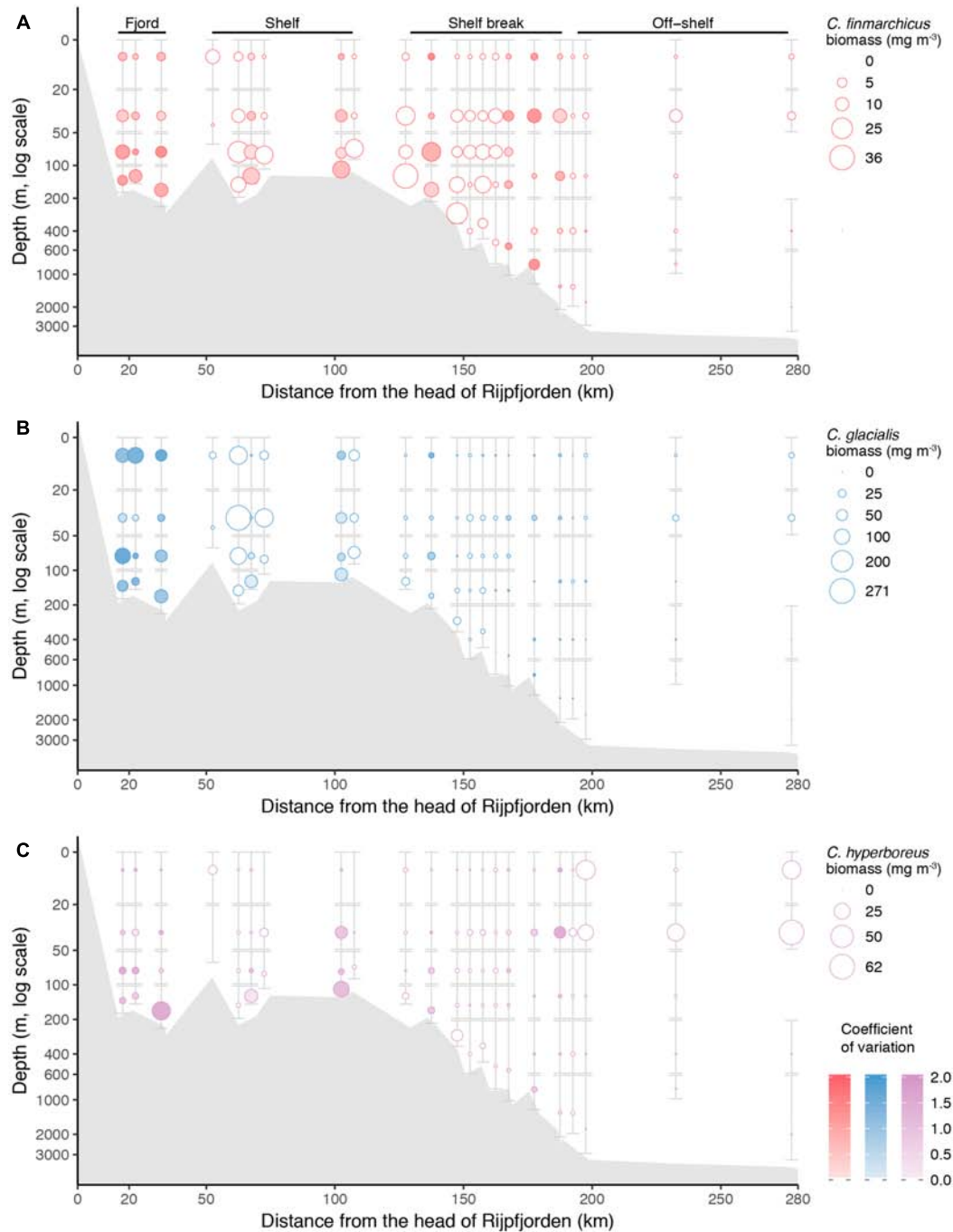


FIGURE 11 | Biomass (mg m^{-3}) of the three *Calanus* species along the transect from Rijpfjorden to the Arctic Ocean with data from all years combined. (A) *C. finmarchicus*, (B) *C. glacialis*, and (C) *C. hyperboreus*. See Figure 10 for explanation of figure elements.

associated with grazing by populations of larval fish and other pelagic zooplanktivorous grazers (e.g., jellyfish and amphipods) following the AW flow (Basedow et al., 2018). The zooplankton have to pass concentrations of Atlantic cod (*Gadus morhua*) and their prey, as well as mesopelagic concentrations of fish and predatory zooplankton at the NW corner of Spitsbergen and along the northern continental shelf (Ingvaldsen et al., 2017;

Knutsen et al., 2017). Diel vertical migration for mesopelagic predators in Fram Strait involved the lower part of the north-flowing AW (Gjøsæter et al., 2017). Seabirds, such as the little auk (*Alle alle*), prey on *Calanus* spp. in the upper part of the water column (e.g., Hovinen et al., 2014).

The population of *C. finmarchicus* diminishes further as it is transported eastward along the Siberian shelf, and this

TABLE 3 | Mean zooplankton biomass (mg dry mass m^{-3}) and standard deviation of major taxonomical groups and 18 taxa with most biomass across the four areas of the study.

Species	Fjord	Shelf	Shelf break	Off-shelf	C:DM
Copepoda	75.3 ± 63.6	61.3 ± 29.2	28.6 ± 7.5	24.7 ± 1.2	0.5
<i>Calanus glacialis</i>	56.2 ± 53.5	43.1 ± 27.7	5.4 ± 5.1	1.2 ± 0.4	
<i>Calanus finmarchicus</i>	7.1 ± 4.4	9.1 ± 3.4	6.5 ± 6.5	1.0 ± 0.5	
<i>Calanus hyperboreus</i>	7.5 ± 9.9	5.6 ± 4.5	4.9 ± 1.8	5.8 ± 0.5	
<i>Paraeuchaeta barbata</i> (AF)	0.5 ± 1.4		3.4 ± 3.3	5.7 ± 1.9	
<i>Paraeuchaeta norvegica</i> (AF)			2.5 ± 1.5	3.7 ± 1.0	
<i>Paraeuchaeta</i> spp. (CI-CV)	0.2 ± 0.3	0.0 ± 0.1	1.7 ± 1.0	2.1 ± 0.1	
<i>Oithona similis</i>	1.8 ± 3.1	1.2 ± 0.9	0.5 ± 0.8	0.1 ± 0.1	
Amphipoda	5.1 ± 6.0	4.2 ± 3.7	7.7 ± 3.7	4.7 ± 2.7	0.5
<i>Themisto libellula</i>	1.5 ± 2.4	3.2 ± 3.4	4.2 ± 3.2	1.2 ± 1.0	
<i>Apherusa glacialis</i>	1.5 ± 1.2	0.2 ± 0.5	1.8 ± 1.4	0.9 ± 1.6	
Euphausiacea	6.6 ± 16.9	1.6 ± 2.3	1.2 ± 1.3	1.3 ± 0.9	0.5
<i>Meganyctiphanes norvegica</i>	4.3 ± 12.2	0.5 ± 1.0	0.2 ± 0.4	0.1 ± 0.2	
Decapoda	0.1 ± 0.1	0.3 ± 0.6	1.2 ± 2.4	3.2 ± 3.2	0.5
Ostracoda	0.0 ± 0.1	0.0 ± 0.0	0.4 ± 0.3	0.6 ± 0.2	0.5
Cirripedia	0.7 ± 0.6	0.7 ± 2.1	0.0 ± 0.0	0.0 ± 0.0	0.5
Cnidaria	1.9 ± 4.4	1.7 ± 2.1	8.8 ± 6.3	12.0 ± 1.3	0.1
<i>Dimophyes arctica</i>		0.4 ± 1.1	6.1 ± 4.2	9.1 ± 0.7	
Ctenophora	3.4 ± 5.0	1.1 ± 0.7	0.2 ± 0.2	0.5 ± 0.7	
<i>Mertensia ovum</i>	3.0 ± 5.2	0.9 ± 0.7	0.1 ± 0.2	0.4 ± 0.7	
Chaetognatha	1.9 ± 1.8	2.3 ± 1.8	12.5 ± 9.7	21.3 ± 9.4	
<i>Eukrohnia hamata</i>	1.1 ± 1.8	1.4 ± 1.7	6.8 ± 2.1	7.1 ± 0.4	
<i>Pseudosagitta maxima</i>			5.4 ± 8.7	13.9 ± 9.0	
Polychaeta	0.0 ± 0.0	0.0 ± 0.0	0.3 ± 0.9	0.8 ± 1.1	0.3
Nemertea		0.0 ± 0.0	0.0 ± 0.0		0.3
<i>Limacina helicina</i>	4.6 ± 7.2	3.0 ± 3.2	0.5 ± 0.7	0.1 ± 0.1	
<i>Clione limacina</i>	3.0 ± 1.6	0.9 ± 0.9	0.1 ± 0.3	0.9 ± 1.5	
Echinodermata	0.1 ± 0.1	0.4 ± 0.4	0.0 ± 0.0	0.0 ± 0.0	0.3
Chordata	1.0 ± 1.1	0.5 ± 0.4	0.3 ± 0.6	0.3 ± 0.3	0.5

Empty cells indicate that the taxon was missing from the particular area. Values of 0.0 mg m^{-3} indicate that the taxon was present but with less than 0.05 mg m^{-3} . Stages (CI-CV) and adult females (AF) are indicated when calculations/observations were limited to those. Carbon:Dry mass (C:DM) conversion factors are indicated for groups or species. For more details, see **Supplementary Table S4**.

species has not yet been observed to reproduce successfully in the Arctic Ocean (Hirche and Kosobokova, 2007; Kosobokova and Hirche, 2009). Thus, it is believed that the population of this species is maintained because of continuous advection (Wassmann et al., 2015). However, recently some zooplankton have shown reproductive activity at high-Arctic latitudes, including krill *Thysanoessa raschii* and the pelagic amphipod

Themisto compressa (Buchholz et al., 2012; Kraft et al., 2013). With increased warming, *C. finmarchicus* may potentially produce two generations in 1 year, by populations inhabiting Atlantic waters in the WSC along the west coast of Spitsbergen (Gluchowska et al., 2017a), and this second reproduction may result in the presence of active, older developmental stages in the middle of winter in surface waters in Fram Strait (Basedow et al., 2018), even if the chances of these instars to survive are probably limited. Furthermore, changes in generation length and population turnover time due to climate warming may diminish the differences in size and lipid content between *C. finmarchicus* and *C. glacialis* and make the *Calanus*-based food chains more efficient (Renaud et al., 2018).

With regard to ocean acidification effects on northern and Arctic crustacean zooplankton, no studies have shown severe effects. Runge et al. (2016) found no effects of elevated CO_2 on vital rates of *C. finmarchicus*. Bailey et al. (2017) determined that early life stages of *C. glacialis* were largely unaffected by increased CO_2 , and Thor et al. (2018b) found no maternal or direct effects of ocean acidification on egg hatching for this species. Weydmann et al. (2012) also found that CO_2 -induced seawater acidification had no significant effect on egg production of *C. glacialis*. However, Thor et al. (2018a) detected negative effects of OA on scope for growth in *C. glacialis* copepodid stage IV at pH 7.87, and Weydmann et al. (2012) noted delayed hatching and possibly reduced overall hatching success for this species at lower pH of 6.9. Opstad et al. (2018) showed little effect of ocean acidification (high CO_2 levels, low pH) on the northern krill *T. inermis*. However, the low Ω_{Ar} saturation value (0.98) observed in surface waters in this study may affect the aragonite-shelled pteropod *L. helicina*, which has a critical Ω_{Ar} limitation of 1.4 (Bednarsek et al., 2014).

Nutritional Status and Successional Stage of High-Arctic Plankton Communities During Summer

Although we do not have information on the nutritional mode of the different protist taxa, it can be assumed that the majority of ciliates and a large fraction of dinoflagellates were characterized by heterotrophic or mixotrophic feeding modes. The same applies to the unidentified flagellates. Thus, with the possible exception of the subsurface blooms in 2014, the planktonic communities along the transect from Rijpfjorden into the Arctic Ocean were net heterotrophic which is consistent with net community production measurements for the Svalbard region in summer (Vaquer-Sunyer et al., 2013). The protist carbon to Chl *a* ratio was generally well above 50, which indicates nutrient limitation but also that a large fraction of the protist biomass was composed of heterotrophs. The 4 years included in this study cover a seasonal gradient from the late bloom phase in the heavy ice year 2014 characterized by subsurface blooms of diatoms and *Phaeocystis pouchetii* and low biomass of larger copepods likely due to less successful recruitment (Leu et al., 2011), to the late post-bloom phase in 2010 characterized by low protist standing stocks, the larger copepods residing at depth and

the zooplankton community predominated by small-sized taxa (e.g., *Oithona similis*, and *Fritillaria biorealis*; **Supplementary Figure S5**). The years 2012 and 2013 fell somewhere in between these two scenarios and had the highest surface zooplankton standing stocks. Our study illustrates how differences in ice cover can modulate phyto- and zooplankton phenology and that the late summer plankton community observed in 2010 might expand over a larger temporal window with the ongoing “Atlantification” of the eastern Arctic.

Future Perspectives

Future warming and reduced ice cover may lead to conditions that are more favorable with regard to survival of Atlantic expatriates in the Arctic Ocean. Rijpfjorden will likely change with climate warming in a direction to resemble Kongsfjorden, as it appeared during the cold years prior to 2006 (Hop et al., 2019; Tverberg et al., 2019). If climate warming continues with temperatures in the range predicted by models (Slagstad et al., 2011, 2015), then Rijpfjorden will continue to develop into a warmer system with higher contribution of boreal species. Thus, it should be continually monitored and models should be applied to the data to forecast regime shifts and resilience in this high-Arctic fjord (Griffith et al., unpublished).

DATA AVAILABILITY

The data are available in the Norwegian Polar Institute's database (<https://doi.org/10.21334/npolar.2019.199f540e>).

AUTHOR CONTRIBUTIONS

Study design and sampling during research cruise involved AW, AF, MD, HH, PA, PD, and MV. Data analyses and assemblage of figures were done by MV assisted by AW and MD. Analyses of carbonates involved AF and MC, nutrients PD and SKr, protists AT, JMW, and JW, and zooplankton MG and SKw. Oceanographic interpretations were performed by AS. Writing of the manuscript was completed by HH with input from all authors.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: <https://www.frontiersin.org/articles/10.3389/fmars.2019.00181/full#supplementary-material>

FIGURE S1 | Depth-integrated (0–50 m) Chl *a* standing stocks (mg m^{-2}) along the transect from Rijpfjorden to the Arctic Ocean for 2010, 2012, 2013, and 2014. Chl *a* standing stocks are averaged for each region.

FIGURE S2 | Average contribution of major protist groups to total protist abundance (cells L^{-1}) along the transect from Rijpfjorden to the Arctic Ocean for 2010, 2012, 2013, and 2014. Samples have been binned vertically to [0, 5], [5, 10], [10, 15], [15, 30], [30, 40], and [40, 50] m depth groups.

FIGURE S3 | Relationship between log transformed abundance (ind. m^{-3}) of common zooplankton species and distance from head of Rijpfjorden. Lines are linear regression lines. *** $p < 0.001$, ** $p < 0.01$, * $p < 0.05$. Left column shows species whose abundance decreases with distance from the head of the fjord, middle column shows species that increase in abundance with distance to the fjord. Right column shows species with non-significant trends ($p > 0.05$) in abundance along the transect.

FIGURE S4 | Relationship between nutrient concentrations and salinities for different regions and water types (light blue = Polar Surface Water (PSW), purple = Winter Cooled Water, red = Atlantic water and dark blue = Arctic Intermediate Water). Lines indicate Local Polynomial Regression (LOESS) fits for PSW and linear regressions for other water types with > 4 observations.

FIGURE S5 | Depth-integrated zooplankton carbon standing stock (g C m^{-2}) in the upper (0–50 m) and lower (50–bottom) water column in the four regions [fjord (F), shelf (Sh), continental slope (CS) and off-shelf (OS)] along the transect from Rijpfjorden to the Arctic Ocean in 2010, 2012, 2013, and 2014.

TABLE S1 | Mean abundance ($\text{cells } 10^3 \text{ L}^{-1}$) and standard error for the main protist taxa for consecutive years and regions of the Rijpfjorden transect. Values are depth-weighted means for the upper 50 m [* – Abundance $< 10 \text{ cells L}^{-1}$].

TABLE S2 | Mean carbon biomass ($\mu\text{g C L}^{-1}$) and standard error for the main protist taxa for consecutive years and regions of the Rijpfjorden transect. Values are depth-weighted means for the upper 50 m [* – Biomass $< 0.01 \mu\text{g C L}^{-1}$].

TABLE S3 | Mean zooplankton abundance (ind. m^{-3}) and standard deviation for all taxa presented in the 4 years and areas of the study. Taxa presented with $< 0.1 \text{ ind. m}^{-3}$ in any of the four areas or years are not included. Empty cells indicate that the species was missing from the particular area. All life stages are included, except when stages (CI-CV) and adult females (AF) are specified for accounts concerning these particular life stages.

TABLE S4 | Mean zooplankton biomass ($\text{mg dry weight m}^{-3}$) and standard deviation for all taxa presented in the 4 years and areas of the study. Taxa presented with $< 0.1 \text{ mg m}^{-3}$ in any of the four areas or years are not included. Empty cells indicate that the species was missing from the particular area. All life stages are included, except when stages (CI-CV) and adult females (AF) are specified for accounts concerning these particular life stages.

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Microzooplankton Distribution and Dynamics in the Eastern Fram Strait and the Arctic Ocean in May and August 2014

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Microzooplankton community structure, distribution, growth, and herbivory were examined in the eastern Fram Strait and Arctic Ocean shelf affected by the Atlantic water inflow in May (during the spring bloom) and August (post-bloom, summer stratification) 2014. In May, integrated microzooplankton biomass in the upper 100 m ranged from 0.16 g C m⁻² above the slope to 2.3 g C m⁻² within the West Spitsbergen Current (0.71 g C m⁻² on average), where it peaked in the mixed layer at 206 μg C L⁻¹. This is the highest volumetric microzooplankton biomass recorded so far in the Arctic. It primarily consisted of mixotrophic oligotrich ciliates from the genus *Strombidium*, which were dominant in the spring and formed a surface bloom (79 × 10³ cells L⁻¹). The heterotrophic dinoflagellates *Gyrodinium* and *Protoberidinium* were abundant at the diatom-dominated stations in the ice-covered waters during both seasons. In the summer, a more diverse community included a large proportion of heterotrophic and mixotrophic dinoflagellates, tintinnids, and other ciliates. Microzooplankton biomass increased to the average of 1.27 g C m⁻². At the ice-covered and open water stations in the Yermak shelf and deep basin, microzooplankton grew at 0.04 to 0.38 d⁻¹; their species-specific growth rates were up to 1.79 d⁻¹. Microzooplankton herbivory on average removed 72% (in two experiments > 100%) of daily primary production with the exception of samples dominated by *Phaeocystis pouchetii* colonies. The results indicate that microzooplankton play a significant role in the carbon cycle in this Atlantic-influenced polar system.

Keywords: microzooplankton, herbivory, growth, mixotrophy, Arctic Ocean

INTRODUCTION

Rapid warming is occurring in the Arctic (IPCC, 2013), where average temperatures have risen twice as fast as those elsewhere in the world (Corell, 2006). The warming trend has resulted in widespread reductions in Arctic ice cover (Kwok and Rothrock, 2009). Sea ice is the central component of the polar environment and its alternations translate global warming to marine ecosystems, including changes in biological productivity, food web structure, and the biogeochemical cycles (Wassmann and Reigstad, 2011; Wassmann and Lenton, 2012). An extended

open-water period in the Arctic Ocean is projected to boost pelagic primary production (Slagstad et al., 2011; Brown and Arrigo, 2012) and increase the role of small-sized phytoplankton (Li et al., 2009). The non-linear nature of ecosystem response to climate change complicates predictions. Understanding and predicting its effects at the system level requires insight into the coupled nature of physical and biological interactions.

An area of special interest in the marine ecosystem studies is carbon flow through pelagic food webs. Even minor climate effects at the lower trophic levels get amplified in food chains (Sarmiento et al., 2010) with significant effects at the higher trophic levels, which are critically dependent on the efficient energy transfer (McBride et al., 2014). In the world ocean, microzooplankton (*sensu lato* phagotrophic protists between 15 and 300 μm , including heterotrophic and mixotrophic ciliates, dinoflagellates, and sarcodines) are main consumers of phytoplankton production (Calbet and Landry, 2004; Schmoker et al., 2013). Recent data show that microzooplankton are a key component of pelagic food webs in productive Arctic shelf systems, such as the Bering Sea (Sherr et al., 2013; Stoecker et al., 2014a) and the Barents Sea (Franzè and Lavrentyev, 2014, 2017).

The Atlantic water is the primary source of heat in the Arctic (Polyakov et al., 2012). Its inflow has intensified (Schauer et al., 2004) and temperature has increased over the last several decades (Lind and Ingvaldsen, 2012). The Fram Strait, a 2500-m deep and 500-km wide passage between the Greenland shelf and Spitsbergen, connects the Atlantic and Arctic Oceans (Cokelet et al., 2008). The eastern Fram Strait is dominated by the West Spitsbergen Current (WSC) – a northward continuation of the Norwegian Atlantic Current and the main conduit of Atlantic Water in the Arctic Ocean (Pnyushkov et al., 2015). In addition, WSC is transporting large quantities of Atlantic phyto- (Paulsen et al., 2016) and zooplankton into the Arctic Ocean (Kosobokova and Hirche, 2009; Basedow et al., 2018).

The Fram Strait is already one of the most productive areas of the Arctic (Slagstad et al., 2011) and is likely become a regional hotspot with increased primary production due to efficient transport of nutrients and the increased light availability in the ice-free water column (Randelhoff et al., 2018). However, microzooplankton remain little studied in this polar region. In the northwestern Fram Strait, dominated by the cold East Greenland Current, heterotrophic and mixotrophic ciliates and dinoflagellates were abundant in the early spring (Seuthe et al., 2011). In the central Fram Strait and the waters north of Spitsbergen, despite considerable ciliate biomass, microzooplankton herbivory was found to be insignificant during the late stages of phytoplankton bloom dominated by the prymnesiophyte *P. pouchetii* (Calbet et al., 2011).

The central goal of our study was to determine microzooplankton quantitative importance in the pelagic food webs within the WSC and the Arctic Ocean shelf affected by the Atlantic water inflow. Extreme seasonality in light typical for the Arctic and strong variability in the sea ice melt across the Fram Strait create a very dynamic and spatially heterogeneous environment. Therefore, we focused our study on two critical phases of the annual cycle: the spring bloom and summer stratification. The study specific questions were: (1) what is the

spatial distribution of microzooplankton biomass and major taxonomic groups? (2) What is the capacity of microzooplankton to use primary production? (3) What are the growth and production rates of microzooplankton?

The Study Sites

The study was conducted in the eastern Fram Strait during the Carbon Bridge cruises aboard the R/V *Helmer Hansen* in May and August 2014 (Figure 1). Samples were collected along two longitudinal transects named C (79.4°N) and D (79.0°N). These transects extended between 10 and 4°E and crossed the warm core of WSC. During both cruises the dominating water mass in the upper 500 m of these transects was Atlantic (Basedow et al., 2018). Its inflow rate did not differ substantially between May and August compared to winter. In May 2014, the Atlantic water (3.5–5.0°C) reached up to the surface between 6 and 8°E. In the western end of transect D, colder, lower-salinity surface waters were observed west of 5°E, closer to the sea ice edge. In August 2014, a fresher (salinity < 34) surface layer extended over most of transect D, with surface temperatures ranging from 7.5°C in the east to 1°C west of 4°E (Randelhoff et al., 2018).

At the shelf break, three ice-covered sites designated further as the process (i.e., experimental) stations were sampled in the inflow region west (P3, P4) and northwest (P1/P5) of Spitsbergen in May (Table 1). In August, we sampled two process stations in the ice fields north of Spitsbergen: P6, representing the deep Arctic basin, and P7, which was selected to represent the area of AW inflow close to the shelf slope. One of the spring process stations (P1/P5), now ice-free, was also sampled in August. See Randelhoff et al. (2018) for a detailed treatment of hydrographic conditions at the process stations.

MATERIALS AND METHODS

Sea temperature and salinity were measured with a Seabird 911 Plus CTD system. Raw fluorescence was measured with the attached fluorometer. Samples were collected from different depths: 2, 5, 10, 20, 30, 40, 50, 100 m and the deep chlorophyll layer (DCL) using Niskin bottles mounted on a rosette. The transect samples were not replicated because it would require three separate CTD casts at each station and wire time was limited during the cruises. Subsamples for examining microzooplankton and chlorophyll concentrations were immediately collected and preserved as described below.

All glass- and plastic ware, and tubing were cleaned with 10% HCl, deionized water, and 0.2- μm filtered seawater prior to sampling. Experimental containers were handled using gloves. For experimental samples, freshly collected seawater was carefully siphoned into a 20 L polycarbonate carboy using submerged silicone tubing, which had one end wrapped in a 153 μm mesh. The collected samples were taken to a shipboard temperature-controlled cold room. All experimental manipulations were conducted at $\pm 1^\circ\text{C}$ ambient sea temperature under dim light. The growth and grazing mortality rates of phytoplankton rates were measured using two-point dilution (Landry et al., 2008). Instead of linear

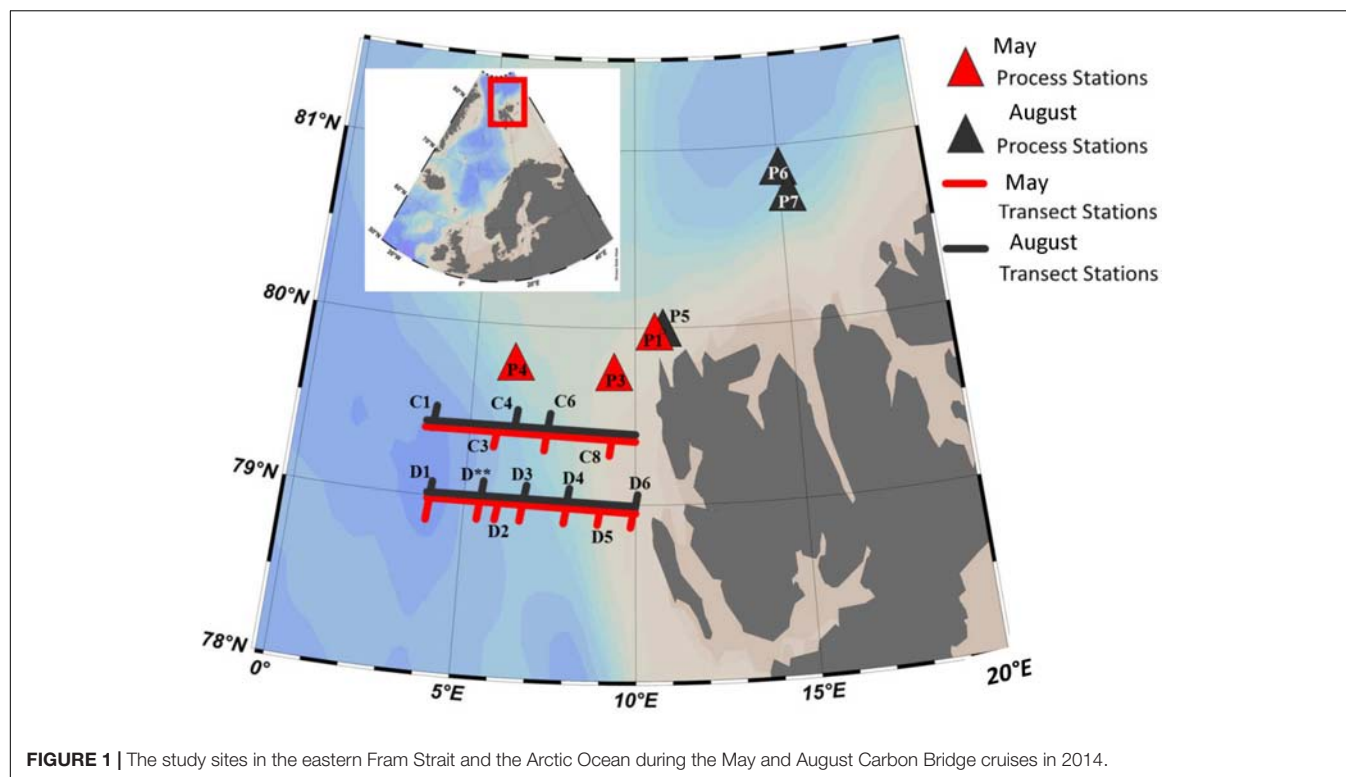


TABLE 1 | Abiotic conditions at the process stations and phytoplankton growth and grazing mortality rates in May and August 2014.

Station	Date	Ice cover	Sample depth (m)	T (°C)	Salinity	Chl ($\mu\text{g l}^{-1}$)	Growth (μ, d^{-1})	SD= standard deviation	Grazing mortality (g, d^{-1})	SD	g/μ
P1/P5	5/19/2014	25%	1	0.0	34.5	5.19	0.27	0.08	0.12	0.03	0.44
P1/P5	5/19/2014		10	-0.5	34.8	5.54	0.31	0.03	0.17	0.01	0.55
P3	5/23/2014	85%	15	0.0	34.2	4.88	-0.24*	0.06	—	—	—
P3	5/23/2014		40	3.0	35.1	4.32	-0.15	0.04	0.17	0.10	—
P4	5/25/2014	40%	1	-1.0	33.7	3.58	0.14	0.05	0.22	0.04	1.57
P4	5/25/2014		15	0.2	34.2	5.20	-0.07	0.03	0.21	0.01	—
P1/P5	8/9/2014	0%	1	6.0	34.9	0.76	0.24	0.06	0.16	0.07	0.67
P1/P5	8/9/2014		18	6.3	34.9	1.05	0.22	0.05	0.08	0.02	0.36
P6	8/12/2014	90%	1	-1.0	31.9	0.13	0.22*	0.08	—	—	—
P6	8/12/2014		25	5.5	34.2	0.95	0.42	0.09	0.29	0.08	0.69
P7	8/14/2014	70%	1	-0.5	31.7	0.16	0.33	0.07	0.40	0.11	1.21
P7	8/14/2014		14	5.0	34.8	0.34	0.37	0.10	0.24	0.01	0.65

*Calculated from the whole seawater treatment.

regression, this method estimates the grazing mortality rate (g) as the difference in phytoplankton growth (μ) between the whole seawater and highly diluted treatments. The diluted treatment approximates “no grazing.” We used this method due to its efficiency and the ability to provide the rates, which are not statistically different from those estimated by the multi-point method (Strom and Fredrickson, 2008; Chen, 2015) even when non-linear responses are taken into account (Morison and Menden-Deuer, 2017).

Seawater was added to 0.6 L Nalgene clear glass bottles. The diluted treatments were prepared by mixing nine parts

filtered seawater ($0.2 \mu\text{m}$ large volume Pall Science pleated capsules using gravity flow) with one part whole seawater to yield a 10% dilution. The capsules were pre-soaked in 5% HCl and thoroughly rinsed with deionized water prior to use. To equalize plankton growth conditions, all triplicated diluted and undiluted samples were amended with dissolved nutrients to final concentrations of $16 \mu\text{M N}$ ($\text{KNO}_3 + \text{NH}_4\text{Cl}$; 15:1 based on N) and $1 \mu\text{M P}$ (K_2HPO_4). These additions correspond to the maximum concentrations of nutrients found in the Fram Strait deep waters (1000 m) during the Carbon Bridge project ($15.7 \mu\text{M NO}_3$ and $1.07 \mu\text{M PO}_3$, Randelhoff et al., 2018).

An additional triplicated set of the whole seawater controls was left unfertilized to test the effect of nutrient additions on phytoplankton growth. All bottles were screened with neutral density filters to mimic light conditions at a certain depth (70 to 4% surface irradiance). Surface samples were incubated on the deck in an open plastic container with running surface seawater for 24 h. The bottles were periodically rotated by hand to avoid particle settling. Samples from deeper layers were incubated in a temperature-controlled deck incubator exposed to natural light and equipped with a plankton wheel (set at 0.25 revolutions per minute). During the experiments, temperature was monitored and remained within $\pm 0.5^\circ\text{C}$ of the initial sea temperature. Samples for chlorophyll and microzooplankton counts were collected at T_0 and T_{24} .

Chlorophyll was collected onto $0.2\ \mu\text{m}$ Nylon membrane filters from 250 to 500 ml samples using low vacuum. The filters were frozen and stored in liquid N_2 . Extraction was done in 90% acetone for 24 h at -20°C . Turner Designs Trilogy fluorimeter was used to measure chlorophyll concentrations via the acidic method (Arar and Collins, 1997). Microzooplankton were preserved with 2% (final concentration) acid Lugol's iodine, stored at 4°C for 24 h, and post-fixed with 1% (final concentration) formaldehyde. Additional plankton samples were fixed with formaldehyde only (1% final concentration) for examination of chloroplast-bearing microzooplankton.

Microzooplankton were settled from 50 to 100 ml sub-samples and examined under an inverted differential interference contrast microscope equipped with fluorescence at 200x. The entire surface area of Utermöhl chambers was scanned. In some cases, additional sub-samples were examined from each bottle in the experiments. Not fewer than 40 cells were measured with an eyepiece micrometer at 400–600x for each abundant taxon. The cell linear dimensions were converted to volume using approximated geometric shapes. The volumes were then converted to carbon (Putt and Stoecker, 1989; Menden-Deuer and Lessard, 2000). Any ciliates in our samples were counted as microzooplankton, whereas dinoflagellates were included only if their maximum linear dimension was at least $>15\ \mu\text{m}$ (Møller et al., 2006). Formaldehyde-only preserved samples were settled and examined similarly using a combination of interference contrast and fluorescence. Ciliates and dinoflagellates with chloroplasts in their cytoplasm were categorized as mixotrophs, and those without chloroplasts as heterotrophs. To calculate the cell chlorophyll quota, we used the chlorophyll vs. volume regression for marine phytoplankton (Montagnes et al., 1994) and assumed that autotrophic and mixotrophic plankton have similar cellular chlorophyll content (Dolan and Perez, 2000).

Phytoplankton apparent growth rates were calculated assuming exponential growth: $\mu = \ln(N_t/N_0)/(t/24)$, where: μ = growth rate (d), N_0 and N_t = chlorophyll concentrations at the beginning and end of the experiment, respectively, and t = time (hours). Grazing mortality rates (g) were determined as the difference between μ measured in the diluted ($\mu_{10\%}$) and whole (μ_{WSW}) seawater samples: $g = \mu_{10\%} - \mu_{\text{WSW}}$. In the experiments where phytoplankton grew slower in diluted samples, or not significantly different from the whole seawater treatment, g was not calculated (since there can be no negative

grazing rate), whereas the growth of phytoplankton was reported from the whole seawater treatment. If chlorophyll concentrations declined in all treatments, phytoplankton decline rate was reported. The average rates used for calculating the grazing to growth ratio (g/μ) calculation did not include the negative values (Stoecker et al., 2014a).

Microzooplankton species-specific instantaneous growth rates (r , d^{-1}) were determined from their initial and final (24 h) concentrations in the triplicated whole seawater control bottles from the simultaneous dilution experiments, assuming exponential growth (Franzè and Lavrentyev, 2014). Microzooplankton community secondary production rates (MzP , $\mu\text{g C l}^{-1} \text{d}^{-1}$) were determined using the following formula: $\text{MzP} = \Sigma r \times b_0$, where b_0 is the initial population biomass of individual taxa (Franzè and Lavrentyev, 2017). The community daily growth rate of microzooplankton was as MzP/B_0 , where B_0 is total initial community biomass.

To estimate dispersion, we used standard deviation throughout the manuscript unless noted otherwise. All pairwise comparisons of the average values of different plankton parameters (chlorophyll a , microzooplankton biomass, and phytoplankton growth and grazing mortality rates) between treatments, stations, and seasons were conducted using a two-tailed t -test assuming unequal variances. The effects of seasonality, depth, sea temperature, salinity, and chlorophyll concentrations on the distribution of total microzooplankton biomass and that of different taxonomic-functional groups along Transect D were examined using a general linear model (GLM) multiple regression. The two study seasons, the spring and summer, and the sampling depth were used as factors (i.e., categorical variables) in GLM, whereas the water column characteristics were used as covariates (i.e., continuous independent variables). The sampling depths were designated as the upper (0–30 m) and lower (31–100 m) layers. These categories were chosen based on the vertical distribution patterns of microzooplankton biomass. In addition to these factors we also included their interaction (i.e., season by layer) to improve the overall model fit. Three outlier samples (the highest microzooplankton biomass values in the upper layer at D5 in May) were excluded from the model. Relationships between plankton growth, production, and mortality rates and sea temperature as well as between microzooplankton biomass and production rates were examined using least square linear regression. All statistical analyses were conducted using Minitab 18.

RESULTS

Microzooplankton Biomass Distribution

Microzooplankton biomass in the upper 100 m of Transit D was distributed unequally along the transect (Figures 2B, 3B). It was elevated in the mixed layer at D1 and D3, and reached its maximum for the whole study period at D5 ($2306\ \text{mg C m}^{-2}$) mostly due to the mixotrophic oligotrich ciliates *Strombidium* sp. ($71000\ \text{cells L}^{-1}$) and *S. conicum* ($8000\ \text{cells L}^{-1}$), which formed nearly 90% of total ciliate biomass ($206\ \mu\text{g C L}^{-1}$) near

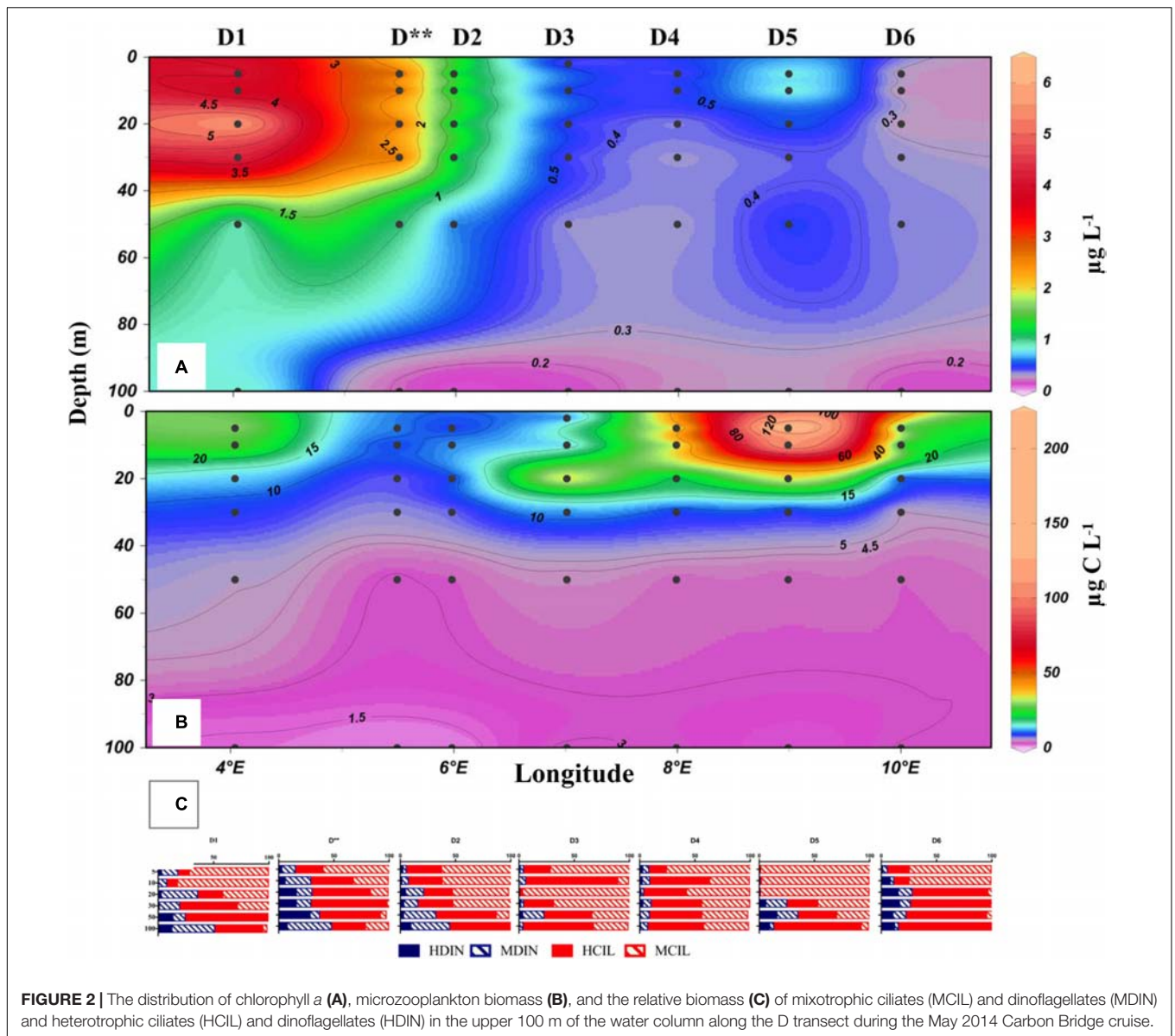


FIGURE 2 | The distribution of chlorophyll a (A), microzooplankton biomass (B), and the relative biomass (C) of mixotrophic ciliates (MCIL) and dinoflagellates (MDIN) and heterotrophic ciliates (HCIL) and dinoflagellates (HDIN) in the upper 100 m of the water column along the D transect during the May 2014 Carbon Bridge cruise.

the surface (Figure 2C). Overall, the average depth-integrated microzooplankton biomass in the upper 100 m in transect D in May was 713 mg C m^{-2} . Similar microzooplankton composition was recorded at the process sites P and Transect C (Figures 4, 5), but microzooplankton biomass in the latter transect was much lower than in Transect D ($<10 \mu\text{g C L}^{-1}$ at C3 and C8). Microzooplankton also accumulated at certain depths, which were not included in the vertical sampling routine. For example, at P1 in May, microzooplankton biomass reached $43 \mu\text{g C L}^{-1}$ at 15 m, mostly due to mixotrophic ciliates, and only 10.1 and $1.3 \mu\text{g C L}^{-1}$ at 10 and 20 m, respectively. Because the 15 m sample was collected separately for incubation, it was not included in the integrated biomass.

Excluding its peak values at D5 in May, microzooplankton biomass was generally higher in August at all studied locations with an increased proportion of dinoflagellates. In Transect

D, microzooplankton peaked at D3 in the mixed layer (Figure 3B) but overall was distributed evenly along the transect compared to May. Its depth-integrated biomass in the upper 100 m averaged 1270 mg C m^{-2} . The most pronounced seasonal changes were observed at C sites (Figure 5), where total microzooplankton biomass increased 3–4 times and dinoflagellates 5–10 times in August compared to May. At the process stations the seasonal trend was similar: depth-integrated microzooplankton biomass (0 to 100 m) increased from 250 to 400 to $>1200 \text{ mg C m}^{-2}$.

Microzooplankton Composition

In addition to the mixotrophic oligotrichs, heterotrophic dinoflagellates, such as *Gyrodinium spirale*, *Protoperdinium bipes*, and *Gymnodinium* sp. were also a significant component of microzooplankton population at the ice-edge and ice-covered

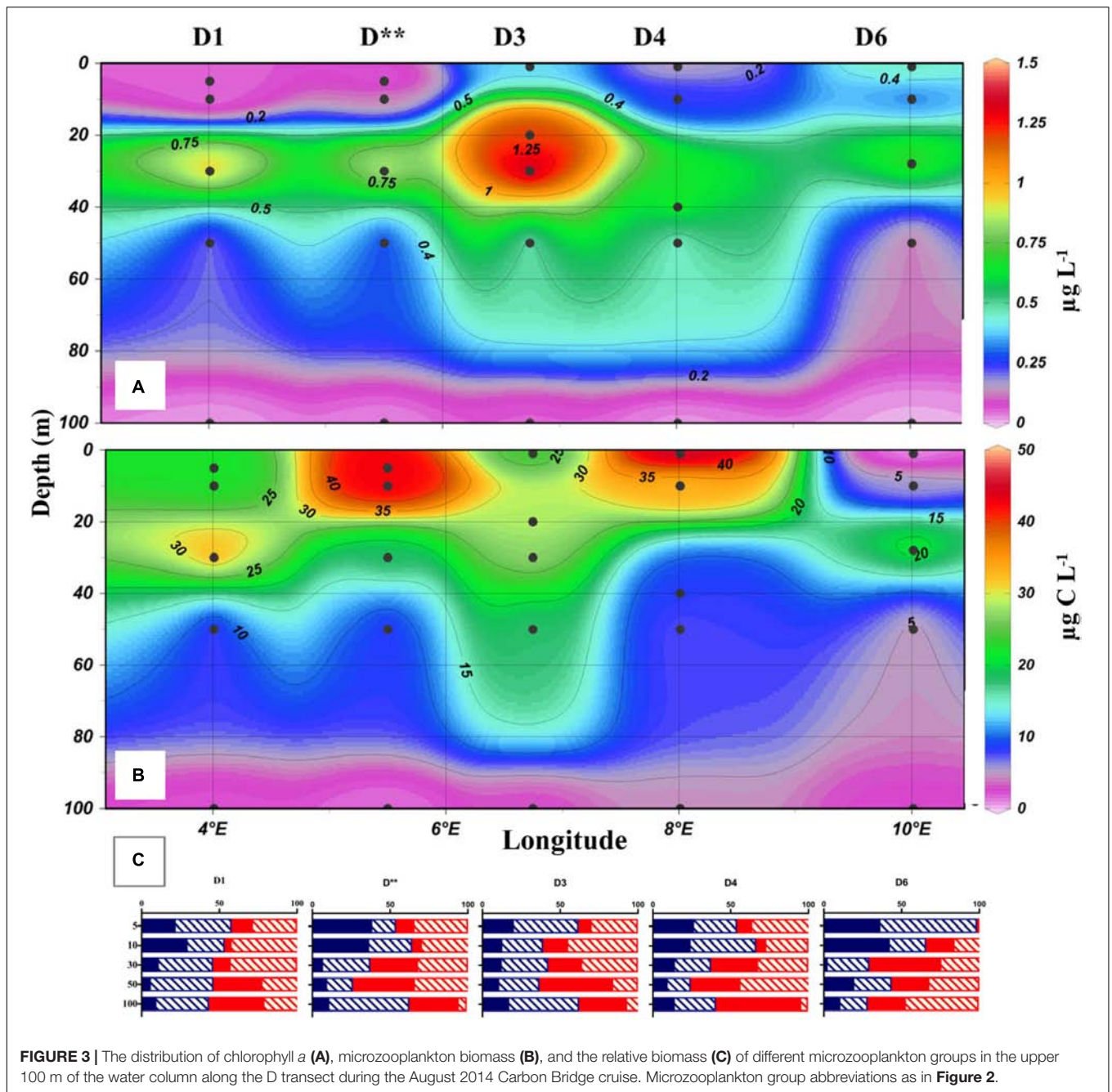


FIGURE 3 | The distribution of chlorophyll *a* (A), microzooplankton biomass (B), and the relative biomass (C) of different microzooplankton groups in the upper 100 m of the water column along the D transect during the August 2014 Carbon Bridge cruise. Microzooplankton group abbreviations as in **Figure 2**.

waters. The kleptoplastidic (e.g., Peltomaa and Johnson, 2017) cyclotrichid ciliate *Mesodinium rubrum* was omnipresent, but only at relatively low abundance (<500 cells L^{-1} , except P3 surface 1120 cells L^{-1}). The heterotrophic choreotrich ciliates *Lohmaniella oviformis* and *Pelagostrobilidium neptuni* were distributed more evenly in the water column and their relative biomass increased at medium depths along with several mixotrophic gymnodiniids.

In August, microzooplankton composition was more diverse (**Figure 3C**). In addition to the species present in the spring assemblage, we also found a diversity of mixotrophic and

heterotrophic dinoflagellates such as *Ceratium arcticum* (*Tripes arcticus*), *Gymnodinium* spp., *Protoperdinium* sp., *Gyrodinium fusiforme*, *Amphidinium* spp., *Dinophysis rotundata*, *Torodinium robustum*, *Pronoctiluca pelagica*. Ciliate biomass was dominated by the mixotrophic oligotrich *Tontonia appendiculariformis* and also included several other mixotrophic (*Laboea strobila*, *Strombidium lynni*, *Didnidium gargantua*, *M. rubrum*) and heterotrophic species (*S. acuminatum*, *Leegardiella sol*, *Balanion comatum*, *Balanion planktonicum*, *M. acarus*, *Urotricha* sp., *U. globose*, *Astylozoon faurei*). In addition, several tintinnid ciliates were also present including *Parafavella faurei* (the most

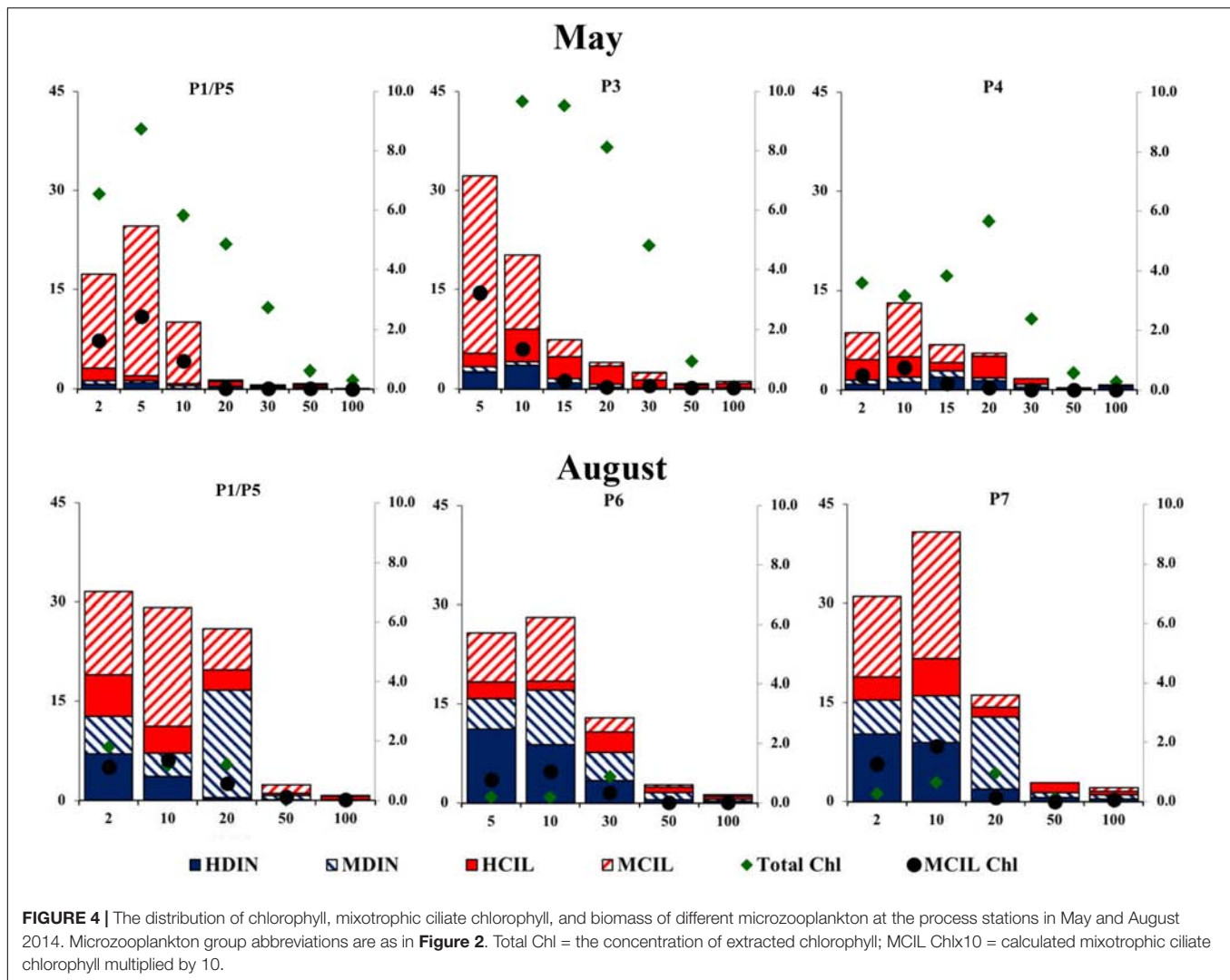


FIGURE 4 | The distribution of chlorophyll, mixotrophic ciliate chlorophyll, and biomass of different microzooplankton at the process stations in May and August 2014. Microzooplankton group abbreviations are as in **Figure 2**. Total Chl = the concentration of extracted chlorophyll; MCIL Chlx10 = calculated mixotrophic ciliate chlorophyll multiplied by 10.

common in our samples), *Acanthostomella norvegica*, *Ptychocylis obtusa*, *Salpignella* sp., and *Leprotintinnus pellucidus*.

Total and Mixotrophic Chlorophyll a Distribution

During the May cruise, the highest chlorophyll values (**Figure 2A**) were found in the western end of Transect D (Stations D1, D**), where diatoms and *P. pouchetti* formed a bloom at the ice edge. At D3, D4, and D6 chlorophyll remained $< 1 \mu\text{g L}^{-1}$. At the process stations further north, chlorophyll was high (up to $13.5 \mu\text{g L}^{-1}$) and concentrated in the shallow mixed layer (**Figure 4**). A bloom of *P. pouchetti* accompanied by diatoms was also in progress, especially at P3. The colonial prymnesiophyte contributed 80–90% of phytoplankton abundance in the ice-covered waters (based on light microscopy, Sanz-Martín et al., 2018). In the summer a DCL at around 20–30 m was present along transect D. Nevertheless, chlorophyll concentrations were much lower in August (**Figure 3A**) than in May. Similar patterns were

observed in Transect C and at the process stations with the exception of P1/P5 (**Figures 4, 5**). Under the ice, diatoms were the dominant group in August (70–80% phytoplankton abundance, Sanz-Martín et al., 2018) with a lesser contribution from *P. pouchetti*.

The average ratio of calculated mixotrophic chlorophyll to total extracted chlorophyll in the surface layer along Transect D was 19% in May and 43% in August (**Figure 6**). The same ratio for depth-integrated values in the upper 50 m was 10 and 9% in May and August, respectively. These average values do not include station D5 in May, where calculated integrated mixotrophic chlorophyll was 83% of total concentration and the ratio in the surface layer exceeded 100% due to the bloom of two mixotrophic oligotrichs. The calculated contribution of *Strombidium* sp. (cell volume $15.5 \times 10^3 \mu\text{m}^3$, chlorophyll content 30 pg cell^{-1}) alone was $\sim 2 \mu\text{g L}^{-1}$. At C sites, the ratio increased from $< 2\%$ in May to 20–50% in the surface layer and 6–18% in the DCL in August (**Figure 5**, absolute values are shown). At the process stations there was an opposite trend despite a decrease in total chlorophyll (**Figure 4**). The ratio declined from 7 to 8% in

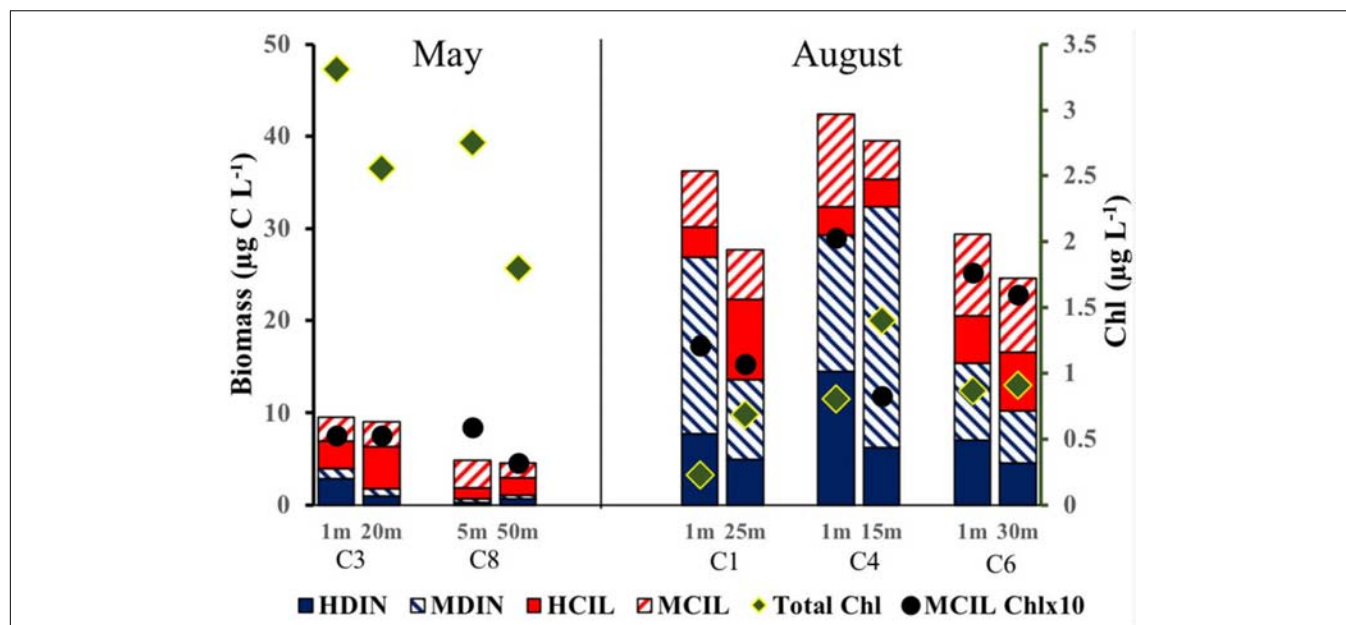


FIGURE 5 | The distribution of chlorophyll (Total Chl), mixotrophic ciliate chlorophyll (MCIL Chl) and biomass of different microzooplankton groups along at selected transect C stations in May and August 2014. Microzooplankton group abbreviations are as in **Figure 2**. Chlorophyll abbreviations as in **Figure 4**.

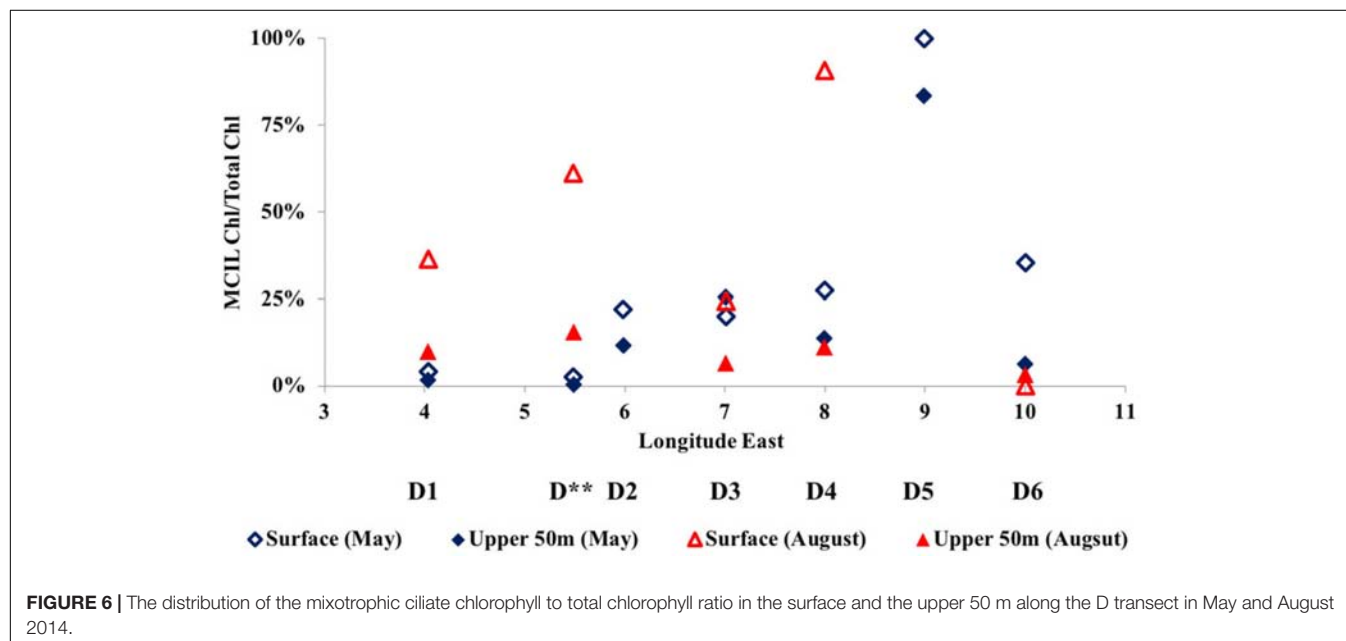


FIGURE 6 | The distribution of the mixotrophic ciliate chlorophyll to total chlorophyll ratio in the surface and the upper 50 m along the D transect in May and August 2014.

the mixed layer in May to 2–3% in August due to the lower abundance of mixotrophic oligotrichs.

The Effects of Environmental Factors on Microzooplankton Distribution

Sampling depth was the only factor that significantly influenced the distribution of total microzooplankton biomass. It also had pronounced effects on different microzooplankton components (mixotrophic and heterotrophic ciliates and

mixotrophic and heterotrophic dinoflagellates): they all decreased with depth (**Table 2**). With the exception of mixotrophic ciliates, all microzooplankton groups were also influenced by seasonality: their biomass increased in the summer. Sea temperature was negatively related to microzooplankton biomass, but its effect was significant only for total microzooplankton and mixotrophic dinoflagellates. Heterotrophic ciliate biomass was positively related to salinity and chlorophyll, but only the former relationship was significant. Overall, the multiple regression model

TABLE 2 | General linear model of microzooplankton biomass distribution vs. season, depth, and environmental parameters along Transect D ($n = 63$).

		Responses				
		MZP	HDIN	MDIN	HCIL	MCIL
Factors	Model r^2 :	48.5	60.0	76.6	35.0	18.2
	Constant	−79.0	59.7	−30.0	−63.8	−45.0
	p -Value	0.57	0.062	0.237	0.005	0.70
Season	F -value	10.6	5.7	45.4	12.2	1.33
	p -Value	0.002	0.02	<0.001	0.001	0.25
	Coef. spring	−9.05	−1.50	−3.38	−1.54	−2.65
	Coef. summer	9.05	1.50	3.38	1.54	0.254
Layer	F -value	18.3	6.16	34.9	11.4	6.60
	p -Value	<0.001	0.016	<0.001	0.001	0.013
	Coef. upper	9.21	1.23	2.29	1.15	4.57
	Coef. lower	−9.21	−1.23	−2.29	−1.15	−4.57
Season * Layer	F -value	7.31	6.25	37.6	7.86	0.52
	p -Value	0.01	0.015	<0.001	0.007	0.47
	Coef. spring upper	−5.13	−1.07	−2.2	−0.84	−1.13
	Coef. spring lower	5.31	1.07	2.2	0.84	1.13
	Coef. summer upper	5.31	1.07	2.2	0.84	1.13
	Coef. summer lower	−5.31	−1.07	−2.2	−0.84	−1.13
Covariates						
Temperature	F -value	4.37	2.12	13	2.05	1.39
	p -Value	0.034	0.15	0.001	0.16	0.24
	Coef.	−4.67	−0.72	−1.39	−0.48	−2.09
Salinity	F -value	0.55	2.86	2.08	8.78	0.23
	p -Value	0.46	0.10	0.155	0.004	0.64
	Coef.	3.08	−1.58	1.08	1.95	1.64
Chlorophyll <i>a</i>	F -value	0.33	2.21	0.01	1.94	0.29
	p -Value	0.57	0.143	0.928	0.17	0.59
	Coef.	−0.70	−0.48	−0.02	0.27	−0.54

Coef., coefficient. Layers: Upper 0–30 m, Lower: 31–100 m. Bold and italic indicate significant coefficients in the regression and the corresponding p and F -values.

explained much larger proportion of dinoflagellate biomass variation (77 and 60% of mixotrophs and heterotrophs, respectively) than that of heterotrophic ciliates (35%). Mixotrophic ciliates displayed little connection to the analyzed environmental variables (only 18% of their biomass variation was explained by the model).

Phytoplankton Growth and Grazing Mortality Rates

The results of dilution experiments at the process stations and the corresponding abiotic conditions in May and August are shown in **Table 1**. The chlorophyll values shown in the table are the initial concentrations in the experimental bottles, which were measured after seawater was screened through a 153 μm mesh to remove large zooplankton. The resulting concentrations were typically 92–98% of ambient, but the screening removed almost 40% of chlorophyll at P3–15 m, where colonial *Phaeocystis* was abundant at the time of experiment. At this station, we used an additional carbon filter to remove potential cytotoxins from 0.2- μm filtered seawater (Stoecker et al., 2015). However, following this treatment chlorophyll strongly decreased in

the diluted treatment (-0.66 d^{-1}) compared to the whole seawater control (-0.24 d^{-1}). Therefore, the growth rate was calculated from the changes in the latter treatment. The same calculation approach was used at P6–1 m, where the initial concentration of chlorophyll in the whole seawater was too low ($0.13 \mu\text{g L}^{-1}$) for reliable growth rate estimates in the diluted treatment.

Phytoplankton growth rates were not stimulated by nutrient additions in any of the 12 experiments except in the open surface water sample at P1/P5 in August (data not shown). The rates varied from -0.24 d^{-1} (P3–15 m) to 0.31 d^{-1} (P1–10 m) in May and 0.22 to 0.42 d^{-1} in August. The highest growth rates were recorded in August at sub-zero temperatures, low salinity (<32), and under the dense (70–90%) ice cover. The rates did not correlate with sea temperature (linear regression, $r^2 = 0.04$, $p = 0.56$), but tended to increase with the ice cover, although the relationship was not significant (**Figure 7**). We found no difference (t -test, $p = 0.4$) between the rates in the surface samples and those collected from DCL despite the fact that light conditions during incubations were very different (70 vs. 4% of surface irradiance). The average growth rates (excluding negative values) were 0.24 d^{-1}

in May and 0.30 d^{-1} in August. The corresponding grazing mortality rates measured in 9 out of 12 experiments did not correlate with temperature or chlorophyll either. Herbivory was measurable in two experiments dominated by *P. pouchetii* (P3-40 m and P4-15 m) and significantly increased with the ice cover (Figure 7). Overall, the grazing rates were similar in May ($0.18 \pm 0.05 \text{ d}^{-1}$) and August ($0.23 \pm 0.12 \text{ d}^{-1}$). In the experiments where both grazing and growth rates were measured, their ratio ($g:\mu$) varied from 0.36 to 1.57. Based on the average growth (0.29 d^{-1}) and grazing (0.21 d^{-1}) rates, microzooplankton herbivory impact at the process stations was 72% of the daily primary production. At sea temperatures above and below 2°C this ratio was 60 and 85%, respectively, although the difference was not statistically significant (t -test, $p = 0.25$).

Microzooplankton Growth and Production Rates

The individual species-specific growth rates of microzooplankton taxa were related to temperature. For example, *P. faureii* grew 0.69 d^{-1} at -0.5°C and 1.25 d^{-1} at 3.0°C ; *T. appendiculariformis* 0.56 d^{-1} at -1.0°C and 0.69 to 1.25 d^{-1} at 6°C . The fastest growing microzooplankton were the ciliates *M. rubrum* (1.39 d^{-1} at 3°C and 0.92 d^{-1} at 6.3°C) and *B. planktonicum* (1.73 d^{-1} at 6.0°C). Many mixotrophic oligotrichs grew fast at low temperatures: for example, *Strombidium* sp. and *S. conicum* 1.00 d^{-1} at 0 and 0.2°C , respectively. The growth rate of *G. spirale* initially increased with temperature from 0.42 d^{-1} at -1°C to 1.12 d^{-1} at 0°C , and then declined to 0.84 d^{-1} at 6.3°C .

The average total microzooplankton growth rates (calculated as the daily P/B ratio) were similar between May and August at the process stations: 0.15 ± 0.10 and 0.14 ± 0.12 , respectively. At temperatures $> 2^\circ\text{C}$, typical for the Atlantic water, the average daily microzooplankton P/B was $0.23 \pm 0.10 \text{ d}^{-1}$.

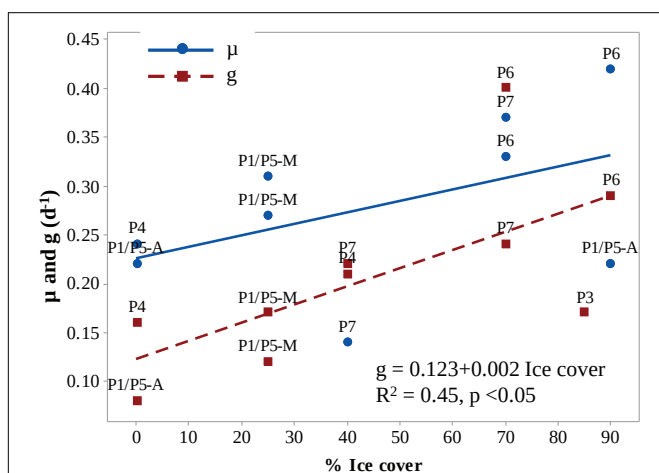


FIGURE 7 | The rates of phytoplankton growth (solid line, circles) and grazing mortality (dashed line, squares) vs. the percentage of sea ice cover at the process stations. P1/P5-M = in May and P1/P5-A = in August.

For those taxa that increased during the experiments, the average taxon-specific growth rates were also similar between the cruises: 0.50 ± 0.19 and 0.40 ± 0.13 . The proportion of these taxa in total microzooplankton biomass also did not change between May and August (33 and 31%, respectively), but varied among the experiments (11% at P6-1 m to 75% at P3-40 m). The maximum average species-specific growth (0.78 d^{-1}) was recorded in the latter experiment at 3°C . Both the growing population (Figure 8A) and total microzooplankton rates (Figure 8B) were positively related to sea temperature with the exception of DCL samples $> 5^\circ\text{C}$ in August. Microzooplankton production rate varied from $0.29 \mu\text{g C L}^{-1} \text{ d}^{-1}$ at P3-40 m (3°C) to $9.2 \mu\text{g C L}^{-1} \text{ d}^{-1}$ at P5-1 m (6.0°C). Production did not correlate with temperature (Figure 8C) or chlorophyll ($r^2 = 0.02$, $p = 0.69$), but the initial biomass of growing populations explained a large proportion of productivity variation ($r^2 = 0.84$, $p < 0.001$). The average rates at the process sites were

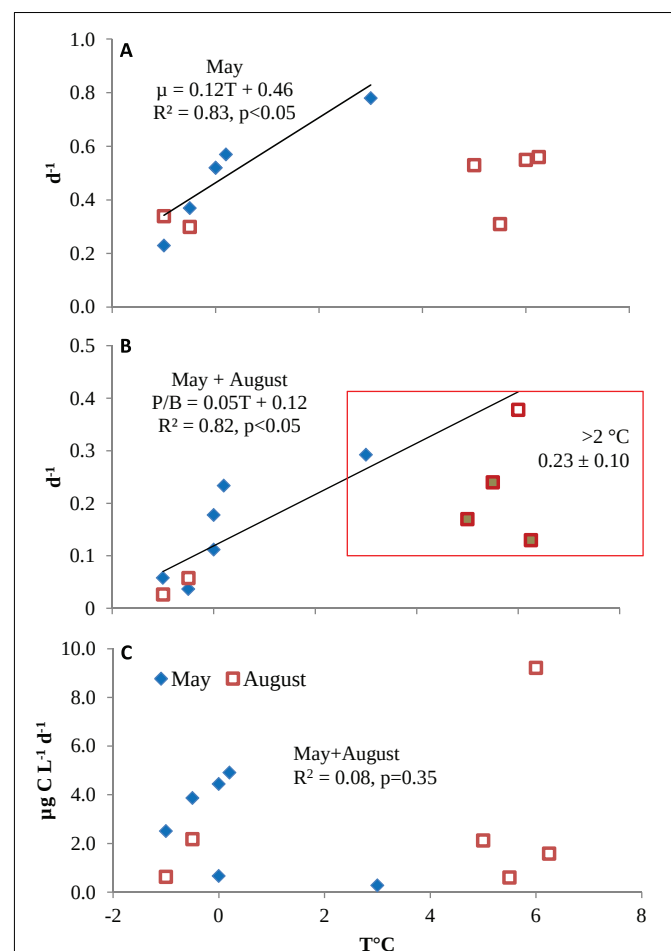


FIGURE 8 | The average growth rates of microzooplankton populations that increased over time in experimental incubations (A) and total microzooplankton growth (B) vs. sea temperature in May (filled triangles) and August (open squares). Filled squares denote regression outliers. (C) Microzooplankton community production.

$2.7 \pm 1.6 \mu\text{g C L}^{-1} \text{ d}^{-1}$ in May and $2.8 \pm 3.0 \mu\text{g C L}^{-1} \text{ d}^{-1}$ in August.

DISCUSSION

Microzooplankton Distribution and the Controlling Factors

Microzooplankton biomass recorded in this study in the upper 0–50 m layer (175 to 2306 mg C m^{-2}) was considerably higher than previously reported values from the northwestern Fram Strait (47 to 108 mg C m^{-2} in 0–60 m, Seuthe et al., 2011). The average volumetric biomass of $22.6 \mu\text{g C L}^{-1}$ in this study was similar to the values reported by Calbet et al. (2011) from the central Fram Strait and the Yermak slope in July ($20.7 \mu\text{g C L}^{-1}$, range 1.84 to $67 \mu\text{g C L}^{-1}$). Both studies have indicated considerable heterogeneity in microzooplankton spatial distribution. Similar microzooplankton biomass values were also reported from the productive Arctic shelf seas (Hansen et al., 1996; Račkova and Wassmann, 2002; Verity et al., 2002; Lavrentyev, 2012; Stoecker et al., 2014b; Franzè and Lavrentyev, 2017). To our knowledge, the biomass of ciliates in the surface layer at D5 in May ($206 \mu\text{g C L}^{-1}$) is the highest microzooplankton biomass reported so far from the Arctic. It exceeds the previous record set in the southeast Bering Sea ($164 \mu\text{g C L}^{-1}$ including ciliates and dinoflagellates $> 10 \mu\text{m}$, Olson and Strom, 2002).

Microzooplankton biomass did not correlate with sea temperature in the northeastern Fram Strait (Seuthe et al., 2011). A negative relationship between total microzooplankton and sea temperature observed in this study was likely due to the fact that microzooplankton increased in August, when their biomass peaked in the cooler surface layer. The positive relationship between heterotrophic ciliates and salinity is probably indirect as well and reflects generally better conditions for this microzooplankton component in the Atlantic waters of WSC. The design of our study was not conducive to isolating the effects of ice cover on microzooplankton distribution and dynamics. Most of our transect stations remained ice-free in the spring and summer, whereas the process stations located further north in the Arctic Ocean were ice-covered during both seasons (except P1/P5 in August). Nevertheless, it should be noted that microzooplankton biomass increased in August in the ice-covered Arctic Ocean waters just like it did in the open Atlantic waters of the eastern Fram Strait. Further, microzooplankton herbivory rates were positively related to the ice cover; the mechanism behind this effect remains to be determined.

Ciliates and dinoflagellates inhabiting polar seas are well-adapted to their cold and icy environment (Sherr et al., 2013; Franzè and Lavrentyev, 2014; Menden-Deuer et al., 2018) and food availability is central among factors controlling their populations dynamics and composition (Caron and Hutchins, 2013). In addition to the distinct vertical patterns, microzooplankton biomass and composition displayed pronounced seasonality. At all examined sites the spring assemblage was dominated by mixotrophic oligotrichs and

large heterotrophic dinoflagellates. The latter group is usually associated with diatom blooms in polar waters (Lovejoy et al., 2002; Olson and Strom, 2002; Sherr et al., 2009, 2013; Franzè and Lavrentyev, 2017). As indicated by the results of regression analyses in this study, total chlorophyll may be too crude a measure to describe the specific resource requirements of microzooplankton. An increase in the abundance of *Synechococcus* in the surface layer in August (Paulsen et al., 2016) and the predominance of nanophytolankton typical for the eastern Fram Strait in summer (Nöthig et al., 2015) could have supported higher and more diverse microzooplankton biomass.

Another factor controlling microzooplankton populations in the ocean is crustacean zooplankton predation (Saiz et al., 2013). The dominant Atlantic expatriate *Calanus finmarchicus* and its Arctic congeners *C. hyperboreus* and *C. glacialis* are opportunistic omnivores that feed on both phytoplankton and microzooplankton (Ohman and Runge, 1994; Levinsen et al., 2000a; Campbell et al., 2009). The surface peak of the plasticid oligotrichs in May corresponded to low concentration of mesozooplankton based on the laser optical plankton counter high frequency vertical profiles (Basedow et al., 2018). In addition, the eastern end of transect D is the zone of fast northward AW flow over the shelf (Basedow et al., 2018) and the ciliates could have been advected there. Given their fast specific growth rates in our experiments ($> 1 \text{ d}^{-1}$), it is also plausible that mixotrophic oligotrichs could have formed a bloom using a temporary relief of top-down control. Inversely, low microzooplankton biomass at C3 and C8 in May could have been due to large *Calanus* spp., which were abundant in the upper part of the water column along transect C. The ratio of microzooplankton biomass (0–100 m) to the biomass of *C. finmarchicus* (0–1000 m) along transect D was 30 to 106% in May and increased to 63 to 123% in August. This ratio demonstrates the quantitative importance of microzooplankton in the eastern Fram Strait. For comparison, the inflow of *C. finmarchicus* with the Atlantic water was estimated to be in the order of 5×10^5 metric tons C y^{-1} (Basedow et al., 2018). At the ice covered process stations, microzooplankton biomass was ca. 40% of *C. finmarchicus* biomass in May and 106% in August (Svensen et al., 2019).

Mixotrophic Microzooplankton and Their Importance

All prior microzooplankton studies in the Fram Strait and the Yermak shelf (Putt, 1990; Calbet et al., 2011; Seuthe et al., 2011) reported significant contribution of mixotrophic ciliates to microzooplankton biomass. Their contribution to total chlorophyll calculated in this study is substantial, particularly in the surface layer. In the adjacent Barents Sea, mixotrophic chlorophyll in DCL varied between 1.5 and 49% (Franzè and Lavrentyev, 2017). In the Bering Sea, ciliate chlorophyll was sometimes over 50% of total chlorophyll (Stoecker et al., 2014a) and 46% in the Kara Sea (Lavrentyev, 2012). In the surface layer at D5 in May, the mixotrophic to total chlorophyll ratio was $\sim 200\%$. Obviously, this is an artifact, but not necessarily stemming from our calculations. Vacuum

filtration through membrane filters commonly used to collect chlorophyll may disrupt fragile ciliate cells and thus lead to losses of mixotrophic chlorophyll (Putt, 1990). The estimates of mixotrophic ciliate chlorophyll made in this study should be treated as tentative. Mixotrophic chlorophyll content was calculated based on algal chlorophyll content (Montagnes et al., 1994), assuming that the volume to chlorophyll relationship is similar to that in autotrophic plankton (Dolan and Perez, 2000). The former study was based on cultures growing under controlled conditions and supplied with sufficient nutrients, thus the physiological state (and consequently chlorophyll quotas) of the cells might be different than those observed in the environment. It should be mentioned, however, that the cell chlorophyll quota of *S. conicum* ($30,000 \mu\text{m}^3$) measured directly in the Barents Sea by Putt (1990) was similar to that estimated in this study using the above assumptions (48 and 55 pg chlorophyll cell⁻¹, respectively). The cell chlorophyll content and kleptoplastid numbers vary widely among different marine oligotrichs (Stoecker et al., 1988; McManus et al., 2012) and can depend on the food availability (Schoener and McManus, 2012). The factors controlling physiology, distribution, and dynamics of mixotrophic ciliates remain poorly understood. Although the distribution of mixotrophic ciliates did not correlate with any of the available environmental variables in this study, their peak abundance was found at low chlorophyll concentrations. Similarly, mixotrophic oligotrichs peaked within the Polar Front, which is characterized by low primary productivity in the Barents Sea (Franzè and Lavrentyev, 2017). These observations may suggest that mixotrophy is a response to oligotrophic conditions. On the other hand, dense populations of mixotrophic ciliates were found in the productive regions of the Kara Sea (Lavrentyev, 2012) and the Bering Sea (Stoecker et al., 2014b). Further studies must clarify the role of mixotrophy, which is widespread among planktonic protists in the polar seas (Stoecker and Lavrentyev, 2018). In general, this trophic mode enhances carbon flow through pelagic food webs by compensating for respiratory losses (Ward and Follows, 2016).

Microzooplankton Herbivory

Planktonic copepods have been considered the main herbivores in the marine food webs (Smetacek, 1999). In contrast to this traditional concept, recent research indicates that copepods primarily rely on ciliates and other microzooplankton as an essential food source except during diatom blooms (Saiz and Calbet, 2011; Ray et al., 2016). Due to their relatively slow growth and long life histories (Hop et al., 2006; Litchman et al., 2013), copepods cannot provide a rapid response to unicellular phytoplankton growth in the spring. On an annual basis the combined grazing by *Calanus* spp. and euphausiids amounts to ca. 30% of the total primary production in the Arctic (Hop et al., 2006). This leaves 70% of primary production available to microbial grazers.

Both dinoflagellates and ciliates can feed on large and chain-forming diatoms (Hansen and Calado, 1999; Olson and Strom, 2002; Aberle et al., 2007; Sherr et al., 2013). The results of dilution experiments in this study demonstrate that microbial grazers can remove a substantial portion of daily phytoplankton

production even during the spring bloom. These data correspond to the previous studies in the Arctic seas (reviewed in Franzè and Lavrentyev, 2017, Table 3). The stimulating effect of ice cover on microzooplankton herbivory in this study is surprising, because in the adjacent Barents Sea, microzooplankton herbivory increased with temperature and was higher in the open waters than under the ice (Verity et al., 2002; Franzè and Lavrentyev, 2017). It is plausible that microzooplankton responded to the ice-induced changes in phytoplankton composition and/or dynamics. Overall, this study demonstrates the capacity of microzooplankton to control primary production in both ice-covered and open waters. For example, the experiments conducted at P1/P5 in May (-0.5 to 0°C , 90% ice cover) and August (6 to 6.3°C , open water) yielded similar depth-averaged grazing rates (0.14 and 0.12 d^{-1} , respectively). In both cases, ca. 50% of daily primary production was removed.

In two surface experiments (P4 and P7), microzooplankton consumed > 100% of primary production. This is not unusual (Calbet and Landry, 2004; Menden-Deuer et al., 2018) and likely reflects the dynamic equilibrium between phytoplankton growth and grazing (Irigoien et al., 2005) and, possibly, the effect of large predator removal. Herbivory, as measured in dilution experiments, is a community process. Based on microscopy, nauplii and other invertebrates were rare in our samples. The most likely contributors to the measured grazing rates were heterotrophic and mixotrophic pico- and nanoflagellates, which were abundant at the process stations, especially in the summer (up to $1500 \text{ cells mL}^{-1}$, Paulsen et al., 2016). Interestingly, in the latter study the flagellates grew faster (up to 0.53 d^{-1}) in <5 μm fraction, whereas their *Synechococcus* prey grew faster in <90 μm fraction, suggesting a picoplankton-nanoflagellate-microzooplankton-copepod trophic cascade.

Although the dilution experiments at P3-15 m technically failed because chlorophyll concentrations declined precipitously in the diluted treatment, it should be noted that colonial *P. pouchetii* formed > 90% of microscopic phytoplankton abundance at this site (Sanz-Martín et al., 2018). Microzooplankton can feed on *P. pouchetii* as evidenced by the outcome of dilution experiments at P3-40 m and P4 and published research (Verity et al., 2007; Grattepanche et al., 2011). However, the presence of colonial *P. pouchetii* is often reported in conjunction with low or insignificant herbivory rates in dilution experiments (Calbet et al., 2011; Stoecker et al., 2015; Menden-Deuer et al., 2018). In addition to forming large colonies, *P. pouchetii* can produce toxic polyunsaturated aldehydes (PUAs) such as 2-*trans*-4-*trans*-decadienal (Hansen et al., 2004). PUA impaired growth of some marine ciliates and dinoflagellates (Lavrentyev et al., 2015). Microzooplankton grew in both experiments at P3, albeit much faster in the seawater collected from 40 m (P/B: 0.29 vs. 0.11 d^{-1} at 15 m). Several abundant species were responsible for this difference (*G. spirale*: 1.08 vs. 0.39 d^{-1} ; *P. bipes*: 0.88 vs. -0.69 d^{-1} ; *M. rubrum*: 1.39 vs. 0.39 d^{-1}), whereas others were not (e.g., *Strombidium* sp.: 0.79 vs. 1.04 d^{-1}). However, the lack of PUA measurements does not allow us to untangle the possible effects of *Phaeocystis*-produced cytotoxins and temperature at different depths. This phenomenon should be investigated further, since *P. pouchetii* is a

very common and often dominant component of phytoplankton assemblages in the Arctic. In addition, dissolved PUA production by marine phytoplankton can create opportunities for bloom development by inhibiting herbivory and stimulating copepod predation on microzooplankton (Franzè et al., 2018).

Microzooplankton Growth and Production

Similar to microzooplankton in the Barents Sea (Franzè and Lavrentyev, 2014), on average one third of the microzooplankton community grew in any given experiments. The rest of the populations either declined or did not change significantly over 24 h. This asynchronicity in the growth of dominant species appears to reflect a general pattern of microzooplankton community dynamics, where multiple populations oscillate out of phase, whereas short-term incubations provide only a snapshot of these dynamics. The rapid species-specific growth rates of ciliates and dinoflagellates in our experiments support the idea that low temperatures do not constrain their growth more than that of their phytoplankton prey (Sherr et al., 2013; Menden-Deuer et al., 2018). Further, the ability of these protists to achieve their intrinsic maxima rapidly is likely an adaptation to the fluctuating and spatially heterogeneous environment (Franzè and Lavrentyev, 2014). Nevertheless, the growth response of microzooplankton community to temperature was evident, particularly at temperatures $\leq 0^{\circ}\text{C}$. Given the current climate change in the Arctic, it is likely that microzooplankton growth will increase in a warmer ocean leading to greater retention of carbon in the mixed layer (Franzè and Lavrentyev, 2017). At the same time, the growth-temperature equations resulting from our field experiments should be used with caution as they may reflect the indirect effects of other factors such as resource limitation (Rose and Caron, 2007) and/or intraguild predation (e.g., Franzè and Modigh, 2013).

Because microzooplankton growth rates were similar between May and August, we can apply the average rate of 0.23 d^{-1} calculated for AW to the depth-integrated (0–100 m) microzooplankton biomass in transect D. The resulting average production rate of $227\text{ mg C m}^{-2}\text{ d}^{-1}$ combined with the growth gross efficiency of 30% commonly reported for zooplankton (Straile, 1997) yields a daily carbon demand of $756\text{ mg C m}^{-2}\text{ d}^{-1}$. Over the 4-month period from May to August microzooplankton production and carbon demand (27.9 and 93 g C m^{-2} , respectively) would equal 23 and 75% of the annual gross primary production in the eastern Fram Strait ($123\text{ g C m}^{-2}\text{ y}^{-1}$, Forest et al., 2010). These calculations depend on primary production estimates, which vary from 80 to $180\text{ g C m}^{-2}\text{ y}^{-1}$ in the WSC (Hop et al., 2006), and do not account for the effects of phytoplankton respiration and exudation, mixotrophy, bacterivory, and copepod predation on microzooplankton. However, they correspond to the average microzooplankton herbivory impact in this study and illustrate the scale of carbon flux through the microbial food web in the Fram Strait and the Arctic Ocean shelf. For comparison, *C. finmarchicus* secondary production in the Atlantic inflow was estimated at $2\text{--}4\text{ g C m}^{-2}\text{ y}^{-1}$ (Slagstad et al., 2011) or

7 to 14% of microzooplankton production estimated in this study. Svensen et al. (2019) estimated *C. finmarchicus* production at 11 to 23% of microzooplankton production at the process stations. Further, microzooplankton growth in the Arctic is not limited to May through August. Protists remain active during the polar winter (Druzhkov and Druzhkova, 1998; Møller et al., 2006) and form considerable biomass in the early spring before the diatom bloom (Levinson et al., 2000b; Seuthe et al., 2011). Therefore, their potential role in polar pelagic food webs may be even greater than suggested by the above estimates.

CONCLUSION

Ciliates and dinoflagellates are an important component of the pelagic food web in both the Atlantic waters of WSC and the ice-covered Arctic shelf waters; their biomass is comparable with that of dominant copepods. Due to their rapid biomass turnover, microzooplankton can produce an order of magnitude more carbon than net zooplankton. Mixotrophic ciliates can form surface blooms and contribute substantially to chlorophyll *a* in the mixed layer, but their role remains to be fully understood. Although microzooplankton biomass and composition displayed strong seasonality, their herbivory remained a major factor controlling primary production except during the peak of colonial *P. pouchetii*. Based on their critical role in the pelagic carbon cycle in the Fram Strait and other polar seas systems, microzooplankton must become a regular component of monitoring programs and models focused on the climate change effects in the Arctic.

AUTHOR CONTRIBUTIONS

PL designed and conducted the experiments, analyzed data, and wrote the manuscript. GF designed and conducted the experiments, analyzed data, and prepared the figures. FM designed experimental equipment and conducted the experiments.

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Seasonal Variation in Transport of Zooplankton Into the Arctic Basin Through the Atlantic Gateway, Fram Strait

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The largest contribution of oceanic heat to the Arctic Ocean is the warm Atlantic Water (AW) inflow through the deep Fram Strait. The AW current also carries Atlantic plankton into the Arctic Basin and this inflow of zooplankton biomass through the Atlantic-Arctic gateway far exceeds the inflow through the shallow Pacific-Arctic gateway. However, because this transport has not yet been adequately quantified based on observational data, the present contribution is poorly defined, and future changes in Arctic zooplankton communities are difficult to project and observe. Our objective was to quantify the inflow of zooplankton biomass through the Fram Strait during different seasons, including winter. We collected data with high spatial resolution covering hydrography (CTD), currents (ADCP and LADCP) and zooplankton distributions (LOPC and MultiNet) from surface to 1,000 m depth along two transects crossing the AW inflow during three cruises in January, May and August 2014. Long-term variations (1997–2016) in the AW inflow were analyzed based on moored current meters. Water transport across the inflow region was of the same order of magnitude during all months (January 2.2 Sv, May 1.9 Sv, August 1.7 Sv). We found a higher variability in zooplankton transport between the months (January 51 kg C s⁻¹, May 34 kg C s⁻¹, August 50 kg C s⁻¹), related to seasonal changes in the vertical distribution of zooplankton. However, high abundances of carbon-rich copepods were observed in the AW inflow during all months. Surface patches with high abundances of *C. finmarchicus*, *Microcalanus* spp., *Pseudocalanus* spp., and *Oithona similis* clearly contributed to the advected biomass, also in winter. The data reveal that the phenology of species is important for the amount of advected biomass, and that the advective input of zooplankton carbon into the Arctic Basin is important during all seasons. The advective zooplankton input might be especially important for mesopelagic planktivorous predators that were recently observed in the region, particularly during winter. The inflow of *C. finmarchicus* with AW was estimated to be in the order of 500,000 metric tons C y⁻¹, which compares well to modeled estimates.

Keywords: advection, West Spitsbergen current, mesozooplankton, laser optical plankton counter, Atlantic Water, seasonal, Arctic Ocean, winter

INTRODUCTION

The Arctic marine environment has undergone major changes in temperature and ice cover over the last decades, and is projected to continue to warm and thaw (Overland and Wang, 2013; IPCC, 2014). The largest oceanic heat transport to the Arctic Basin is the warm Atlantic Water (AW) inflow through the deep Fram Strait (Beszczynska-Möller et al., 2011). Over the last decades this AW inflow has become warmer (Beszczynska-Möller et al., 2012), and it has been identified as the main mediator of climate change in the Arctic marine environment (Spielhagen et al., 2011; Polyakov et al., 2012; Onarheim et al., 2014). In addition to heat, the AW current transports phytoplankton (Hegseth and Sundfjord, 2008; Metfies et al., 2016) and zooplankton of Atlantic origin, and with different functional roles (Kosobokova and Hirche, 2009; Kraft et al., 2013; Gluchowska et al., 2017b). Changes in ecosystem structure at lower latitudes are thus advected into the Arctic Basin and affect productivity and carbon cycling (Hunt et al., 2016). The input of zooplankton biomass through the Atlantic-Arctic gateway far exceeds the input through the shallow Pacific-Arctic gateway due to the large differences in water volume advected (Bluhm et al., 2015; Wassmann et al., 2015). However, this input has not yet been adequately quantified based on observational data, therefore the present contribution is poorly defined, and future changes in Arctic Basin zooplankton communities are still difficult to project and observe.

Atlantic expatriates in the Arctic Basin can considerably influence the composition of Arctic zooplankton communities; they might exert top-down control on primary production, and may also be an important food source for higher trophic levels (Olli et al., 2007; Kosobokova et al., 2011; Falk-Petersen et al., 2014). How the inflow of Atlantic species will manifest itself in Arctic food webs in the future is less clear. For example the Atlantic copepod *Calanus finmarchicus* contributes 30–40% to zooplankton biomass in the western Nansen basin (Mumm, 1993; Kosobokova and Hirche, 2009; Wassmann et al., 2015), but so far this species has not been able to reproduce in the Arctic Ocean and high non-predatory mortality is observed (Hirche and Kosobokova, 2007; Daase et al., 2014). The reasons for this are not fully understood, but low temperatures in the upper layer may slow development considerably, leading to a failure of reaching the main overwintering stages within one season (Hirche and Kosobokova, 2007; Daase et al., 2014). The delayed onset of the phytoplankton bloom in the Arctic domain also impacts survival and reproductive success of Atlantic copepods, by hindering development, maturation and egg production the following spring (Niehoff and Hirche, 2000). A warmer AW current might thus not only bring new species into the Arctic Ocean, but may also affect survival of those that are transported there.

North Atlantic and Arctic zooplankton species have adapted their life cycles to the pronounced seasonality at higher latitudes. Many herbivorous copepods tend to leave the productive epipelagic zone in winter, but variability occurs in the timing of their seasonal migrations throughout the Arctic (Daase et al., 2013). Other, omni- and detritivore species remain in the epipelagic (e.g., *Oithona similis*) or the mesopelagic zone (e.g.,

Triconia borealis) throughout the year, as a seasonal study from the Canadian Arctic has shown (Darnis and Fortier, 2014). The AW inflow in the Fram Strait stretches over the epipelagic into the mesopelagic zone and occupies roughly the upper 600–800 m. Species that stay in the epipelagic throughout the year will thus be advected into the Arctic Basin continuously, while species that perform seasonal migrations below the AW will be advected mainly during spring and summer. Seasonal variability occurs also in the strength and extension of the AW inflow: in summer the baroclinic offshore branch of the West Spitsbergen Current (WSC) is absent (Wekerle et al., 2017), such that in winter the WSC tends to be wider and stronger with two-fold higher transport (Beszczynska-Möller et al., 2012). The interplay between the seasonality of the currents and the variable seasonal migrations of zooplankton as part of their life cycle therefore strongly affects the potential of different species to be advected into the Arctic Basin.

The dominating Atlantic copepod *C. finmarchicus* has its core habitat in the Norwegian Sea, where it migrates to depths below the AW layer for overwintering (Gaardsted et al., 2011). During spring and summer *C. finmarchicus* stays in the upper layer and is then advected with AW to areas downstream (Edvardsen et al., 2003). In the region of AW inflow into the Arctic Basin *C. finmarchicus* recently has been observed in surface waters as early as January (Daase et al., 2014; Berge et al., 2015; Blachowiak-Samolyk et al., 2015). Winter data on zooplankton vertical distribution from Arctic regions are still scarce, but these recent observations challenge our understanding of the life cycle of one of the most well-studied copepods. A reduced understanding of fundamental principles also hinders the modeling of zooplankton transport into the Arctic Basin correctly, and stresses the need for seasonal observations.

Not all the AW that flows through the Atlantic gateway enters the Arctic Basin, in fact large amounts recirculate and eventually turn southwards (Hattermann et al., 2016; von Appen et al., 2016). However, a narrow barotropic branch flows northwards with high velocity along the steep continental slope in the eastern Fram Strait. Most of this water likely enters the Arctic Basin across the southeastern Yermak Plateau, although mesoscale instabilities shed off eddies that propagate westwards (Hattermann et al., 2016; von Appen et al., 2016). To the west of this continental slope current, to approximately 5°E, the fate of the AW and included zooplankton is less certain. The AW flows northwards to the Yermak Plateau before either recirculating west- and southwards or entering the Arctic Basin across or around the perimeter of the plateau (Koenig et al., 2017). To the west of 5°E the AW is likely recirculated. Zooplankton studies from the AW inflow in the northern Fram Strait so far have been limited to few (<10) stations and were mostly restricted to the upper 200 m (Hirche et al., 1991; Blachowiak-Samolyk et al., 2007; Svensen et al., 2011; Nöthig et al., 2015; Gluchowska et al., 2017a,b).

Time series of 9–14 years from the WSC indicate that with a warming AW we can expect higher abundances of the Atlantic-boreal species *C. finmarchicus* and *Oithona similis* (Weydman et al., 2014; Gluchowska et al., 2017a). However, based on optical data with high spatial resolution the generally patchy distribution

of zooplankton has been confirmed for a region of the AW inflow in the Fram Strait (Trudnowska et al., 2016). Spatial variability explained as much of the variability in the analyzed time series as environmental factors did (Weydman et al., 2014). Often, statistical analyses of net samples are complicated by the spatial resolution of the nets not matching the spatial resolution of the physical parameters. In this respect optical and acoustical methods that are collected in concert with physical parameters have the potential to greatly enhance our understanding of factors governing zooplankton distributions (Wu et al., 2014). In addition, these methods allow the collection of high-resolution data both in the vertical and horizontal plane, which needs to be taken into account when quantifying advection of zooplankton into the Arctic Basin.

Our main objective is to quantify the zooplankton biomass entering the Arctic Basin through the Fram Strait during different seasons, including winter. Based on an extensive biophysical dataset with high spatio-temporal resolution we aim to answer (1) how the interplay between the seasonal variability in AW inflow and zooplankton vertical distributions determines the advection of zooplankton species with different life cycles, and (2) how the input of external zooplankton biomass into the Arctic Basin compares to Arctic secondary production.

MATERIALS AND METHODS

Field Sampling

Physical-biological data on the seasonal variation in hydrography, currents and plankton distributions were collected with high spatial resolution along two transects (referred to as C and D for consistency with other publications in this issue) crossing the Atlantic Water inflow into the Arctic Basin during three research cruises with R/V Helmer Hanssen in January, May and August 2014 (Figure 1, Table 1). Only one transect was completed in January due to time constraints. During the research cruises, currents were measured using a ship-mounted Acoustic Doppler Current Profiler (ADCP, RDI 75 kHz) along transects and a lowered ADCP (LADCP, RDI 300 kHz) profiling at stations. For an increased temporal resolution we used data from 6 moorings placed in the study region in 2014, and analyzed variations in the northward flow of Atlantic Water in 2014 compared to the long-term mean from 1997 to 2016 (von Appen et al., 2016). The moorings were located along 78°50'N, 79°N and 79°45'N near the 2,500 m isobaths. They contained rotor current meters and upward looking ADCPs at 250 m depth. More details on the mooring setup can be found in Beszczynska-Möller et al. (2012).

To obtain high spatial resolution data on water mass properties and plankton distributions we used a free-fall Moving Vessel Profiler (MVP, ODIM Brooke Ocean, Rolls Royce Canada Ltd., Herman et al., 1998) that was equipped with a Conductivity-Temperature-Depth and a Fluorescence sensor (CTD, Applied Microsystems Micro CTD; F, WET Labs FLRT Chl *a* fluorometer), as well as a Laser Optical Plankton Counter (LOPC; ODIM-Brooke Ocean Rolls Royce Canada Ltd., Herman et al., 2004). These instruments provide quantitative data at a rate of 4 Hz (CTD-F) or 2 Hz (LOPC) on hydrography,

fluorescence and mesozooplankton abundance. All instruments on the MVP are contained in a “fish” that is controlled by a remotely-operated winch system. In ice-free waters the MVP was used in free-wheel mode while the ship moved forward along transects. In this mode data are collected along profiles while the fish falls freely through the water column at 3.5–4 m s⁻¹ vertical speed, and is then retrieved automatically by the winch. Sampling depth was from surface to 10 m above the bottom, but restricted to 1,000 m at maximum, which is well below the Atlantic Water layer (Table 1). Ship velocity along transects was 6–7 knots (3–3.6 m s⁻¹) and bottom depth ranged between ca. 200 m on the shelf to >1,000 m offshore, resulting in a distance between starting points of individual profiles of ca. 0.5 km on the shelf and ca. 5.5 km offshore. When ice conditions did not permit continuous sampling, single profiles were taken with the MVP and the winch was then operated in continuous rounds-per-minute mode, resulting in downward velocities of the fish of ca. 3 m s⁻¹. Alternatively, if conditions in total were too risky to deploy the MVP (i.e., a combination of darkness, sea ice, strong winds and high waves), the LOPC was mounted on a sturdy rosette frame together with a different CTD (Seabird 19plusV2, Seabird Electronics Inc., USA) and fluorescence sensor (WETLabs EcoFl, Seabird Electronics Inc., USA). In this case the instruments were deployed vertically at stations along the transects, and lowered with a speed of 0.7–0.8 m s⁻¹.

To analyze the depth distribution of species and to aid interpretation of the high-resolution data, species composition in the study region was investigated based on vertically stratified net samples. These were collected by a MultiNet Midi (180 μm mesh size, 0.25 m² mouth opening, Hydro-Bios, Kiel, Germany) that was deployed vertically at stations along transects (Table 1). Hauling speed was 0.5 m s⁻¹. Samples were preserved in a solution of 80% seawater and 20% fixation agent (75% formaldehyde buffered with hexamine, 25% anti-bactericide propandiol), resulting in a final formaldehyde concentration of 4%.

Raw Data Analyses

Analyses of Water Masses

CTD data were screened for out-of-range values, which were removed prior to further analyses. Potential temperature (Θ) and density (σ_Θ) were computed from a running mean over 2 m of pressure, temperature and salinity using the seawater package (version 3.3.4) in python (www.python.org, version 2.7). Based on this, T-S diagrams (not shown) were made to help identifying water masses.

Analyses of Water Currents

The climatological northward transport for each month of the year was established based on mean gridded current data from the moorings as described in Beszczynska-Möller et al. (2012), but the data set was extended by 2 years, ranging from 2002 to 2012. Not all the moorings could be recovered in 2015, therefore we followed the approach of von Appen et al. (2016) to judge how similar 2014 was compared to the climatology. Current data obtained from the vessel-mounted ADCP and

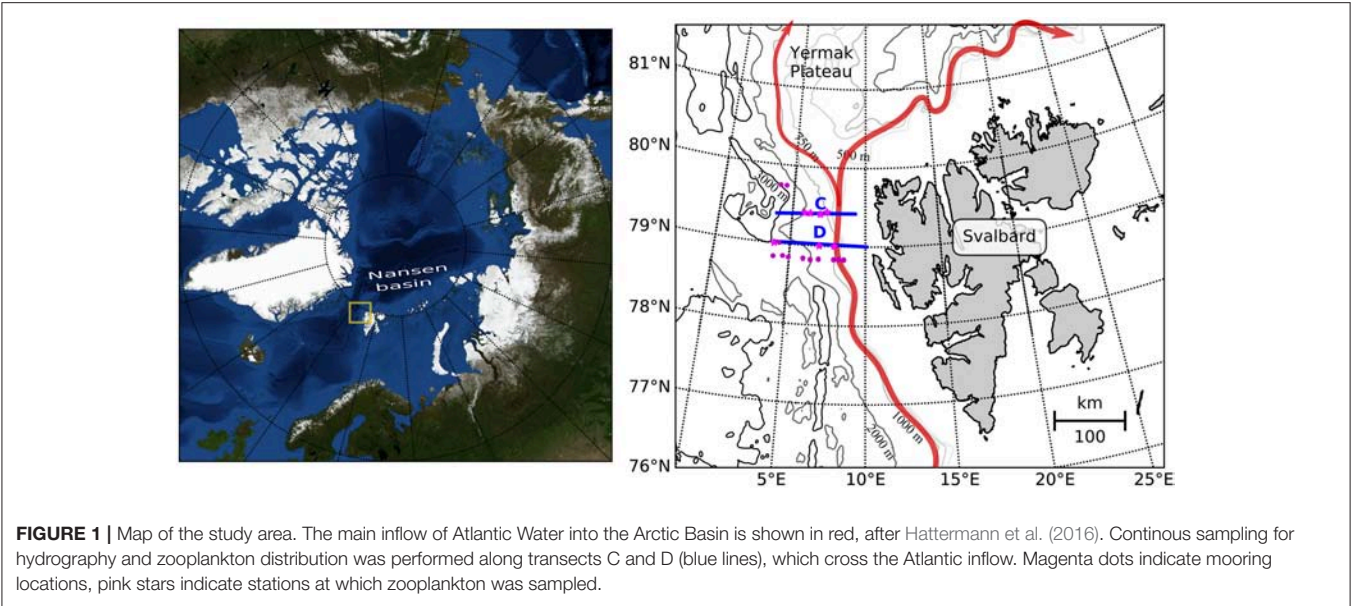


TABLE 1 | Seasonal sampling for mesozooplankton across the Atlantic Inflow west of Svalbard in January, May, and August 2014.

Station/transect	Date	UTC	Gear	Lat (°N)	Lon (°E)	Bottom depth (m)	Sampling depth (m), notes
D – start	12 Jan	10:39	MVP	79.00	08.78	227	0–bottom or 1,000 m
D – end	12 Jan	20:03	MVP	79.02	04.28	2,589	
D1	12 Jan	22:44	MultiNet	79.00	04.36	2,564	1,000–600–200–100–50–0
D3	13 Jan	06:19	MultiNet	78.99	07.01	2,422	1,000–600–200–100–50–0
D4	13 Jan	11:45	MultiNet	79.00	08.00	1,087	1,000–600–200–100–50–0
D – start	16 May	07:14	MVP	79.00	09.90	278	0–bottom or 1,000 m
D	16 May	16:27	MVP	79.00	05.22	2,399	Ice, over to frame
D	16 May	19:35	Frame	79.00	04.80	2,454	0–1,000 m
D – end	16 May	21:17	Frame	79.00	04.00	2,717	0–1,000 m
D1	17 May	01:20	MultiNet	78.99	04.02	2,717	1,000–600–200–100–50–0
D3	17 May	15:10	MultiNet	78.99	07.00	1,216	1,000–600–200–100–50–0
C – start	27 May	01:00	Frame	79.40	04.94	2,415	0–1,000 m
C – end	27 May	13:09	Frame	79.42	09.33	134	0–125 m
C5	28 May	08:38	MultiNet	79.40	06.98	1,225	1,000–600–200–100–50–0
C3	28 May	17:13	MultiNet	79.41	05.89	1,855	1,000–600–200–100–50–0
D – start	07 Aug	09:29	MVP	79.00	10.09	269	0–bottom or 1,000 m
D – end	07 Aug	22:36	MVP	79.01	04.01	2,411	
D1	08 Aug	01:43	MultiNet	79.01	04.00	2,410	1,000–600–200–100–50–0
D3	08 Aug	13:48	MultiNet	79.00	06.76	1,247	1,000–600–200–100–50–0
C – start	16 Aug	03:47	MVP	79.42	09.31	135	0–bottom or 1,000 m
C – end	16 Aug	12:54	MVP	79.38	03.98	3,476	
C1	16 Aug	14:37	MultiNet	79.35	03.75	3,816	1,000–600–200–100–50–0
C4	17 Aug	01:38	MultiNet	79.41	06.29	1,595	1,000–600–200–100–50–0
C6	17 Aug	09:18	MultiNet	79.43	07.44	940	900–600–200–100–50–0

The Moving Vessel Profiler (MVP) contained a laser optical plankton counter (LOPC) together with a CTD and a fluorescence sensor (F), continuous profiles were taken while moving along transects. Also the rosette frame (Frame) was equipped with a LOPC-CTD-F, it was deployed vertically at stations. The MultiNet was deployed vertically and sampled several depth layers. For details see section Materials and Methods.

L-ADCP data were first processed by standard routines and afterwards tides were subtracted based on AOTIM (Padman and Erofeeva, 2004). The current data along transects were gridded using multivariate interpolation as specified in the function griddata in scipy.interpolate (www.scipy.org, version 0.18.1).

Two regions of possible inflow of AW into the Arctic Ocean were identified based on flux across transect D as observed by the moored instruments in this study, and as modeled in the study region (Hattermann et al., 2016): (1) The Inflow region in the upper 700 m along the continental slope between 8 and 9 °E, and (2) the Uncertain Fate region in the upper 700 m between 5.5 and 8 °E. Water and zooplankton in the Inflow region have a high likelihood of entering the Arctic Ocean, while in the Uncertain Fate region water and zooplankton may eventually end up in the Arctic Ocean or may be recirculated southwards in the East Greenland Current. We also analyzed the transport in the 700–1,000 m layer below both regions to estimate the transport of zooplankton residing below the AW layer.

Analyses of Zooplankton Distributions

Zooplankton distributions were analyzed with high spatial resolution based on LOPC data. The LOPC counts and measures particles that pass through its sampling channel while the instrument is towed through the water (Herman et al., 2004). Two types of particles are registered by the LOPC, single element particles (SEPs) and multi element particles (MEPs). SEPs are smaller particles which darken one to two of the 49 photodiodes of the LOPC, MEPs are larger particles that darken more than two photodiodes. Typically SEPs dominate in the size range below 0.6–0.8 mm equivalent spherical diameter (ESD), above which MEPs dominate. For MEPs additional features are registered, e.g., the transparency of particles, which is usually calculated as attenuation index (AI) that ranges from zero (completely transparent) to one (completely opaque). The size range of particles detected and registered by the LOPC is 0.1 µm to 35 mm ESD, but only particles between ca. 0.2 and 4 mm ESD are counted quantitatively. We analyzed particles in this size range as described in Basedow et al. (2014), which included thoroughly checking the quality of the data as described in Schultes and Lopes (2009) and Espinasse et al. (2017). The ESD is a relative measure of the diameter a particle has, in case of the LOPC it is the diameter equivalent to black calibration spheres. This means for example that large, transparent particles can have a relatively small ESD. The LOPC does not give any taxonomic information, and nets are not suited to capture marine snow or fragile zooplankton. Therefore, it is often unclear if transparent particles are marine snow or transparent zooplankton, and this varies in all likelihood regionally and seasonally (Ohman et al., 2012; Basedow et al., 2013). To separate zooplankton from other particles we followed the method developed by Espinasse et al. (2017) that indicates the ratio of zooplankton to detritus among small (SEPs) and large (MEPs) particles by analyzing two simple indicators, the percentage of MEPs in all counts, and the mean AI of MEPs.

During all months few faulty MEPs (as defined in Schultes and Lopes, 2009) were observed and the total number of MEPs was far below 10^6 , showing that the LOPC was not overloaded and counted the correct amount of particles (Table A1). In January the mean AI was high (>0.2) and MEPs were relatively large (>1 mm ESD), which is typical for polar systems dominated by larger copepods (Basedow et al., 2013; Espinasse et al., 2017). In May and August parts of the transects (6 out

of 9 files) were characterized by a high percentage of MEPs ($\geq 2\%$) in combination with a low (August) to very low AI (May), Table A1. This is typical for hydrologically stratified systems, when the LOPC counts phytoplankton aggregates, other detritus and/or transparent zooplankton along with more opaque zooplankton (Espinasse et al., 2017). In May very high chlorophyll concentrations (up to 11.6 mg m^{-3}) were observed in the area, indicating that phytoplankton aggregates might have contributed to LOPC counts. In August chlorophyll concentrations were lower ($<4 \text{ mg m}^{-3}$) indicating that detritus and/or transparent zooplankton might have contributed most to the large amount of transparent particles. More information on the distribution of chlorophyll can be found in Randelhoff et al. (this issue).

We divided particles into three different size groups and excluded transparent particles, i.e., MEPs with an AI < 0.4 , from our analyses so that the large size group consisted of zooplankton only, while the medium size group consisted of zooplankton for the most part. For the small size group, which consists mostly of SEPs, a division based on the transparency of particles is not possible, therefore the small size group in May and August most likely consisted of a mixture of zooplankton and detrital material. In January, however, the indicators developed by Espinasse et al. (2017) and applied to our data suggest that the small size group consisted mostly of zooplankton. The following three size groups were analyzed: small (S, 200–600 µm ESD), medium (M, 0.6–1.5 mm ESD) and large particles (L, 1.5–4 mm ESD). This size classification was chosen to separate dominating species in the study area into different groups, where possible (Basedow et al., 2014, and references therein).

Abundance of the three size groups was estimated based on particle counts and the water volume flowing through the sampling channel. For data that were collected during retrieval of the MVP “fish,” the water volume calculated based on LOPC data differed strongly from the water volume estimated trigonometrically from wire length, cable speed and the ships velocity. It is uncertain which of the estimated volumes is the correct one, therefore we constrained abundance analyses to downward profiles.

Analyses of the Zooplankton Community

From the fixed MultiNet samples zooplankton were counted and identified to the level of species (most copepods), genus or family (other groups). Conspicuous, large zooplankton (>5 mm, chaetognaths >10 mm) were identified and enumerated from the entire sample. From the rest of the sample, at least 500 individuals from a minimum of three sub samples (2 ml, obtained with an automatic pipette with tip end cut to leave a 5 mm opening) were identified, staged to life cycle and counted. This procedure allows for the analysis of abundance of common species and taxa with 10% precision and at a 95% confidence level (Postel, 2000). Copepods of the genus *Calanus* were identified to species based on their size (Kwasniewski et al., 2003). Specimens other than copepods were measured and sorted into different size categories (<5 , 5–10, and 10–20 mm).

Analyzing Seasonal Variation in Transport of Zooplankton Into the Arctic Ocean

Transport of zooplankton biomass (kg C s^{-1}) across the four different areas (Inflow region, Uncertain Fate region, and the layers below both, see section Analyses of Water Currents) was calculated by multiplying mean biomass in an area (mg C m^{-3}) with mean northward water transport across that area (in $\text{Sv} = 10^6 \text{ m}^3 \text{ s}^{-1}$). Mean northward water transport was calculated based on the long-term data from 1997 to 2012 (Beszczynska-Möller et al., 2012, 2015), because we judged this to be more representative for the seasonal variation than the short-term data from the ship-mounted ADCP. Due to eddy activity in the region measured currents at any given time are representative for a few days only. Biomass transport was calculated for January, May and August, which in combination with the vertical distribution of zooplankton allowed us to analyze seasonal variation in the advection of zooplankton. A two-factorial analysis of variances (ANOVA) was performed to test if the depth distribution of zooplankton was significantly different between months and transport regions. Mean biomass was determined based on the zooplankton biovolume observed by the LOPC in each area. For this, biovolume was converted into carbon using a fixed ratio of $0.03 \text{ mg C mm}^{-3}$ (Zhou et al., 2010). Biomass data from the downward profiles were gridded using multivariate interpolation as specified in the function `griddata` in `scipy.interpolate` (www.scipy.org, version 0.18.1). For each area the average carbon content per m^3 was then computed based on the gridded data. Incorrectly interpolated data from depths below sampled depths at the shelf break were excluded from the analyses.

RESULTS

Water Masses

During all cruises the dominating water mass in the upper 500 m was Atlantic Water (AW, $\Theta > 2^\circ\text{C}$, $\sigma_T < 27.97$, Rudels et al., 2005), **Figure 2**. Along transect D in January AW was observed from surface down to ca. 700 m along most of the transect, and down to ca. 400 m west of 5.6°E . West of 5.6°E the conductivity sensor was not working properly and this area is indicated by a gray rectangle in **Figure 2**. Also in May and August AW was observed all along the transect, but stretched down to ca. 450 m only and was overlain by a layer (ca. 50 m) of warm Polar Surface Water (wPSW, $\Theta > 0^\circ\text{C}$, $\sigma_T < 27.7$, Rudels et al., 2005). The layer of wPSW originates from sea ice that is melted by the relatively warm AW or by solar radiation (Rudels et al., 2005), see **Figure 2** and **Figure A1** for the distribution of wPSW along the transects in individual months. Below the warmer, less dense AW ($\Theta > 2^\circ\text{C}$) a part of AW with lower temperature was observed, down to ca. 900 m in January and ca. 750 m in May and August. This colder, denser AW, often called Arctic Atlantic Water, is characterized by $0^\circ\text{C} < \Theta < 2^\circ\text{C}$, $\sigma_T > 27.97$, $\sigma_{0.5} < 30.444$, and by Θ and salinity increasing with depth (Rudels et al., 2005; Marnela et al., 2016). The main water mass below both these AW water masses was characterized by $\Theta < 0^\circ\text{C}$ and $\sigma_T > 27.97$, properties typical for Arctic Intermediate Water (AIW, Marnela et al., 2016).

Currents

Short-Term Currents Measured During the Cruises

In the Inflow region along the shelf break between 8 and 9°E , both the ship-mounted ADCP (**Figure 3**) and the lowered ADCP (**Figure 4**) recorded a northward directed flow during all months. According to the ship-mounted ADCP the northward current was fastest in August, with more than 50 cm s^{-1} , in an area not sampled by the LADCP. Conversely, in January the LADCP measured high current speed with nearly 50 cm s^{-1} at 8°E , which was not detected by the ship-mounted ADCP. The northward flow was restricted to the upper 700 m during all sampled months. Below 700 m along the shelf break the current was flowing with variable velocities toward the southeast in January and May, and with low velocities toward the southwest in August (**Figure 4**). In the region of Uncertain Fate, between 5.5 and 8°E , both instruments detected variable currents, with relatively strong northward velocities at times but also relatively strong southward velocities at other times, up to 30 cm s^{-1} at ca. 7.5°E in January (**Figure 3**, top). West of 8°E current direction below 700 m was mostly toward the northwest and the current speed was mostly low (**Figure 4**).

Long-Term Currents Observed by the Moorings

The currents observed by the ship-mounted ADCP and the LADCP (**Figures 3, 4**) at transect D were generally consistent with the currents observed at the mooring locations (**Figure 5**). Averaged over 1 to 31 January 2014 and 1 to 31 May 2014 a consistent northward flow at 75 m and 250 m was observed at the moorings along the continental slope (**Figure 5**). This is in agreement with the long-term measurements at the moorings, which showed a strong northward current in January, May and August (**Figure 5**, right panels). However, averaged over 1 to 31 August 2014 currents with highly variable directions were observed in the Inflow region, contrary to the long-term northward flow. During all months currents were more variable and weaker in the Uncertain Fate region than in the Inflow region along the shelf break. Currents at 250 m were not noticeably weaker than at 75 m (**Figure 5**), which is in agreement with the LADCP data that did not show a decrease in current velocity in the upper 500 m at most of the stations (**Figure 4**).

Zooplankton Distribution

The distribution of zooplankton in the area indicates their potential of entering the Arctic Basin, depending on their vertical position in the water column (upper part or at depths $> 600 \text{ m}$), and whether they are in the Inflow region (along the continental slope between 8 and 9°E) or in the region of Uncertain Fate (5.5 – 8°E). Significant seasonal differences were observed in the distribution of all zooplankton size groups (**Figures 6–8**, **Table A2**). In January, patches with high abundances of all size groups were observed in the surface layer, where they are subject to higher current velocities. Relatively high abundances were also observed below ca. 500 m, i.e., below the core of AW inflow (**Table 2**, **Figures 6–8**, top). In May, most medium-sized and large zooplankton was concentrated in AW, and very low abundances were observed below 700 m (**Table 2**, **Figures 7, 8**). In August, medium and large zooplankton were

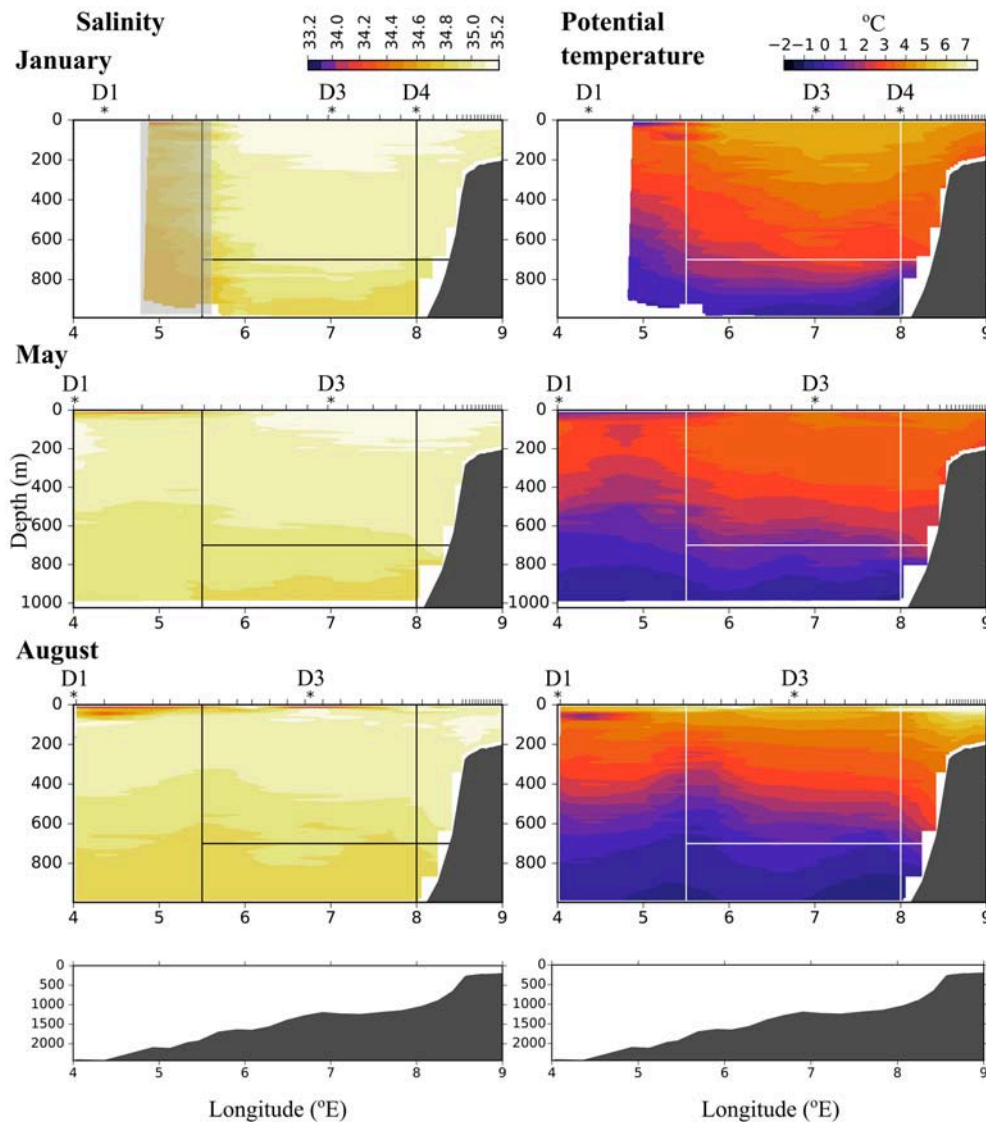
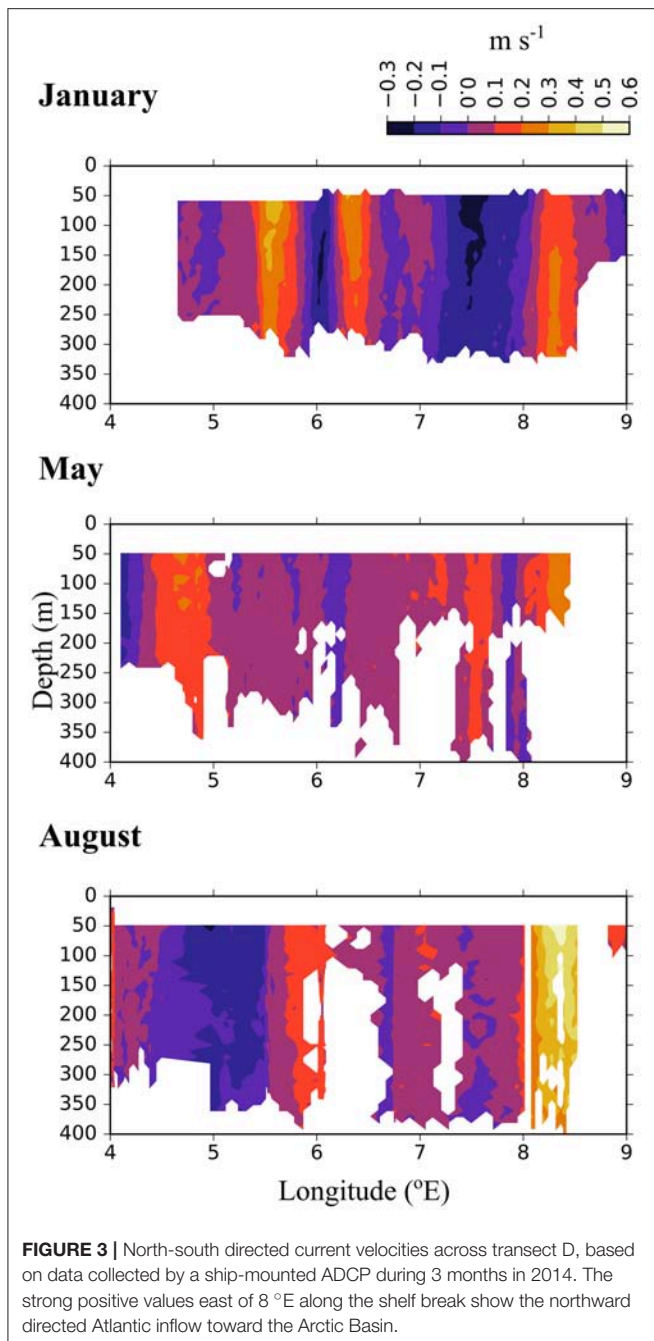


FIGURE 2 | Salinity (Left) and potential temperature (Right) along transect D in January (Top), May (Middle), and August (Bottom). Ticks along the top axis indicate start points for vertical sampling profiles. Stars with labels depict stations at which zooplankton was sampled. In January, the conductivity sensor was not working properly west of 5.6 °E, this area is indicated by a gray rectangle. Black (Left) and white (Right) lines indicate the areas that were used for calculating flux. The bottom panels show the bottom topography along the transect.

found in the entire water column, with the highest abundances of medium zooplankton in the upper 500 m (Figures 7, 8). The surface patches in January consisted predominantly of *Calanus finmarchicus* CIV and CV, but *Microcalanus* spp. and *Pseudocalanus* spp. also had high abundances, as well as the cyclopoid copepod *Oithona similis* (Table 2, and data for specific depth layers, not shown). Below the AW water layer these species, along with *Metridia longa*, were by far the dominating constituents of the zooplankton community in January.

Relatively low abundances ($<1,000$ individuals m^{-3}) of small plankton were observed offshore between 100 and 200 m in January, and below 200 m east of 5 °E in May (Figure 6). Significantly higher abundances were observed along the shelf

break in the Inflow region in January and also in May (Figure 6, Table A2). Keep in mind that the small size group likely contained a mixture of zooplankton and other particles in May and August, see Methods. In August, the distribution of small plankton and particles was very uniform along the transect, with very high abundances (between 10^4 and $10^6 m^{-3}$) in the epipelagic zone and high abundances (10^3 – $10^4 m^{-3}$) below (Figure 6). Net samples showed highest abundances of small zooplankton in the upper 600 m in May and August. Very high abundances of copepod nauplii, *Oithona similis* and *Microcalanus* spp. were observed in May. In August copepod nauplii, young stages of *C. finmarchicus*, *Microcalanus* spp. and *Oithona similis* dominated. *Triconia borealis* had very high



abundances below the AW layer in May, and in the AW layer in August.

The distribution of medium-sized zooplankton in January was similar to the distribution of small zooplankton in this month, with highest abundances in patches in the surface layer (up to 10^5 ind. m^{-3}), **Figure 7**. Relatively high abundances (up to $1,000$ ind. m^{-3}) were also observed in the Inflow region along the shelf break, and in a large area below 400 m and between approximately 5.5 and 7.5 °E. The dominating species in the medium size group were *C. finmarchicus* CII-CIV and *Metridia longa* (**Table 2**). In January and May, the areas of low abundances

of medium-sized zooplankton coincided with areas in which low abundances of small plankton and particles were observed. In August, the distribution of medium-sized zooplankton seemed to be less uniform than that of the small size group (**Figure 7**). Lowest abundances were observed in the surface layer in the center of transect D, in wPSW, while highest abundances were observed in the center of transect C.

Large zooplankton was distributed more patchily than the other two size groups (**Figure 8**). *C. finmarchicus* CV was by far the dominating copepod in the large size group (**Table 2**, **Figure 9**). In January patches of more than $1,000$ ind. m^{-3} were observed in the surface layer, and large zooplankton resided either close to the surface or below 600 m in the region of Uncertain Fate (**Figure 8**). In May, scattered patches were observed in AW along transect D, while highest abundances were found at the surface in wPSW along transect D and C. Almost all large zooplankton was concentrated in wPSW along transect C in May. The distribution of large zooplankton in August was patchy, but patches (with 100 – $1,000$ ind. m^{-3}) were distributed all along the transects and at all depths (**Figure 8**). Along transect C in August more patches were observed along the shelf break than farther west.

Zooplankton and Water Transport

Northward water transport across transect D was in the same order of magnitude during all months, but largest in January and lowest in August (**Table 3**). Across the Inflow region northward transport was roughly 2 Sv during all months, while transport across the Uncertain Fate region was more variable with approx. 3 Sv in January, 2 Sv in May, and 1 Sv in August. Below 700 m depth water transport was generally much lower with ca. 0.1 Sv below the Inflow region and 0.3–0.7 Sv below the Uncertain Fate region. These low transport rates nevertheless have the potential to transport substantial amounts of zooplankton residing at depth during the winter months.

Northward transport of zooplankton across the Inflow region during the different months was more variable than water transport (**Table 3**). In total about 50 kg C s^{-1} were transported across the Inflow region in January and August, and are highly likely to reach the Arctic Basin and to impact the ecosystem there. In May the total amount of carbon transported was lower, with about 34 kg C s^{-1} (**Table 3**). Additionally, a large but variable amount of carbon was transported northward across the Uncertain Fate region.

About 9,000 individuals m^{-3} of small zooplankton occurred in the Inflow region in January, mostly *Microcalanus* spp., *Pseudocalanus* spp., and *Oithona similis* (**Table 2**). This corresponded to a transport of ca. 11 kg C s^{-1} over the entire Inflow region (**Table 3**). In May and August about 19 kg C s^{-1} of small plankton and particles were transported across the Inflow region. The relative contribution of non-zooplankton particles was likely highest at depth, below the Inflow and Uncertain Fate regions, where net samples showed relatively low abundances of small zooplankton, but where the LOPC recorded moderate to high numbers of plankton and particles (**Table 2**, **Figure 6**).

Across the Inflow region northward biomass transport of medium-sized zooplankton was lowest in May (ca. 4 kg C s^{-1}),

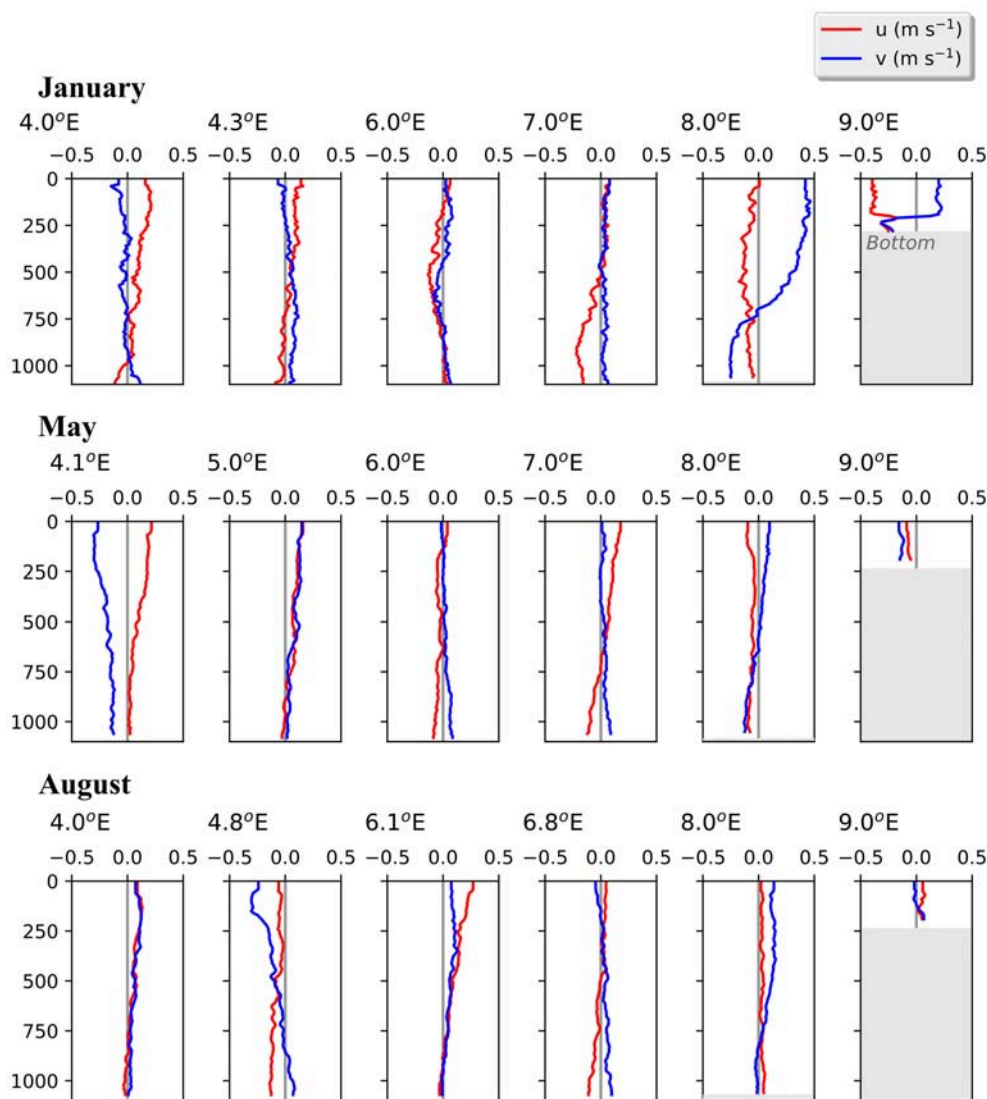


FIGURE 4 | Vertical profiles of current velocities at six stations along transect D. Based on data collected by a lowered-ADCP during 3 months in 2014. Northward (v , blue) and eastward (u , red) directed currents are shown.

higher in August (ca. 14 kg C s^{-1}) and highest in January (ca. 17 kg C s^{-1}), **Table 3**. The medium size group consisted mostly of CII-CIV copepodids (**Table 2**), which in January and May were predominantly CIV, whereas in August they were CIII and CII (data not shown). The average carbon content per individual (mean biomass m^{-3} divided by mean abundance m^{-3} , **Table 3**) that was estimated for the medium group was lower in May than in January and August, and abundances were lower in May, resulting in a comparatively low biomass transport in May (**Table 3**). The high abundances of the dominating *C. finmarchicus* CIV in the upper layer in January (**Table 2**), together with the slightly higher average carbon content in this month (**Table 3**), and the slightly larger water transport compared to August, all resulted in the large transport of

medium-sized zooplankton carbon across the Inflow region in winter (**Table 3**).

The same tendency that was observed for the medium size group was also seen for the large size group. In January, large zooplankton resided in the upper layer, had a relatively high average carbon content and a relatively large water transport was measured. Thus, a high amount of large zooplankton biomass was transported across the Inflow region in January (23 kg C s^{-1} , **Table 3**). Transport of large plankton across the Inflow region was also relatively high in May and August, 12 and 17 kg C s^{-1} , respectively, **Table 3**. Substantial amounts of large zooplankton were also transported northward across the Uncertain Fate region, between 4 kg C s^{-1} in May and 16 kg C s^{-1} in January (**Table 3**). Below the Inflow region transport differed by three

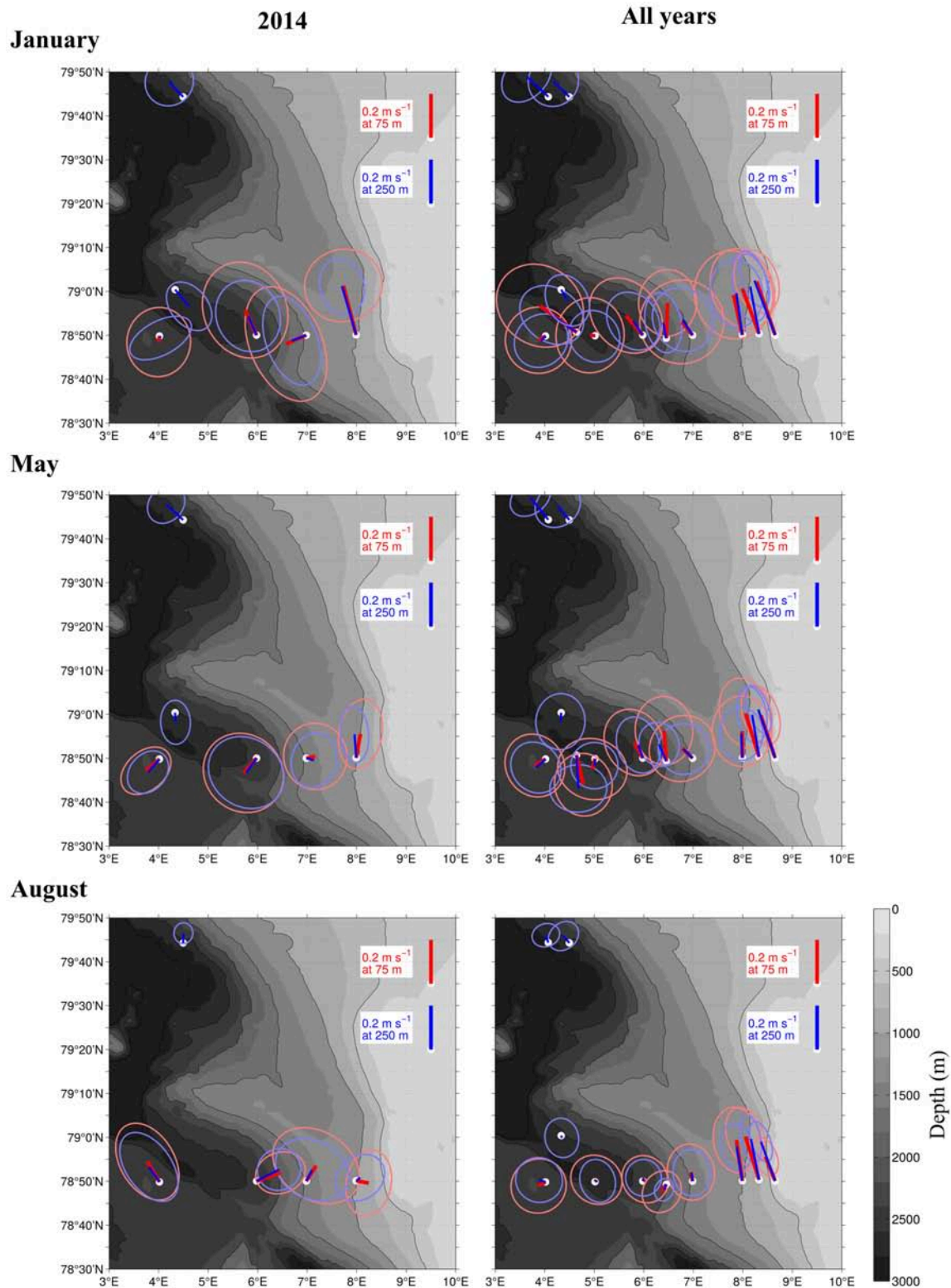


FIGURE 5 | Current strength and direction (lines) in an area of the Atlantic Water inflow toward the Arctic Basin during 3 months in 2014 (**Left**), and averaged over 15 years from 1997 to 2012 (**Right**). Based on moored ADCPs that were placed at 75 m (red) and 250 m (blue). The ellipses around the lines show standard deviations of the currents. The averaging period was January 1–31st (top), May 1–31st (**Center**), and August 1–31st (**Bottom**).

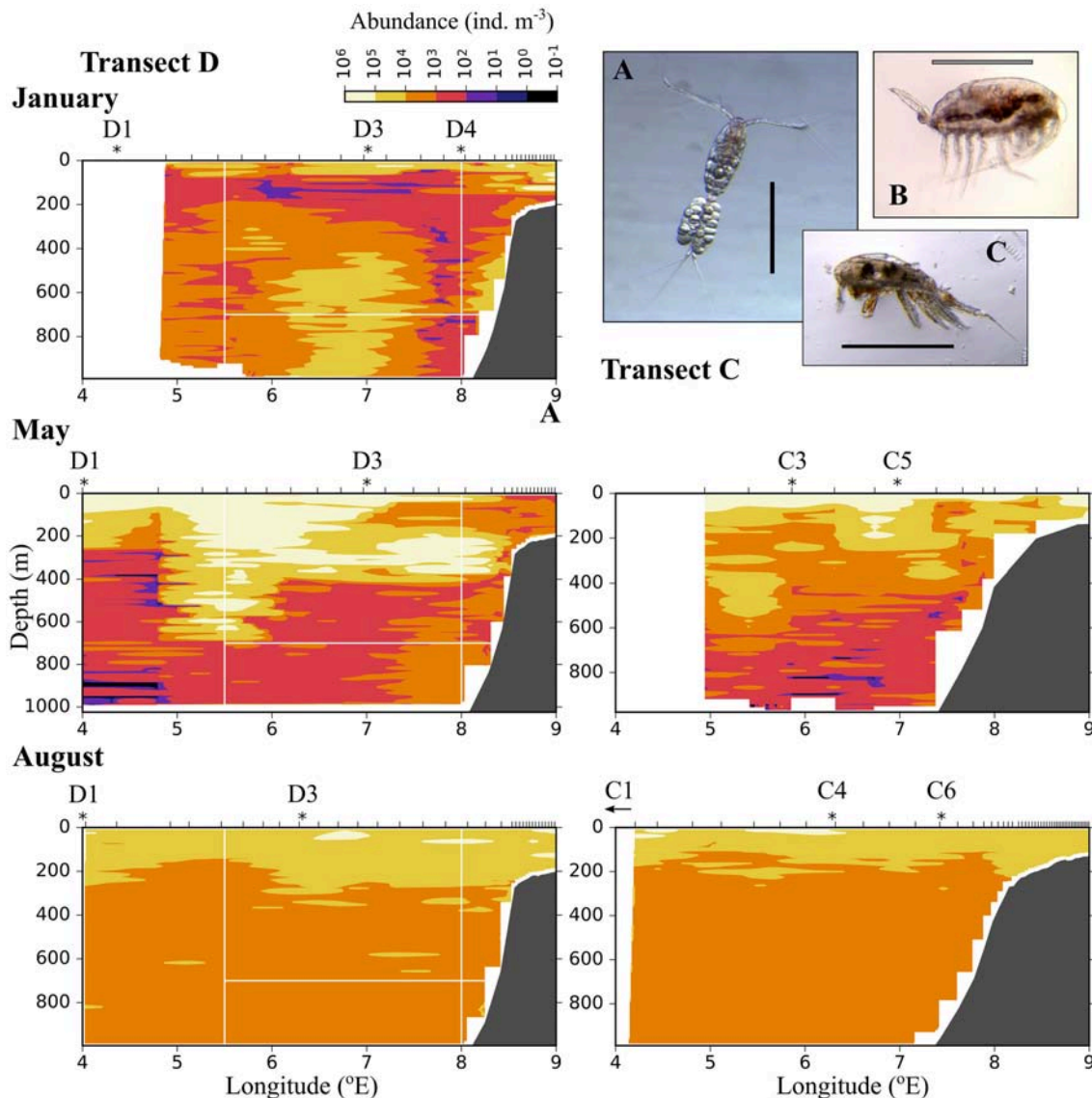


FIGURE 6 | Distribution of small plankton and particles (200–600 μm equivalent spherical diameter) along three transects crossing the Atlantic inflow into the Arctic Basin. Based on data collected by a laser optical plankton counter (LOPC) in January (**Top**), May (**Middle**), and August (**Bottom**). See **Figure 1** for location of transects. Ticks along the top axis indicate start points for vertical sampling profiles with the LOPC, stars denote the approximate position of MultiNet stations that were sampled after completion of sampling with the LOPC. A small arrow indicates that the MultiNet station lay outside the transect. Three of the most abundant zooplankton species in the MultiNet samples in this size range are shown: (A) *Oithona similis*, (B) *Microcalanus* sp., (C) *Triconia borealis*. The black scale bar is 0.5 mm, the gray scale bar is approximately 0.5 mm.

orders of magnitude between 2 g C s^{-1} in January and 1 kg C s^{-1} in August.

DISCUSSION

This study provides the first quantification of abundance and biomass of zooplankton that flows with Atlantic Water (AW) through the Fram Strait into the Arctic Basin (AB). The occurrence of carbon-rich species in the upper 600 m, where northward current velocities were strongest, resulted in large

amounts of carbon being transported with the AW across the Inflow region. Furthermore, some of the zooplankton that is transported northward across the Uncertain Fate region may reach the AB, and likely more so in winter than in summer (Koenig et al., 2017). This suggests that the external input of zooplankton carbon, on the order of $34\text{--}50 \text{ kg C s}^{-1}$ depending on the season (**Table 3**), is important for AW-influenced areas of the AB during all seasons, including winter. Below we discuss how the interplay between zooplankton phenology and physical factors influences the advection of zooplankton into the AB (sections Zooplankton Phenology and

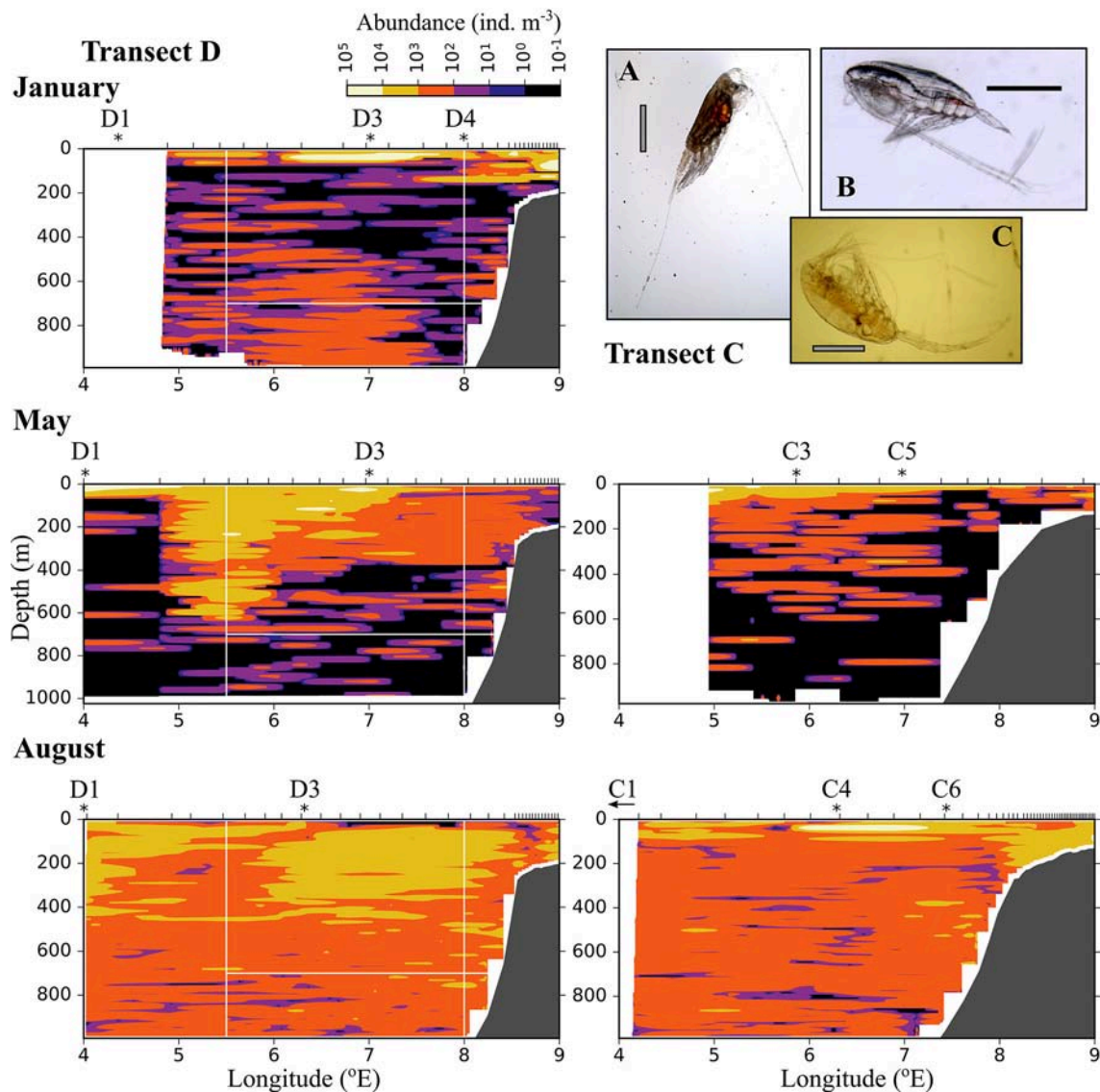


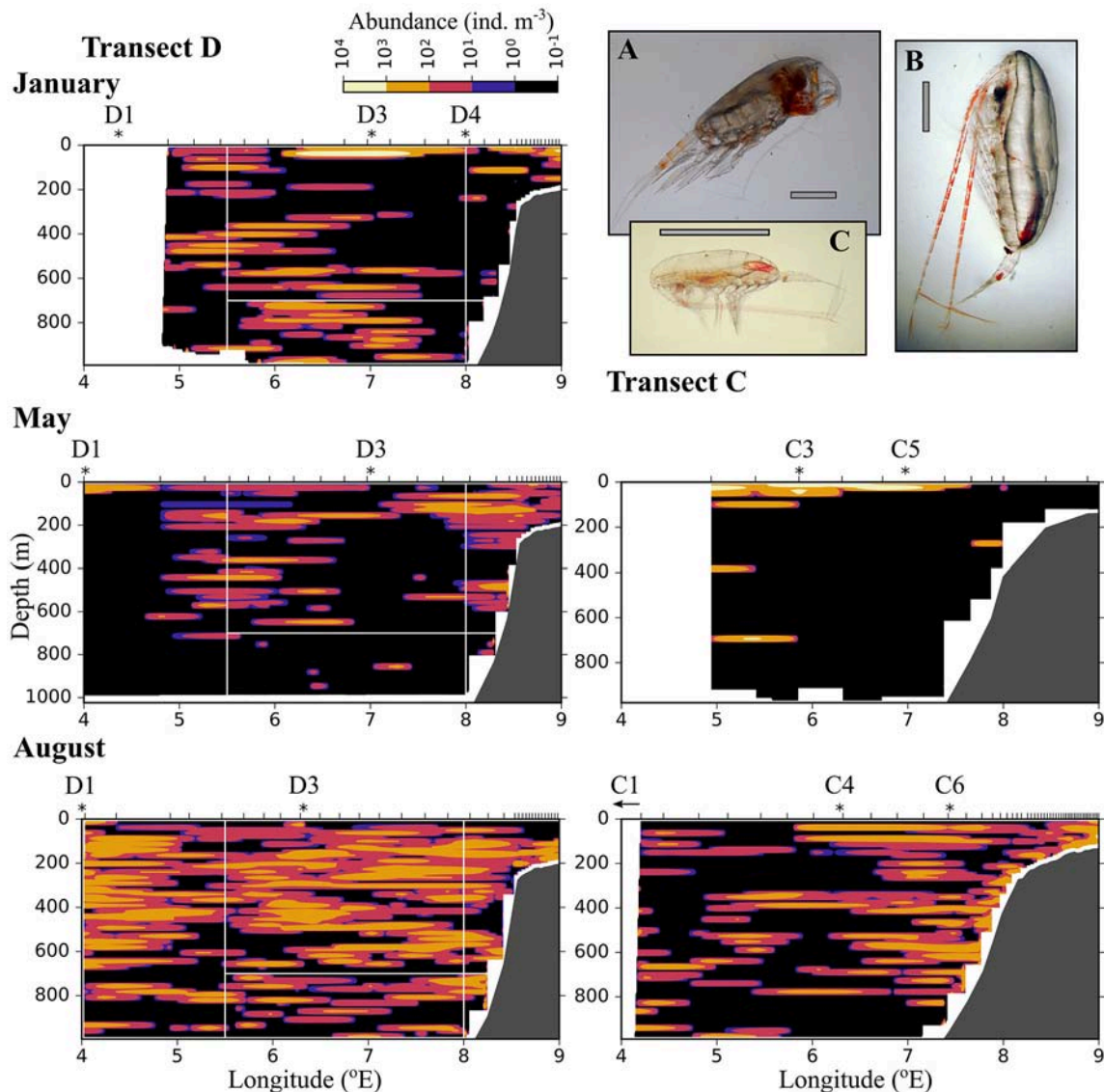
FIGURE 7 | As **Figure 6**, but for medium-sized zooplankton (0.6–1.5 mm equivalent spherical diameter). (A) *Heterorhabdus norvegicus* (B) *Calanus finmarchicus* CIV, (C) *Metridia longa* female. The black scale bar is 1 mm, the gray scale bar is approximately 1 mm.

Implications for Their Advection Toward the AB and Eddy Activity and Zooplankton Transport). Based on our data we perform calculations to relate our estimates of zooplankton input into the AB to observed and modeled zooplankton advection and to Arctic secondary production (sections Advection of the Atlantic Copepod *C. finmarchicus* to Implications of Advected Biomass for Arctic Productivity and Higher Trophic Levels).

Zooplankton Phenology and Implications for Their Advection Toward the AB

We observed a lower variability in water transport than in zooplankton transport between the months, indicating that zooplankton patchiness and vertical migrations influenced the advected biomass. Zooplankton patchiness is well known (e.g.,

Trudnowska et al., 2016) and also clearly visible in our data, e.g., when comparing the abundance of large zooplankton between transect D and C in May (**Figure 8**). This highlights the necessity to sample with high spatial resolution for an increased certainty when quantifying transport. Many species carried out seasonal vertical migrations between the upper 600 m and greater depths below the AW inflow (**Table 2**). In this study from an open ocean area with bottom depths >2,000 m we observed large and significant variations in vertical distribution of zooplankton between the months, also for those species that were mostly confined to certain depth ranges in the relatively shallow (<500 m) Amundsen Gulf of the Canadian Arctic (Darnis and Fortier, 2014). For example, the abundant, small cyclopoid *Triconia borealis* occurred mostly below 600 m in January and



May, and mostly above 600 m in August. Thus, these copepods were transported rapidly northward in summer, when they stayed in the layer with higher current velocities, compared to winter and spring, when they stayed in the 700–1,000 m layer, where southward currents were observed and where northward transport was very small.

The occurrence of high abundances of *C. finmarchicus* CV in the upper layer in January contradicts their classic life cycle, which postulates that the copepods overwinter at depths below 600 m from late summer/autumn to early spring (e.g., Edvardsen et al., 2006). Our observations are, however, in line with recent observations from the AW inflow region in January that also show high abundances of *C. finmarchicus* in the surface layer during winter months (Daase et al., 2014; Berge et al., 2015).

It is unclear how universal this observed behavior is, and if *C. finmarchicus* in this region does overwinter at depth at all, or if they stay in the upper layer throughout autumn and winter. Our data indicate that the copepods might start their downward migration in August, when they were distributed over the entire water column, and might ascend already in December. In January high abundances were observed in the surface layer but also at greater depths. The *C. finmarchicus* abundances observed in the surface layer in January were comparable to abundances observed elsewhere in its distribution range during summer (Melle et al., 2014).

This unexpected phenology has large impacts on the potential of these dominating copepods being advected into the AB. Ontogenetic migrations may help to maintain populations at

TABLE 2 | Abundance of zooplankton species (individuals m⁻²) collected by a 180 μ m-mesh MultiNet at stations across the Atlantic Water inflow into the Arctic Ocean in January, May and August 2014.**JANUARY**

	Stations					
	D1		D3		D4	
	uL	IL	uL	IL	uL	IL
LARGE						
<i>Calanus finmarchicus</i> CV-CVI	14,284	5,100	3,831	13,920	6,833	10,800
<i>C. hyperboreus</i> CIV-CVI	157	344	36	124	60	616
<i>C. glacialis</i> CV-CVI	260	64	132	80	37	–
<i>Paraeuchaeta</i> spp. CIV-CVI	159	8	32	8	68	32
<i>Scaphocalanus magnus</i>	43	–	–	–	–	–
<i>Augaptilus glacialis</i>	–	36	–	–	–	–
MEDIUM						
<i>Calanus finmarchicus</i> CII-CIV	5,300	2,300	654	2,480	1,030	2,600
<i>C. hyperboreus</i> CI-CIII	–	132	–	28	–	24
<i>C. glacialis</i> CII-CIV	24	–	38	–	20	–
<i>Paraeuchaeta</i> spp. CI-CIII	112	100	57	108	72	48
<i>Metridia longa</i> CII-CVI	1,996	3,932	943	1,708	1,784	1,160
<i>M. lucens</i>	138	–	286	28	197	44
<i>Pleuromamma robusta</i>	19	–	–	–	7	–
<i>Gaetanus tenuispinus</i>	279	68	21	80	65	68
<i>G. brevispinus</i>	17	–	40	80	–	132
<i>Chiridius obtusifrons</i>	23	–	–	28	40	44
<i>Heterorhabdus norvegicus</i>	206	168	105	108	84	112
<i>Paraheterorhabdus compactus</i>	–	68	–	–	–	–
<i>Aetideopsis minor</i>	16	32	–	–	–	–
<i>A. rostrata</i>	–	32	–	52	–	112
SMALL						
Copepoda nauplii	35	200	34	80	–	132
Calanoida indet.	–	32	37	–	–	24
<i>Metridia longa</i> CI	69	–	8	80	–	–
<i>Pseudocalanus</i> spp.	1,309	3,064	2,201	960	2,836	848
<i>Microcalanus</i> spp.	9,299	3,132	2,698	3,120	3,146	2,156
<i>Spinocalanus</i> spp.	152	700	–	–	–	88
<i>Scaphocalanus brevicornis</i>	6	68	–	28	–	24
Aetideidae CI-CIII	16	200	8	80	–	24
<i>Scolecithricella minor</i>	184	–	48	108	199	224
<i>Temorites brevis</i>	16	32	–	–	–	–
Cyclopoida indet.	19	–	–	–	–	–
<i>Oithona similis</i>	5,204	1,600	1,501	1,440	3,172	224
<i>O. atlantica</i>	1,306	400	123	400	924	200
<i>Triconia borealis</i>	248	10,000	86	2,240	287	3,000
<i>Triconia conifera</i> (cf.)	–	100	–	28	–	–
<i>Oncaea</i> spp.	16	1,200	12	28	–	24
<i>Acartia longiremis</i>	–	–	12	–	–	–
Harpacticoida indet.	50	–	–	–	–	–
<i>Microsetella norvegica</i>	57	–	6	–	–	–
<i>Neomormonilla minor</i>	22	200	–	80	–	68

(Continued)

TABLE 2 | Continued

MAY	Stations							
	D1		D3		C3		C5	
	uL	IL	uL	IL	uL	IL	uL	IL
LARGE								
<i>Calanus finmarchicus</i> CV-CVI	17,787	292	11,047	708	1,407	132	16,199	84
<i>C. hyperboreus</i> CIV-CVI	3,472	248	2,598	728	369	60	484	68
<i>C. glacialis</i> CV-CVI	161	–	33	–	50	–	267	–
<i>Paraeuchaeta</i> spp. CIV-CVI	81	68	20	80	81	88	48	60
<i>Scaphocalanus magnus</i>	12	16	–	–	28	32	100	108
<i>Augaptilus glacialis</i>	–	8	–	–	–	–	–	–
<i>Pseudohaloptilus pacificus</i>	–	–	–	–	–	32	–	–
MEDIUM								
<i>Calanus finmarchicus</i> CII-CIV	7,810	24	7,852	668	1,464	96	6,647	28
<i>C. hyperboreus</i> CI-CIII	111	24	–	–	657	–	267	108
<i>C. glacialis</i> CII-CIV	–	–	14	44	102	–	584	–
<i>Paraeuchaeta</i> spp. CI-CIII	190	116	326	220	602	264	873	216
<i>Metridia longa</i> CII-CVI	5,411	668	2,670	752	2,836	228	4,648	112
<i>M. lucens</i>	–	–	68	–	91	–	32	–
<i>Spinocalanus antarcticus</i>	28	44	–	–	–	100	–	80
<i>S. horridus</i>	–	–	–	–	28	–	–	80
<i>Pleuromamma robusta</i>	28	24	–	–	–	–	–	–
<i>Gaetanus tenuispinus</i>	165	68	–	224	160	32	240	–
<i>G. brevispinus</i>	67	136	139	132	–	132	–	132
<i>Chiridius obtusifrons</i>	97	–	14	88	80	32	68	–
<i>Heterorhabdus norvegicus</i>	245	88	132	1,200	437	232	642	452
<i>Paraheterorhabdus compactus</i>	–	24	–	–	–	–	–	28
<i>Aetideopsis minor</i>	284	68	–	176	–	100	100	80
<i>A. rostrata</i>	–	68	–	44	–	68	–	28
<i>Haloptilus acutifrons</i>	–	–	–	–	–	–	–	28
<i>Undinella oblonga</i>	–	–	–	–	–	32	–	–
SMALL								
Copepoda nauplii	20,717	332	1,512	44	16,754	300	34,800	240
Calanoida indet.	–	24	–	–	28	–	–	–
<i>Calanus finmarchicus</i> CI	878	68	544	–	1,222	28	2,792	200
<i>C. glacialis</i> CI	89	–	38	–	322	28	775	–
<i>Metridia longa</i> CI	177	–	71	132	790	80	1,467	–
<i>Pseudocalanus</i> spp.	3,435	336	1,779	1,064	4,258	188	3,091	132
<i>Microcalanus</i> spp.	16,116	6,200	24,239	14,004	29,024	12,960	35,509	14,600
<i>Spinocalanus</i> spp.	111	376	–	44	80	960	232	68
<i>Scaphocalanus brevicornis</i>	17	356	–	132	28	268	–	132
Aetideidae CI-CIII	45	332	–	44	28	240	100	100
<i>Scolecithricella minor</i>	390	24	435	256	631	52	843	32
<i>Temorites brevis</i>	–	24	–	–	–	28	–	32
Tharybidae	–	68	–	–	–	–	–	–
<i>Oithona similis</i>	47,920	668	23,054	1,200	41,620	456	21,500	4,900
<i>O. atlantica</i>	2,212	24	2,200	532	3,253	28	2,084	32
<i>Triconia borealis</i>	1,267	13,268	620	12,800	4,634	3,520	6,334	5,000
<i>Triconia conifera</i> (cf.)	–	24	–	44	–	–	–	–
<i>Oncaea</i> spp.	97	2,800	–	268	80	1,600	–	1,068
<i>Neomormonilla minor</i>	–	332	–	–	–	320	32	700

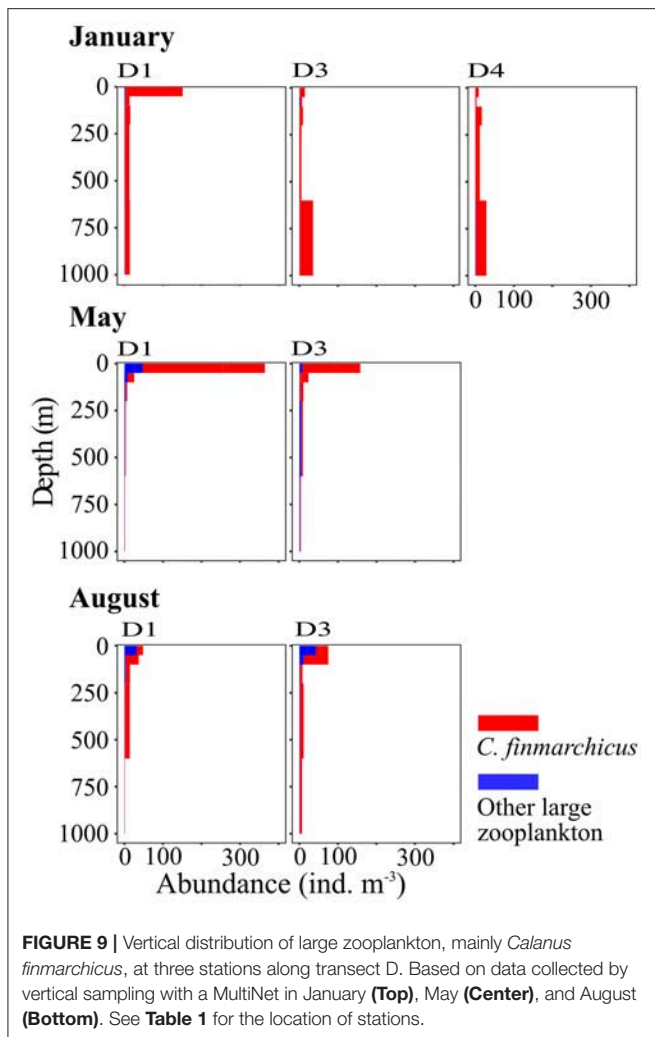
(Continued)

TABLE 2 | Continued

AUGUST

	Stations							
	D1		D3		C4		C6	
	uL	IL	uL	IL	uL	IL	uL	IL
LARGE								
<i>Calanus finmarchicus</i> CV-CVI	8,820	232	9,335	2,312	9,746	3,800	12,000	5,000
<i>C. hyperboreus</i> CIV-CVI	1,398	144	1,324	320	1,394	332	185	151
<i>C. glacialis</i> CV-CVI	876	32	1,646	44	894	468	1,191	600
<i>Paraeuchaeta</i> spp. CIV-CVI	84	56	274	68	202	84	101	6
<i>Scaphocalanus magnus</i>	16	16	68	44	112	136	–	–
<i>Augaptilus glacialis</i>	–	32	–	–	–	68	–	3
MEDIUM								
<i>Calanus finmarchicus</i> CII-CIV	19,396	96	83,645	1,064	29,318	200	117,494	1,868
<i>C. hyperboreus</i> CI-CIII	738	32	1,444	132	229	400	286	67
<i>C. glacialis</i> CII-CIV	390	–	334	–	134	–	–	–
<i>Paraeuchaeta</i> spp. CI-CIII	474	164	758	220	507	136	1,069	133
<i>Metridia longa</i> CII-CVI	6,368	260	7,623	528	13,850	1,604	12,801	2,268
<i>M. lucens</i>	68	32	132	–	179	68	108	–
<i>Spinocalanus antarcticus</i>	132	168	132	44	332	–	–	–
<i>S. horridus</i>	–	132	–	44	–	–	–	–
<i>Pleuromamma robusta</i>	68	–	68	–	–	–	–	–
<i>Gaetanus tenuispinus</i>	668	100	312	224	332	200	105	67
<i>G. brevispinus</i>	–	64	–	88	–	68	–	200
<i>Chiridius obtusifrons</i>	68	–	200	–	224	–	212	–
<i>Heterorhabdus norvegicus</i>	732	132	1,133	268	756	732	2,187	267
<i>Paraheterorhabdus compactus</i>	68	32	–	–	–	–	–	–
<i>Aetideopsis minor</i>	68	32	132	88	–	200	–	67
<i>A. rostrata</i>	–	4	–	44	–	–	–	267
<i>Haloptilus acutifrons</i>	–	–	–	–	–	68	–	–
<i>Undinella oblonga</i>	–	32	–	–	–	–	–	–
SMALL								
Copepoda nauplii	145,720	3500	465,067	2,400	24,282	3,800	99,360	1,401
<i>Calanus finmarchicus</i> CI	21,788	200	133,133	400	9,818	–	64,698	400
<i>C. glacialis</i> CI	–	–	1,067	–	–	–	–	200
<i>Metridia longa</i> CI	5,050	–	6,933	132	5,250	1,200	3,680	67
<i>Pseudocalanus</i> spp.	5,126	132	37,579	1,688	8,313	2,868	31,404	3,065
<i>Microcalanus</i> spp.	39,800	14,600	57,845	13,600	54,986	14,000	49,245	11,403
<i>Spinocalanus</i> spp.	668	68	689	756	224	468	108	200
<i>Disco hartmanni</i>	132	32	–	–	–	–	–	–
<i>Scaphocalanus brevicornis</i>	–	132	–	176	–	332	–	200
Aetideidae CI-CIII	68	100	444	800	112	600	907	200
<i>Jaschnovia brevis</i>	120	–	–	–	112	–	–	–
<i>Scolecithricella minor</i>	1,122	32	2,113	–	2,485	200	1,688	133
<i>Temorites brevis</i>	–	32	–	–	–	68	–	–
Tharybidae	–	–	–	–	–	–	–	67
<i>Oithona similis</i>	378,060	4,900	952,935	8,268	174,901	8,400	1,021,120	16,002
<i>O. atlantica</i>	3,330	32	11,267	44	7,734	68	13,067	200
<i>Triconia borealis</i>	21,340	5,000	55,933	11,868	9,568	25,800	40,907	14,799
<i>Triconia conifera</i> (cf.)	–	–	–	–	–	68	–	–
<i>Oncaea</i> spp.	4,630	1,068	31,733	1,600	1,216	1,000	8,427	800
Harpacticoida indet.	68	–	–	–	117	–	–	–
<i>Microsetella norvegica</i>	440	–	1,067	44	362	2,000	534	–
<i>Neomormonilla minor</i>	600	700	68	668	–	200	–	–

Only species/groups with ≥ 10 ind. m^{-2} in any depth layer are listed. Several depth layers were sampled vertically (Table 1), here they are grouped into upper layer (uL, 600–0 m) and lower layer (IL, 1,000–600 m). –, No individual observed in depth layer.



the center of their distribution in advective environments (Kimmerer et al., 2014), as we observed southward flow toward the core habitat of *C. finmarchicus* in the Norwegian Sea at depth. However, the occurrence at the surface would transport *C. finmarchicus* rapidly into the AB and thereby out of the area where they can complete their life cycle; they would reach the western Nansen Basin within approximately 3 weeks (Hattermann et al., 2016). In a warmer climate zooplankton species might modulate their phenology as a response to temperature (Mackas et al., 2012), and our data are an example showing that slight changes in the phenology, e.g., in the timing of overwintering, can transport populations into habitats with very different abiotic conditions that may or may not be suitable. The *Calanus* sp. CV that were observed in the upper layer in August may also represent a second generation that could develop under favorable conditions further south (Weydman et al., 2014). This alternative scenario suggests another possible mechanism of increasing advection of zooplankton biomass into the Arctic Basin as a result of climate change.

The data reveal that the amount of zooplankton biomass that is transported into the AB depends strongly on the phenology of

the species. If *Calanus* sp. would follow their classical life cycle and overwinter at depths below the inflowing AW for up to 6 months, as it is observed in its core habitat (Gaardsted et al., 2011), biomass in the Inflow region would be lower than observed during our study. Assuming that *Calanus* sp. overwinters at depths during 3–4 months would reduce our estimates of its annual transport into the AB by 25–33%.

Uncertainty in the Carbon Estimates

Our carbon estimates are based on a fixed conversion from biovolume to carbon, which is not realistic since carbon content of same-sized plankton varies. Our estimates of carbon flux are thus somewhat uncertain. Changing the conversion ratio by 10% has been modeled to change growth rate estimates based on carbon by 3% (Basedow et al., 2014). At the same time, our data are based on several million data points, compared to traditional sampling that often is limited to <10 stations. The increased certainty due to the large amount of data will therefore ameliorate the increased uncertainty due to a fixed conversion ratio. The LOPC counts all particles, although fragile ones are likely destroyed when towing it. Analyses of the particles showed that in May and August non-zooplankton particles also contributed to the counts in the small size group, especially at greater depths, see section Materials and Methods. Thus, the estimates of carbon transport of the small size group in May and August include both the abundant small zooplankton species, and an unknown fraction of non-zooplankton particles.

Eddy Activity and Zooplankton Transport

The variable current directions that were observed in the Uncertain Fate region during our cruises are consistent with the large eddy activity known in this recirculation region (Hattermann et al., 2016; von Appen et al., 2016; Wekerle et al., 2017). Although we show the northward flux of zooplankton across the Uncertain Fate region in Table 3, this zooplankton biomass may or may not reach the AB (Hattermann et al., 2016; Koenig et al., 2017). Instead, zooplankton in the Uncertain Fate region might remain in recirculating AW, and could also be transported westward toward Greenland (Hattermann et al., 2016). Model simulations have shown that episodic events can transport cod larvae hatched outside the Norwegian coast toward Northeast Greenland, by taking the route with AW northward toward Svalbard and then westward across Fram Strait (Strand et al., 2017). The high abundances of *Calanus* sp. that were observed also in the Uncertain Fate region could be a potential source of food for these cod larvae on their way toward potential new habitats. Additionally, a potential second generation of *C. finmarchicus* that develops in concert with the cod larvae might be very favorable for these larvae. Eddy activity was also indicated by the pronounced switches between north- and southward currents (Figure 3). The horizontal distance between these switches matches the size of mesoscale eddies at this latitude very well, as those would typically have a size similar to the local Rossby deformation radius, around 5 km (Nurser and Bacon, 2014). While it is difficult to identify similarly clear signatures of eddies in the hydrography, the combination of downward doming temperature at 4.5 E and upward at 5.5 E in August

TABLE 3 | Seasonal variation in northward water flux (Sv, $10^6 \text{ m}^3 \text{ s}^{-1}$) and in mean abundance (Abu, individuals m^{-3}) and biomass (C, mg C m^{-3}) of three zooplankton size groups (small S, medium M, large L) transported across four regions of transect D.

		Inflow			Uncertain Fate			Below Inflow			Below Uncertain		
		Sv			Sv			Sv			Sv		
Water	Jan	2.21			3.09			0.16			0.74		
	May	1.93			2.19			0.13			0.73		
	Aug	1.70			1.24			0.09			0.28		
		Abu	C	Flux	Abu	C	Flux	Abu	C	Flux	Abu	C	Flux
S	Jan	9,027	5.21	11.51	5,848	3.01	9.30	652	0.32	0.05	6,927	3.70	2.74
	May	17,303	9.80	18.91	62,252	40.83	89.42	1,543	0.54	0.07	788	0.30	0.22
	Aug	22,987	11.19	19.02	15,753	8.02	9.94	5,228	2.85	0.26	2,952	1.62	0.45
M	Jan	1,629	7.70	17.02	825	4.72	14.59	48	0.16	0.03	496	1.79	1.33
	May	649	2.03	3.88	5,716	18.17	39.79	35	0.10	0.01	33	0.15	0.11
	Aug	1,924	8.06	13.70	2,088	9.64	11.95	839	4.37	0.39	447	2.19	0.61
L	Jan	128	10.29	22.74	206	16.28	50.31	0.5	0.01	0.002	81	6.33	4.68
	May	91	6.00	11.59	52	3.57	7.82	2	1.57	0.20	4	0.35	0.26
	Aug	172	9.98	16.97	211	14.27	17.69	198	11.80	1.06	75	7.00	1.96
All	Jan	51.27			74.20			0.08			8.75		
	May	34.38			146.90			0.28			0.59		
	Aug	49.69			39.58			1.71			3.02		

The northward carbon flux (Flux, kg C s^{-1}) of these groups and of total biomass transport (All, kg C s^{-1}) across the four regions was calculated based on water flow and on mean biomass. The cross section area (in 10^6 m^2) of the four regions is 11.25 (Inflow), 37.10 (Uncertain Fate), 1.79 (Below Inflow), and 15.90 (Below Uncertain).

(Figure 2) is an example that could be associated with a dipole pair of anticyclonic and cyclonic eddies, respectively, centered at those longitudes. The high biomass that we observed in the upper layer in August might result in part from a concentration of copepods in an eddy, instead of a continuous northward flow. This is supported by our observations compared to long-term averages; the shelf break branch of the West Spitsbergen Current (WSC) was much weaker in August 2014 compared to the long-term data. Observed currents that deviate from long-term observations are common, and in January we also observed a weak southward flow in the offshore branch of the WSC, contrary to the climatological northward flow (Figure 5).

Advection of the Atlantic Copepod *C. finmarchicus*

Based on our data a very rough estimate of an annual *C. finmarchicus* inflow of about 500,000 metric tons (t) C y^{-1} through the Fram Strait into the AB can be calculated. This is based on the assumption that the large group consisted exclusively of *C. finmarchicus* (Figure 9). The average inflow equals then $(22.74 + 11.59 + 16.97)/3 \sim 17 \text{ kg C s}^{-1}$ over the 3 months January, May and August (Table 3). Assuming further that the medium group consisted of 50% *C. finmarchicus* (Table 2), this results in an average inflow of $0.5 * (17.02 + 3.88 + 13.7)/3 \sim 5.8 \text{ kg C s}^{-1}$ (Table 3). Combining both $(17 + 5.8 = 22.8 \text{ kg C s}^{-1})$, and multiplying by 31.536 million s y^{-1} , this yields 719,020,800 kg C y^{-1} , or roughly 720,000 t C y^{-1} . As stated above, the copepods likely overwinter at depth for 3–5 months (ca. 0.3 y), during which they would stay below the Inflow region.

Our estimate for the annual transport would thus be ca. 220,000 t C lower $(720,000 \text{ t C y}^{-1} * 0.3 \text{ y} \sim 222,000 \text{ t C})$, which yields a transport of ca. 500,000 t C y^{-1} . Obviously this is a very rough estimate only, but it gives an idea on the order of magnitude of the amount of *C. finmarchicus* that is transported from population centers further south toward the AB.

The annual estimate of 500,000 t C y^{-1} compares very well to modeled advection of *C. finmarchicus* into the AB. Wassmann et al. (2015) modeled a transport of 1,674 t C d^{-1} , whereas our estimate corresponds to 1,369 t C d^{-1} . However, the model indicates lowest transport rates during winter and peak advection during summer, while we observed similar rates in winter and summer. The model uses the classical life cycle that is known for *C. finmarchicus*, with long overwintering at depth. This might be refined once we get more seasonal observations and thus a better understanding on the factors that govern the copepods life cycle in Arctic regions.

Annual production estimates of *C. finmarchicus* range between 75 Mega tons C y^{-1} for the Nordic Seas to 300 Mt C y^{-1} for the Norwegian Sea alone, with one Mt = 10^9 kg (Aksnes and Blindheim, 1996; Skjoldal, 2004). More recently a stock size of 150 Mt C was estimated for the copepod in the Norwegian Sea (Hjøllo et al., 2012). An advection of about 500,000 t C into the AB thus constitutes between 2 and 7 per mille of the annual production or about 3 per mille of the standing stock of *C. finmarchicus*. Large amounts of *C. finmarchicus* are also advected with AW into the Barents Sea (Edvardsen et al., 2003; Gluchowska et al., 2017a). Edvardsen et al. (2003) calculated an inflow of about 250,000 t C zooplankton, mainly *C. finmarchicus*,

for the month of June. This is ca. 4 times more than what is advected into the AB, according to our monthly estimate for August.

Advection of the Arctic Copepod *C. glacialis*

C. glacialis is an Arctic key zooplankton species that is mostly observed in the Arctic shelf seas, where high production rates have been observed (Kosobokova, 1999). Conversely, in the Arctic Basin modeled production of *C. glacialis* is very low and in fact mostly negative, especially along the Eurasian shelf break (Slagstad et al., 2011). This negative production in the model results when respiration is larger than production, and thus is an indication of advection of biomass from areas with positive production. Based on our data and on the observed biomass of *C. glacialis* in the Nansen Basin, we can roughly calculate the equivalent biomass of *C. glacialis* that is advected from the Barents and Kara Seas.

In the Nansen Basin the observed biomass of the Arctic copepod *Calanus glacialis* is ca. 19% of total mesozooplankton biomass, while the biomass of the Atlantic copepod *C. finmarchicus* constitutes ca. 9.5% (Kosobokova and Hirche, 2009). Thus, the observed biomass of *C. glacialis* is nearly twice as large as the biomass of *C. finmarchicus* in the Nansen Basin. In the AW inflow we observed a clear dominance of *C. finmarchicus*, and the biomass of *C. glacialis* ranged between 0.5 and 3.5% (Table 2, Inflow and Uncertain Fate region combined). This implies that the difference between 200% *C. glacialis* in the Nansen Basin and 0.5–3.5% *C. glacialis* in the AW inflow either is produced locally or is advected from the Barents and Kara Seas. If we take our estimate of an inflow of $500,000 \text{ t C } \gamma^{-1}$ of *C. finmarchicus*, and assume that (1) 50% *C. finmarchicus* biomass is lost on the way to the Nansen Basin (Wassmann et al., 2015) and (2) that local *C. glacialis* production is negligible, we can calculate the biomass of *C. glacialis* that is advected from the adjacent shelf seas. This *C. glacialis* biomass in the Nansen Basin is on the order of $491,250\text{--}498,750 \text{ t C } \gamma^{-1}$ (196.5–199.5% of $250,000 \text{ t C } \gamma^{-1}$), with a mean of $495,000 \text{ t C } \gamma^{-1}$, i.e., very similar to the calculated inflow of *C. finmarchicus* through the Fram Strait. This crude estimate is based on our calculations of the advection of *C. finmarchicus* and thus has a higher uncertainty; it is also sensitive to the underlying data on *C. glacialis* and *C. finmarchicus* biomass in the Nansen Basin (Kosobokova and Hirche, 2009). Our estimate ($1,356 \text{ t C d}^{-1}$) compares well to the modeled advection from the Barents Sea of $1,712 \text{ t C d}^{-1}$ (Wassmann et al., 2015). More data on the distribution and local production of *C. glacialis* in the Nansen Basin will likely refine both our estimate and the model.

Implications of Advected Biomass for Arctic Productivity and Higher Trophic Levels

Data on mesozooplankton production in the AB are scarce making it difficult to compare our data with others, but the observed biomass transport between 12 kg C s^{-1} (May) and 23 kg C s^{-1} (January) of large herbivores and similar

amounts of smaller zooplankton species certainly is important. To compare, the total allowable catch of Northeast Arctic cod (*Gadus morhua*) for 2018 is set to 775,000 t (weight, not carbon). This indicates that an advective inflow on the order of $500,000 \text{ t C } C. finmarchicus$ with AW through the Fram Strait, plus ca. $500,000 \text{ t C } C. glacialis$ from the Barents Sea surely contributes significantly to the marine food web in the Nansen Basin.

The Arctic marine environment is characterized by a pulsed production of zooplankton, which is strongly bottom-up driven and thus coupled to the peak of the primary production (Søreide et al., 2010; Leu et al., 2011; Daase et al., 2013). Recently this view has been challenged based on a high level of biological activity that was observed in an Arctic fjord (Kongsfjorden) in January (Berge et al., 2015). However, this fjord is an advective fjord heavily influenced by AW (Basedow et al., 2004; Pavlov et al., 2013). Our data also show a northward flow of zooplankton carbon with AW in the West Spitsbergen Current during winter when local production presumably is low. This continuous transport might serve as another form of bottom-up forcing of the ecosystem and might in part explain the biological activity that was observed during winter in Kongsfjorden.

Recent observations indicate high abundances of mesopelagic predators during early autumn and winter in the southwestern Nansen basin, where the AW inflow is pronounced (Gjøsæter et al., 2017). Many of the most abundant predators that were observed in this layer are planktivorous, e.g., herring (*Clupea harengus*), Lion's mane jellyfish (*Cyanea capillata*) and the carnivorous amphipod *Themisto libellula*. For these predators the advected zooplankton carbon might be a significant part of their diet, especially in winter. Historically, the southwestern Nansen Basin has been known as an area of high abundances of whales (Falk-Petersen et al., 2014), which might be related to the additional biomass input of zooplankton that serves as food for higher trophic levels.

CONCLUSION

This study provides the first quantification of abundance and biomass of zooplankton that flows with Atlantic Water through the Fram Strait and into the Arctic Basin. This quantification was possible because seasonal data on zooplankton abundance was combined with concurrent data on ocean current direction and velocity, all collected with high spatial resolution down to 1,000 m. Seasonal variability in zooplankton transport was higher than the variability in water transport, but contrary to our expectations the seasonal variation on the inflow of zooplankton biomass into the Arctic Basin was not pronounced. High abundances of lipid-rich zooplankton species were observed in the core of the Atlantic Water inflow during all seasons, and the advective input presumably far exceeded local production. The phenology of different zooplankton species had a large impact on their advection, exemplified by the unexpected occurrence of *C. finmarchicus* in the surface layer in January.

DATA AVAILABILITY

The datasets analyzed for this study can be found in the PANGAEA data base in the following data sets:

[Data set] Basedow, S.L. (2017) CarbonBridge January 2014: Zooplankton abundance, biovolume and size structure along transect D crossing the Fram Strait. PANGAEA, <https://doi.org/10.1594/PANGAEA.879799>

[Data set] Basedow, S.L. (2017) CarbonBridge May 2014: Zooplankton abundance, biovolume and size structure along transect D crossing the Fram Strait. PANGAEA, <https://doi.org/10.1594/PANGAEA.879808>

[Data set] Basedow, S.L. (2017) CarbonBridge August 2014: Zooplankton abundance, biovolume and size structure along transect D crossing the Fram Strait. PANGAEA, <https://doi.org/10.1594/PANGAEA.879805>

[Data set] Basedow, S.L. (2017) CarbonBridge May 2014: Zooplankton abundance, biovolume and size structure along transect C crossing the Fram Strait. PANGAEA, <https://doi.org/10.1594/PANGAEA.879814>

[Data set] Basedow, S.L. (2017) CarbonBridge August 2014: Zooplankton abundance, biovolume and size structure along transect C crossing the Fram Strait. PANGAEA, <https://doi.org/10.1594/PANGAEA.879811>

[Data set] Bauerfeind, E., Beszczynska-Möller, A., von Appen, W.-J., Soltwedel, T., Sablotny, B., Lochthofen, N. (2015) Physical oceanography and current meter data from mooring FEVI27 at Hausgarten North. Alfred Wegener Institute, Helmholtz Center for Polar and Marine Research, Bremerhaven, PANGAEA, <https://doi.org/10.1594/PANGAEA.845621>

[Data set] Bauerfeind, E., Beszczynska-Möller, A., von Appen, W.-J., Soltwedel, T., Sablotny, B., Lochthofen, N. (2015) Physical oceanography and current meter data from mooring FEVI28 at Hausgarten IV. Alfred Wegener Institute, Helmholtz Center for Polar and Marine Research, Bremerhaven, PANGAEA, <https://doi.org/10.1594/PANGAEA.845622>

[Data set] Halvorsen, E., Kwasniewski, S. (2017) CarbonBridge January 2014: Mesozooplankton species composition and abundance. The Arctic University of Norway, PANGAEA, <https://doi.org/10.1594/PANGAEA.881889>

[Data set] Halvorsen, E., Kwasniewski, S. (2017) CarbonBridge May 2014: Mesozooplankton species composition and abundance. The Arctic University of Norway, PANGAEA, <https://doi.org/10.1594/PANGAEA.881892>

[Data set] Halvorsen, E., Kwasniewski, S. (2017) CarbonBridge August 2014: Mesozooplankton species composition and abundance. The Arctic University of Norway, PANGAEA, <https://doi.org/10.1594/PANGAEA.881893>

[Data set] Randelhoff, A., Sundfjord, A. (2017). Carbon Bridge CTD hydrography 2014. Norwegian Polar Institute. <https://doi.org/10.21334/npolar.2017.f40317d5>

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[Data set] von Appen, W.-J., Beszczynska-Möller, A., Fahrbach, E. (2015) Physical oceanography and current meter data from mooring F3-15. Alfred Wegener Institute, Helmholtz Center for Polar and Marine Research, Bremerhaven, PANGAEA, <https://doi.org/10.1594/PANGAEA.853902>

[Data set] von Appen, W.-J., Beszczynska-Möller, A., Fahrbach, E. (2015) Physical oceanography and current meter data from mooring F4-15. Alfred Wegener Institute, Helmholtz Center for Polar and Marine Research, Bremerhaven, PANGAEA, <https://doi.org/10.1594/PANGAEA.853903>

[Data set] von Appen, W.-J., Beszczynska-Möller, A., Fahrbach, E. (2015) Physical oceanography and current meter data from mooring F5-15. Alfred Wegener Institute, Helmholtz Center for Polar and Marine Research, Bremerhaven, PANGAEA, <https://doi.org/10.1594/PANGAEA.853904>

[Data set] von Appen, W.-J., Beszczynska-Möller, A., Fahrbach, E. (2015) Physical oceanography and current meter data from mooring F7-12. Alfred Wegener Institute, Helmholtz Center for Polar and Marine Research, Bremerhaven, PANGAEA, <https://doi.org/10.1594/PANGAEA.853905>

AUTHOR CONTRIBUTIONS

SB and MR outlined the study. AS collected and interpreted the ship-borne ADCP data. W-JvA was responsible for and interpreted the data from the moored ADCPs. SK and EH analyzed the MultiNet data. SB analyzed the LOPC data, prepared most figures and wrote most of the MS. All authors contributed with text and comments on the whole manuscript and approved the final version.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: <https://www.frontiersin.org/articles/10.3389/fmars.2018.00194/full#supplementary-material>

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Summer Mesozooplankton Biomass Distribution in the West Spitsbergen Current (2001–2014)

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Marine ecosystems in Arctic regions are expected to undergo large changes, driven by sea ice retreat and increasing influence of warmer and saline waters. We examined changes in the hydrography and mesozooplankton from a 14-year long time series in the West Spitsbergen Current during the summer period. The aim was to provide a contemporary description of spatial and temporal variations in the zooplankton community inhabiting the surface layer (0–60 m), over an area extending 6 latitudinal degrees and nearly 20 longitudinal degrees. A total of 296 samples were partitioned into three groups, based on salinity and temperature signatures, representing the western, eastern, and coastal branches of the West Spitsbergen Current. Only the waters of the eastern branch, influenced by north-flowing Atlantic water, showed significant temporal trend in salinity, whereas no significant time trend was found for temperature in any of the three branches in the surface layer studied. Zooplankton biomass generally decreased from south to north in the western and eastern branches, suggesting poleward net loss of zooplankton, whereas relatively constant biomass in the coastal branch was likely sustained by higher production at the shelf break. The biomass remained constant over the study period for all three branches. Four species (*Calanus finmarchicus*, *Calanus glacialis*, *Calanus hyperboreus*, and *Eukrohnia hamata*) contributed almost 90% of the mesozooplankton biomass in all branches, with *C. hyperboreus* and *C. glacialis* being relatively important in the western and coastal branches, respectively. *Calanus finmarchicus* became increasingly important over time in the eastern branch, almost doubling its biomass and contributing more than 50% of the total biomass at the end of the study period. This increase was not associated with a general tendency toward more mature stages. *C. finmarchicus* copepodid CV and adults constituted > 80% of this species biomass in the western and eastern branches. In general, the relatively long time series, for Arctic standards, could not confirm expected drastic trends, but showed subtle changes over time overlaid by considerable interannual variability. Given the large inherent variability in zooplankton data, time series extending more than 14 years are needed for assessing trends in the West Spitsbergen Current.

Keywords: Arctic, Atlantic water, *Calanus finmarchicus*, climate change, copepod, Fram Strait, trends, zooplankton community

INTRODUCTION

Sea ice is rapidly retreating and thinning in the Arctic (Carstensen and Weydmann, 2012), potentially rendering the area ice-free in summer by 2030 (Stroeve et al., 2012). Increasing area and period with open water has enhanced primary production in the Arctic, particularly along shelf breaks where upwelling of nutrient-rich waters stimulate phytoplankton growth (Arrigo and van Dijken, 2015). Since phytoplankton constitute the base of the Arctic food web, changes in the spatial and temporal distribution of primary production will essentially affect all organisms at higher trophic levels. Mesozooplankton plays a central mediating role in the Arctic food webs as grazers of the primary production and food source for fish (e.g., Gislason and Astthorsson, 2002), bird (e.g., Karnovsky et al., 2003) and whale populations (e.g., Heide-Jørgensen and Acquarone, 2002). However, whereas spatial and temporal changes in surface primary production largely can be assessed through remote sensing (Matrai et al., 2013), this is not possible for mesozooplankton yet and consequently, our knowledge on the distribution of the mesozooplankton community remains limited.

Over the past 2–3 decades, research cruises have been the main vehicle for studying mesozooplankton in the Arctic and sub-Arctic, but such isolated expeditions are not optimal for quantifying distribution pattern over time and space. There are only few examples of consistent monitoring in the Arctic region, suitable for analyzing changes in biological communities over time. The Hausgarten observatory is probably the most well-known Arctic research infrastructure that has delivered insight into seasonal and long-term changes in numerous biological variables in Fram Strait, the only deep-water connection between the Arctic Ocean and the Nordic Seas (Soltwedel et al., 2015). Another long-term monitoring effort in this region is carried out by the Institute of Oceanology of the Polish Academy of Sciences (IO PAN), where zooplankton has been sampled along a number of latitudinal transects across the West Spitsbergen Current (WSC) since 2001. For Arctic standards, this data set is unique due to its spatial and temporal coverage. While these data have been used to analyze how environmental variables shape the distribution of key *Calanus* species (Carstensen et al., 2012), zooplankton community structure (Weydmann et al., 2014; Gluchowska et al., 2017a), zooplankton structural and functional diversity (Gluchowska et al., 2017b), and population development of *Calanus finmarchicus* (Gluchowska et al., 2017a; Weydmann et al., 2018), the spatial and temporal variability in the zooplankton community has not yet been fully explored.

The importance of Atlantic Water (AW) in the WSC varies substantially among years, and many studies suggest its increasing role signified by rising temperature and salinity (Beszczynska-Möller et al., 2012; Gluchowska et al., 2017a). Associated with this trend, Gluchowska et al. (2017a) also found increasing biomass of *C. finmarchicus* and zooplankton in total in the WSC, but this was analyzed for a single transect located at 76°30' N. The WSC is the main conduit of AW into the Arctic Ocean (Rudels et al., 2004, 2005; Walczowski et al., 2012), and the combination of increasing primary production, stronger AW transport in the WSC, and increasing zooplankton biomass and

dominance of expatriate Atlantic species (e.g., *C. finmarchicus*) may drastically change the functioning of the Arctic Ocean in the future (Wassmann et al., 2015). Given that the Arctic Ocean most probably will undergo large changes, describing current spatial and temporal variations in the zooplankton community in the WSC will constitute a baseline for future studies.

Therefore, the main objective of this study was to describe temporal variations in the zooplankton community over a 14-year period (2001–2014) across a broad spatial domain (from 73°30' N to 78°50' N) in the WSC during the summer period. In particular, we addressed the questions:

- (1) What are the key species, in terms of biomass, and how are they distributed over time and space in this large area?
- (2) Is there supporting evidence for increasing contribution of AW associated species in the WSC zooplankton community?
- (3) Is the WSC a simple conduit of zooplankton or are there sources/sinks along the northbound transport?
- (4) Are there consistent time trends in the zooplankton community over the 14-year period?

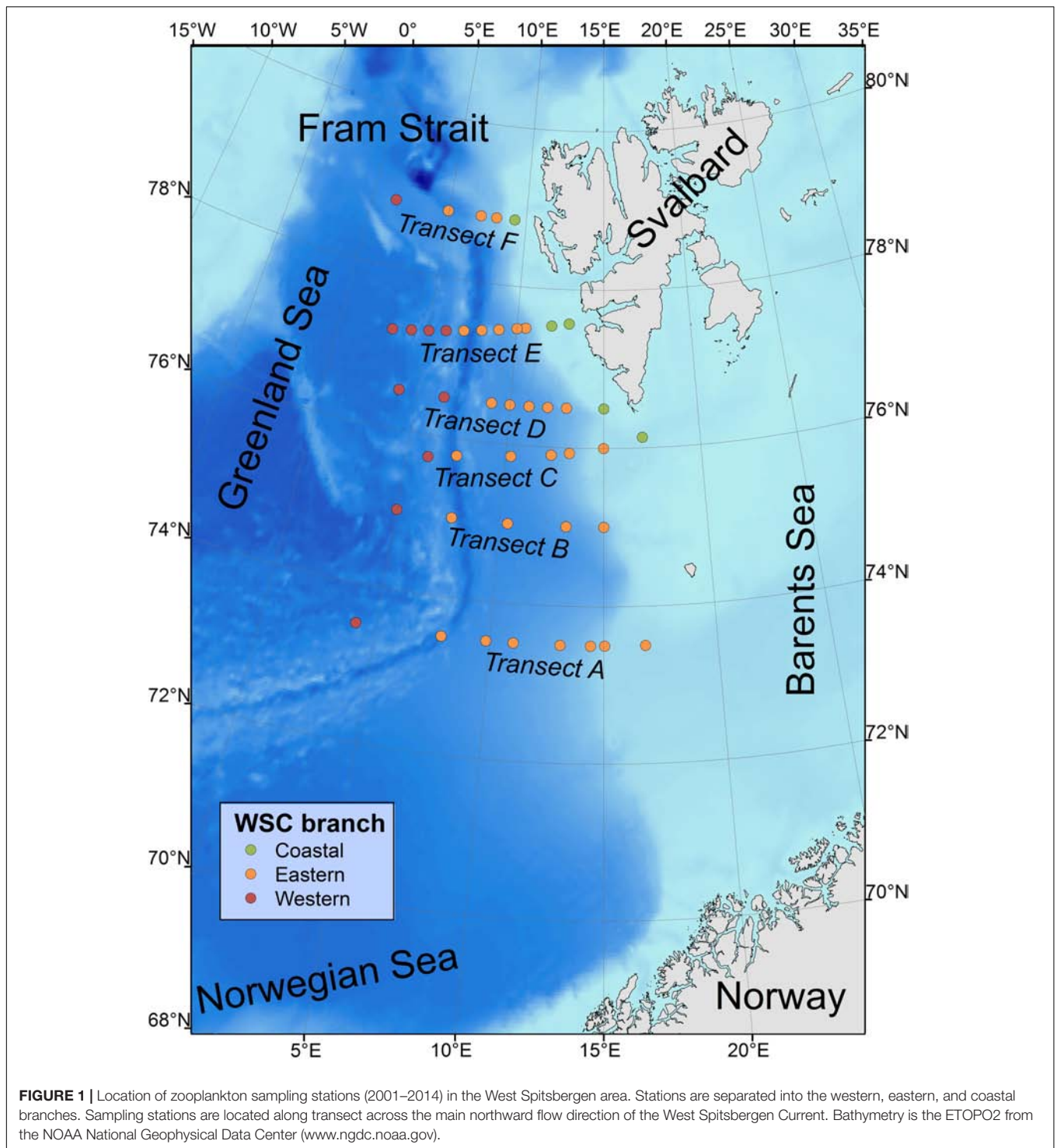
MATERIALS AND METHODS

Zooplankton Sampling

Zooplankton was sampled across six latitudinal transects (A–F) spanning across the core of the WSC (Figure 1). A total of 44 stations were sampled over the 14-year period, although only a subset of these were sampled each year. On a few occasions, zooplankton was sampled at locations next to each other and these were associated to the same station name. The number of zooplankton samples ranged from 15 in 2002 to 28 in 2009, and the six transects were sampled with similar intensity over the study period, with each transect typically represented by 3–5 samples from a given year, although there were four occasions where a transect was characterized by one station only or none.

Sampling typically took place over a 3-week period from end of June to mid-July, and the timing of the cruise was relatively consistent over years shifting by less than 10 calendar days.

At each station, depth-stratified hauls were made using a standard mesozooplankton net of WP-2 type with 0.25 m² square opening and 0.180 mm mesh size gauze, equipped with mechanical closing device (UNESCO, 1968). The depth stratification of sampling was determined on every station, based on the temperature-salinity distribution profile taken prior to collecting zooplankton. Sampling was conducted in three layers within the epipelagial (the upper 200 m of the sea), the layer within which most of the zooplankton in oceanic waters of the higher latitudes concentrates during summer (Wiborg, 1955; Longhurst and Williams, 1979; Gluchowska et al., 2017b). The depth-stratified net sampling was meant to provide data on vertical distribution patterns of zooplankton in relation to water mass structure, however, this study concerns only the upper mixed layer and the pycnocline



(typically 0–60 m), where the zooplankton abundance was the highest. The WP-2 net with 0.180 mm mesh samples typically mesozooplankton (by definition multicellular, heterotrophic organisms with linear size between 0.2–20 mm), therefore we do not have data on smaller (microzooplankton, protoplankton) or larger (macrozooplankton) organisms, but we will refer to our data as zooplankton.

Immediately after sampling, zooplankton were preserved in a 4% solution of formaldehyde in seawater buffered with borax. The samples were analyzed afterward in the laboratory at IO PAN, and zooplankton were identified to the lowest possible taxonomic level, including distinguishing the copepodids developmental stages for *C. finmarchicus*, *Calanus glacialis*, *Calanus hyperboreus*, *Pseudocalanus acuspes/minutus*, and

Paraeuchaeta norvegica (Kwasniewski et al., 2003; Weydmann and Kwasniewski, 2008). Nauplii of Calanoida were also counted, although not identified to species level. Due to the mesh size of the gauze, they were representing predominately *Calanus* species, and therefore assumed to be distributed among the three species proportionally to relative abundances of their copepodid stages I and II. Zooplankton carbon biomass (mg C m^{-3}) was calculated from abundances using taxon- and stage-specific dry mass values and factors for dry mass to carbon conversion (references in Gluchowska et al., 2017a and unpublished data).

The physical properties of the water column were determined with a Sea-Bird 911 + CTD instrument (for details see Walczowski et al., 2012). Salinity and temperature of the upper mixed layer were found by averaging the CTD profiles taken at each station, over the depth stratum used for zooplankton sampling (here 0–60 m).

Data Analyses

Zooplankton samples were categorized into three different groups according to water mass types present at the station, characteristic for western, eastern and coastal WSC branches, based on visual inspection of temperature and salinity (T-S plots) of the water mass (**Supplementary Figure S1**). This separation into different branches follows the approaches in previous studies (Carstensen et al., 2012; Weydmann et al., 2014; Gluchowska et al., 2017b), but in contrast to these studies, that used fixed station-specific associations, a flexible approach was applied using transect-specific thresholds for salinity and temperature to identify the eastern branch (**Table 1**), located in between the two other branches. The WSC eastern branch is characterized by higher temperature and salinity that gradually decrease toward north. Samples not fulfilling these criteria were allocated to either western branch or coastal branch, depending on whether they were located to the west or east, respectively, of those samples on the given transect fulfilling the criteria for the eastern branch. This classification approach was adopted because the eastern branch has a highly distinctive T-S signature, whereas the ones of the two other branches are more variable.

Spatial variation among transects and temporal variation among years for temperature, salinity, and various zooplankton variables (see below) were investigated with a linear mixed model for the three WSC branches separately.

$$Y_{ijk} = t_i + y_j + S_k(t_i) + T_i \times Y_j + Y_j \times S_k(t_i) + e_{ijk} \quad (1)$$

The model described the common spatial (t_i , $i = 1, \dots, 6$) and temporal (y_j , $j = 1, \dots, 14$) trends and assessed the significance of these against the random variation among stations within transects ($S_k(t_i)$), interannual changes in the spatial variation among transects ($T_i \times Y_j$), interannual changes in the spatial variation among stations within transects [$Y_j \times S_k(t_i)$] and residual variation (e_{ijk}). The residual variation described the variation between samples within the same year from nearby locations associated with the same station name. Since this sampling pattern only occurred on rare occasions (five in total), the degrees of freedom for estimating residual variation were low and hence, variance estimates for the residual variation relatively

TABLE 1 | Transect-specific criteria for temperature (T) and salinity (S) to identify the WSC eastern branch.

Transect A	$T > 5.0$	$S > 34.9$
Transect B	$T > 4.95$	$S > 34.9$
or	$T > 4.75$	$S > 35.0$
Transect C	$T > 4.95$	$S > 34.9$
or	$T > 4.75$	$S > 35.0$
Transect D	$T > 4.9$	$S > 34.9$
Transect E	$T > 4.7$	$S > 34.9$
Transect F	$T > 4.0$	$S > 34.8$

For transect B and C, the WSC eastern branch was identified by either of the two criteria.

uncertain. However, test statistics for common spatial (t_i) and temporal (y_j) variations depended more strongly on the other sources of random variation [$S_k(t_i)$, $T_i \times Y_j$, and $Y_j \times S_k(t_i)$] and were relatively unaffected by residual variation.

In addition to temperature and salinity, the mixed model was employed to the log-transform of biomass of the entire zooplankton community and the most dominant species as well as the logistic transformation of the biomass proportion of the most dominant species. Marginal means of t_i (representing transect means across all years) and y_j (representing yearly means across all transects) were computed from the parameter estimates of the mixed model. For the log-transformed zooplankton variables, marginal means were back-transformed with the exponential function representing geometric means. Similarly, the inverse logistic transformation was used for calculating geometric means of biomass proportions. Finally, the marginal means of y_j were analyzed for systematic trends using linear regression.

Since *C. finmarchicus* was the predominant species in all three WSC branches, we further analyzed the biomass proportion of different developmental stages over time and transects. Biomass proportions of nauplii, CI to CV, and adults were modeled as nominal variables (i.e., representing consecutive development stages) using a multinomial logistic regression model with the same structure as Eq. 1. Essentially, the model estimated the maturity of the *C. finmarchicus* population across transects and years based on biomass proportions. Marginal means for the stage-specific biomass proportion were computed from the parameter estimates of the model. Systematic time trends in the stage development were investigated by linear regression of the y_j parameters from the model.

RESULTS

A total of 296 samples were grouped into 59, 198, and 39 observations for the WSC western, eastern and coastal branches with distinct T and S signatures (**Supplementary Figure S1**). These distinctive characteristics were quite clear for all transects except the northernmost Transect F, where the three branches converge (**Supplementary Figure S1**). The eastern branch had the highest temperature and salinity, whereas the western and coastal branches had similar and lower temperature, but differed

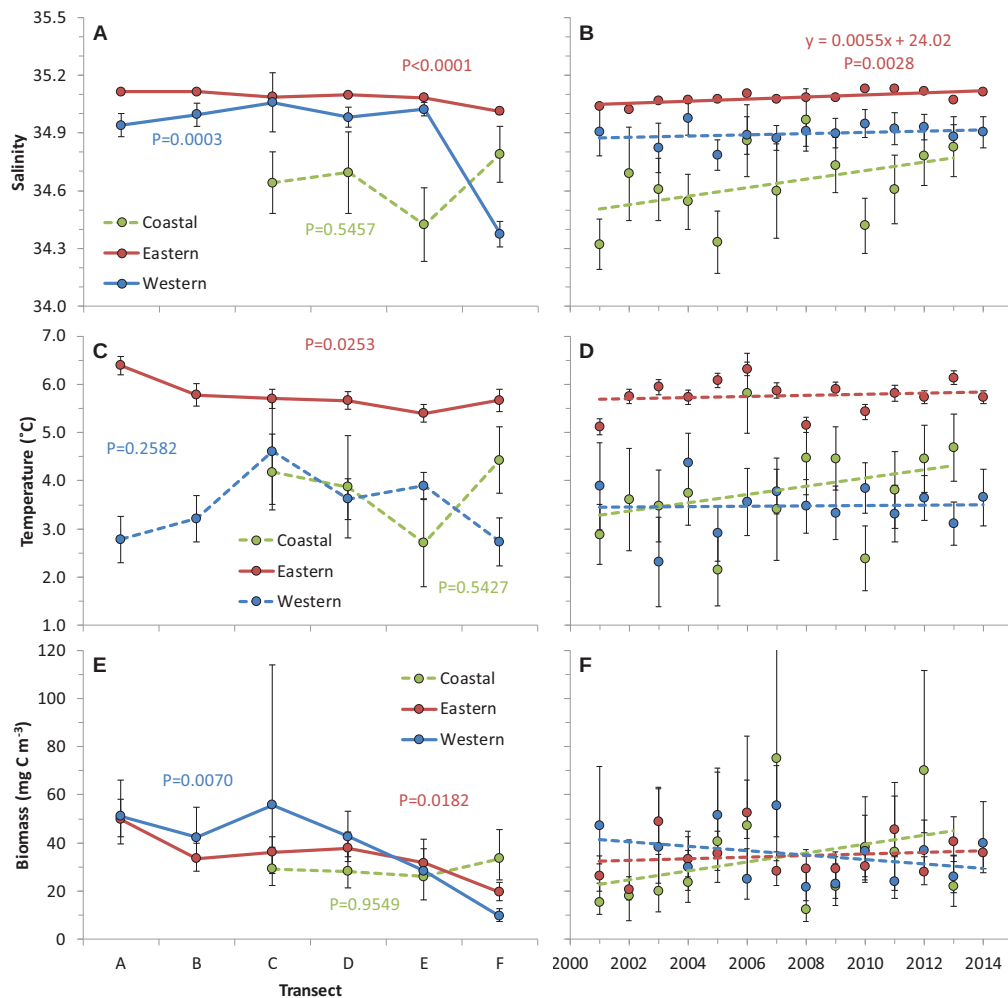


FIGURE 2 | Spatial and temporal trends for salinity (A,B), temperature (C,D) and total mesozooplankton biomass (E,F) for the three branches of the West Spitsbergen Current. Error bars represent the standard error of the marginal means. Significance of the spatial variation from the mixed model (Eq. 1) and linear regression of annual means (only for regression with $P < 0.05$) are inserted. Non-significant spatial trends and linear time trends are indicated with dashed lines.

from each other in salinity, with the coastal branch having lower salinity among the three branches (Figure 2). The eastern branch exhibited significant spatial trends of decreasing temperature and salinity from south to north, which was partly mirrored for salinity in the western branch. No significant spatial patterns were observed for temperature and salinity in the coastal branch as well as temperature in the western branch (Table 2).

Interannual variations among years were significant for both temperature and salinity in the eastern branch (Table 2), exhibiting a significant increase of 0.0055 yr^{-1} (± 0.0015) for salinity (Figure 2B) and no linear trend for temperature ($P = 0.5984$) (Figure 2D). There were no systematic temporal trends in the western and coastal branches for neither temperature nor salinity. However, the relatively low number of observations for the western and coastal branches could impede the analysis of temporal and spatial variations.

Biomass of the entire zooplankton community attained similar levels across the three branches, but exhibited different

spatial gradients (Figure 2E). The western and eastern branches had significant variation across transects, showing declining biomass in the northward direction. The coastal branch did not display significant variation among transects. Moreover, there was no significant variation among years for any of the three branches, despite that marginal means for y_j varied by factors 2–4 (Figure 2F). The large standard error of the marginal means and the lack of significance was mainly caused by large random variation in the spatial patterns across years [random factors $T_i \times Y_j$ and $Y_j \times S_k(t_i)$] (Supplementary Table S1), i.e., spatial trends in zooplankton biomass were not consistent but highly variable across the 14 years (Supplementary Figure S2).

Zooplankton Community

There were 68 species or genera and 20 taxa of higher rank identified in the zooplankton samples from the West Spitsbergen Current (Supplementary Table S2), representing all important marine zooplankton taxa (at the rank of

TABLE 2 | Statistical tests (*P*-values) for variation among transects (*t_i*) and years (*y_j*) in the WSC branches using Eq. 1.

WSC western branch			WSC eastern branch			WSC coastal branch		
Variable	P(<i>t_i</i>)	P(<i>y_j</i>)	Variable	P(<i>t_i</i>)	P(<i>y_j</i>)	Variable	P(<i>t_i</i>)	P(<i>y_j</i>)
Temperature	0.2582	0.7688	Temperature	0.0195	<0.0001	Temperature	0.5427	0.1758
Salinity	0.0003	0.9289	Salinity	<0.0001	<0.0001	Salinity	0.5457	0.2028
Total biomass	0.0182	0.4117	Total biomass	0.0253	0.2934	Total biomass	0.9549	0.5378
C.f. stages	0.0286	0.3740	C.f. stages	0.2414	<0.0001	C.f. stages	0.3075	0.2622
Dominant species	P(<i>t_i</i>)	P(<i>y_j</i>)	Dominant species	P(<i>t_i</i>)	P(<i>y_j</i>)	Dominant species	P(<i>t_i</i>)	P(<i>y_j</i>)
<i>Eukrohnia hamata</i>	B 0.0556	0.4080	<i>Calanus finmarchicus</i>	B 0.0517	0.2459	<i>Calanus finmarchicus</i>	B 0.9174	0.7165
	P 0.3043	0.2945		P 0.0859	0.0123		P 0.6945	0.3194
<i>Calanus finmarchicus</i>	B 0.0638	0.2638	<i>Eukrohnia hamata</i>	B 0.2755	0.0517	<i>Calanus glacialis</i>	B 0.8639	0.1185
	P 0.2336	0.5300		P 0.4090	0.1497		P 0.5059	0.2701
<i>Calanus hyperboreus</i>	B 0.0166	0.1334	<i>Aglantha digitale</i>	B 0.0066	<0.0001	<i>Eukrohnia hamata</i>	B 0.6371	0.7937
	P 0.3147	0.1122		P 0.0173	<0.0001		P 0.6347	0.2885
<i>Oithona similis</i>	B 0.2658	0.3112	<i>Calanus hyperboreus</i>	B 0.2394	0.0296	<i>Calanus hyperboreus</i>	B 0.4870	0.2181
	P 0.0528	0.2226		P 0.1129	0.0027		P 0.6931	0.3367
<i>Pseudocalanus acuspes/minutus</i>	B 0.1110	0.3842	<i>Calanus glacialis</i>	B 0.0035	0.0009	<i>Parasagitta elegans</i>	B 0.5572	0.1000
	P 0.9231	0.2598		P <0.0001	<0.0001		P 0.4134	0.1298

The model was employed for temperature, salinity, total zooplankton biomass, biomass (B) and proportion (P) of the five most dominant species, and *Calanus finmarchicus* development stage. Significant tests ($P < 0.05$) are highlighted in bold. Temporal variations from the mixed model are shown in **Figures 2, 4, 5**, and spatial variations are shown in **Figures 2, 5** (spatial trends for dominant species are not shown).

TABLE 3 | Frequency of occurrence, average biomass (mg C m⁻³) and proportion for the most dominant mesozooplankton species in samples from the West Spitsbergen Current (2001–2014).

Samples and taxa	Western branch			Eastern branch			Coastal branch		
	<i>n</i> = 59 samples and <i>n</i> = 53 taxa			<i>n</i> = 198 samples and <i>n</i> = 85 taxa			<i>n</i> = 39 samples and <i>n</i> = 67 taxa		
Dominating taxon	Occurrence	Biomass	Proportion	Occurrence	Biomass	Proportion	Occurrence	Biomass	Proportion
<i>Calanus finmarchicus</i>	100.0%	10.19	26.1%	100.0%	24.24	52.2%	100.0%	16.77	47.2%
<i>Eukrohnia hamata</i>	100.0%	12.99	33.3%	99.0%	10.93	23.5%	100.0%	1.43	4.0%
<i>Calanus hyperboreus</i>	100.0%	10.25	26.3%	97.5%	1.88	4.0%	94.9%	0.59	1.7%
<i>Calanus glacialis</i>	91.5%	0.71	1.8%	82.3%	1.59	3.4%	100.0%	12.46	35.1%
<i>Oithona similis</i>	100.0%	1.74	4.5%	100.0%	1.18	2.5%	100.0%	0.65	1.8%
<i>Aglantha digitale</i>	39.0%	0.02	0.0%	83.8%	1.97	4.2%	74.4%	0.12	0.4%
<i>Themisto abyssorum</i>	94.9%	0.64	1.6%	99.0%	0.55	1.2%	94.9%	0.20	0.6%
<i>Pseudocalanus</i> spp.	100.0%	0.85	2.2%	100.0%	0.20	0.4%	100.0%	0.25	0.7%
<i>Parasagitta elegans</i>	45.8%	0.03	0.1%	65.7%	0.00	0.0%	97.4%	0.81	2.3%
<i>Oikopleura</i> spp.	86.4%	0.08	0.2%	87.9%	0.24	0.5%	94.9%	0.25	0.7%
<i>Metridia longa</i>	64.4%	0.36	0.9%	74.7%	0.00	0.0%	84.6%	0.11	0.3%
<i>Themisto libellula</i>	91.5%	0.35	0.9%	69.2%	0.00	0.0%	69.2%	0.05	0.1%
<i>Thysanoessa inermis</i>	8.5%	0.09	0.2%	18.2%	0.78	1.7%	15.4%	0.17	0.5%

Total number of samples and taxa recorded are listed for each branch. Species contributing more than 10% to the total biomass are highlighted in bold.

phylum and class). Most speciose were Copepoda Calanoida (24 species/genera), several taxa were less diverse, among them Amphipoda (7), Cyclopoida (6), Hydromedusae (6), and Euphausiacea (4). The remaining zooplankters were represented by yet less species/genera, for example, Pteropoda (3) and Chaetognatha (3); however, in some cases, species level identification was challenging or impossible due to difficulties in recognizing taxonomic features of specimens fixed in formaldehyde solution (*Oikopleura*), because of lack of species

descriptions (Polychaeta larvae) or because of lack of taxonomic expertise at the time of sample processing (Harpacticoida).

Three *Calanus* copepods (*C. finmarchicus*, *C. glacialis*, and *C. hyperboreus*) and chaetognaths *E. hamata* constituted the bulk of the zooplankton biomass in the WSC (**Table 3**). Zooplankton biomass was almost equally dominated by *E. hamata*, *C. finmarchicus*, and *C. hyperboreus* in the western branch, tallying almost 90% of the total biomass, whereas *C. finmarchicus* dominated in the eastern and coastal branches,

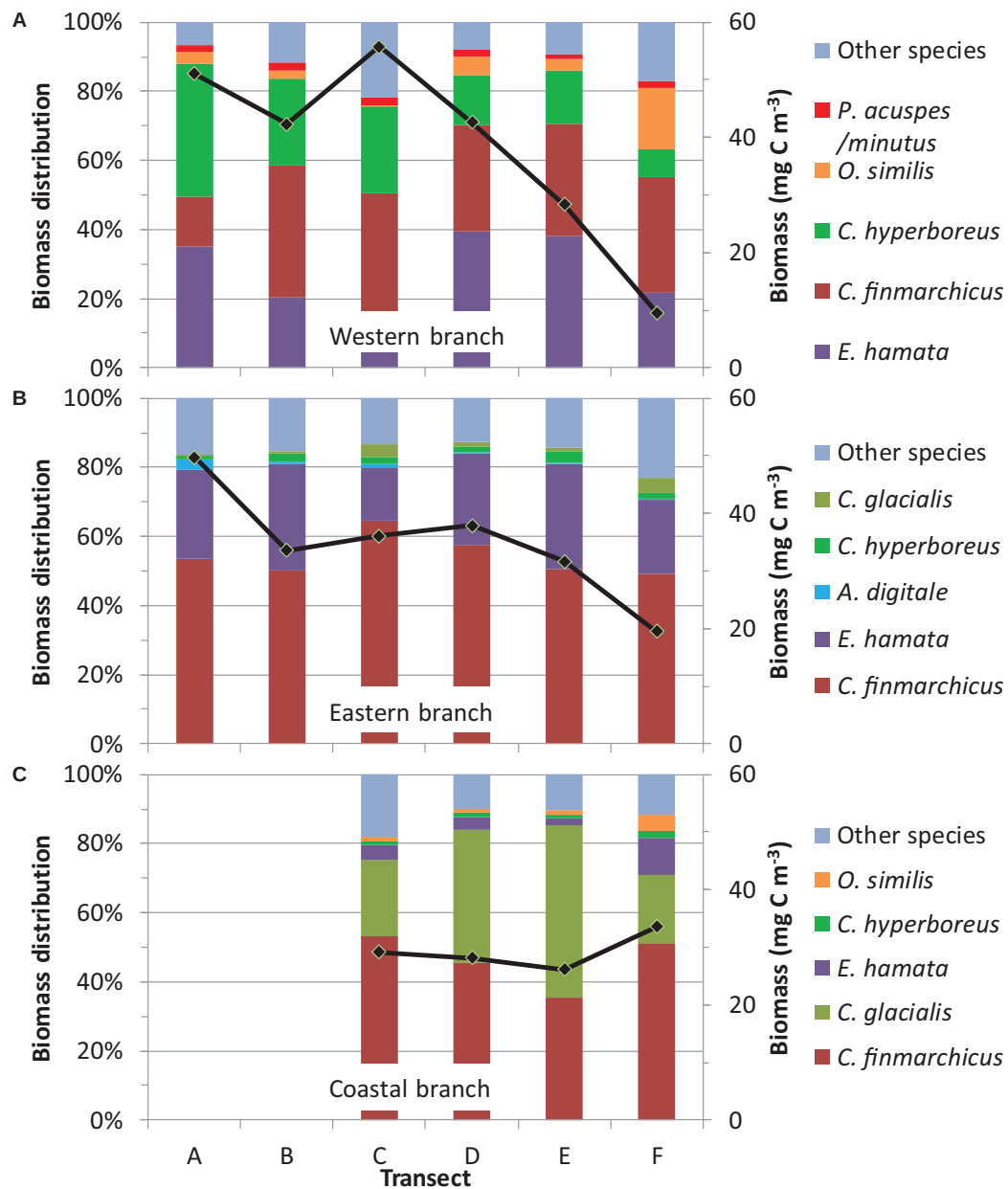


FIGURE 3 | Spatial distribution of dominant mesozooplankton species for the three branches of the West Spitsbergen Current (**A**: western branch, **B**: eastern branch, and **C**: coastal branch). Biomass proportions were modeled using Eq. 1 for the five dominant species in each branch as well as all other species. For comparison with the species distribution the total mean biomass for the different transects is also plotted (cf. Figure 2).

constituting there about half of the biomass. *E. hamata* was also important for the zooplankton biomass in the eastern branch, whereas *C. glacialis* contributed about one-third biomass in the coastal branch. In addition to the differences regarding the four bulk biomass species, there were also well-defined spatial patterns across the three branches for other zooplankton species. In the western branch, other important species were *Oithona similis*, *Pseudocalanus* (most probably *P. minutus*), and *Themisto abyssorum*. In the eastern branch, the two main zooplankton species (*C. finmarchicus* and *E. hamata*) were seconded by

hydromedusae *Aglantha digitale* and copepods *C. hyperboreus*, *C. glacialis*, and *O. similis*. In the coastal branch, *Parasagitta elegans*, *Oikopleura*, and *O. similis* were also important biomass contributors in addition to the four bulk biomass species.

In the western branch, *C. hyperboreus* showed significant latitudinal differences (Table 2), although the significance was not particularly strong. *C. hyperboreus* was relatively more dominant at the three southern transects (~30% of biomass) and less dominant at the three northern transects (~10% of biomass) (Figure 3A). Variations among years were not

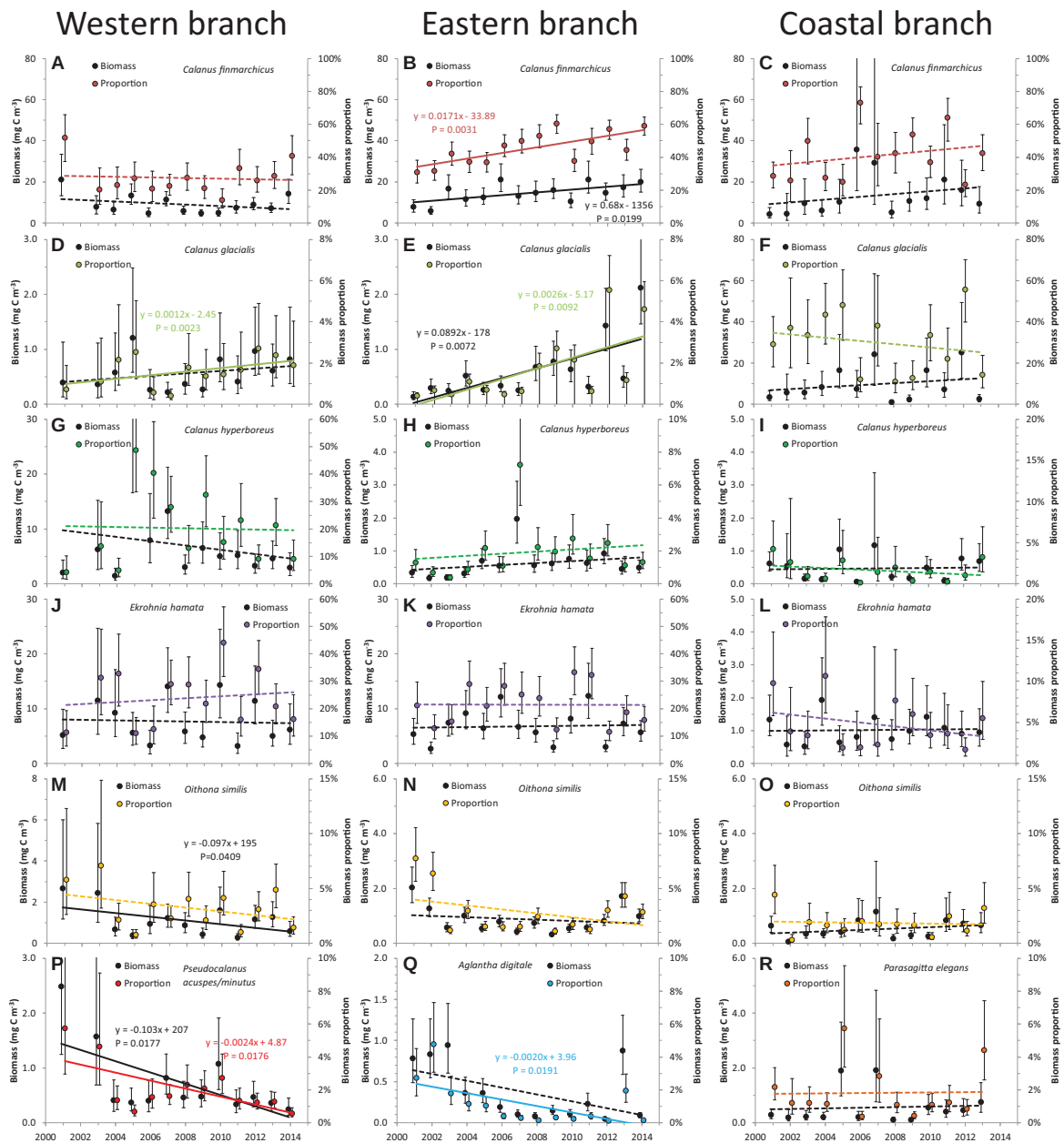


FIGURE 4 | Changes in biomass and relative proportion of five dominant mesozooplankton species over time for the three branches of the West Spitsbergen Current (A–R: combinations of dominant species and branches). Error bars represent the standard error of the means. Significant linear regressions of annual means ($P < 0.05$) are shown with solid lines and statistics inserted, whereas non-significant linear trends are indicated with dashed lines. Note the different scaling on the y-axes.

significant for any of the five most dominating species (Table 2), yet the biomass proportion of *Pseudocalanus acutispinus/minutus* decreased significantly over time due to relatively high biomass in the first years of the study period (Figure 4P). The most pronounced change over time was the increasing biomass (both absolute and relative) of *C. glacialis*, increasing its presence in the western branch from almost absent to ~2% in recent years (Figure 4D).

In the eastern branch, significant and opposing spatial trends were observed for *A. digitale* and *C. glacialis* (Figure 3 and Table 2). The proportion of *A. digitale* was around 2.5% at the southernmost transect, but less than 1% further north. On the other hand, the proportion of *C. glacialis* was less than 1% at transect A and B, but increased to ~2% at transects C–F. These two species, together with *C. finmarchicus* and *C. hyperboreus*, also exhibited significant interannual variations (Table 2).

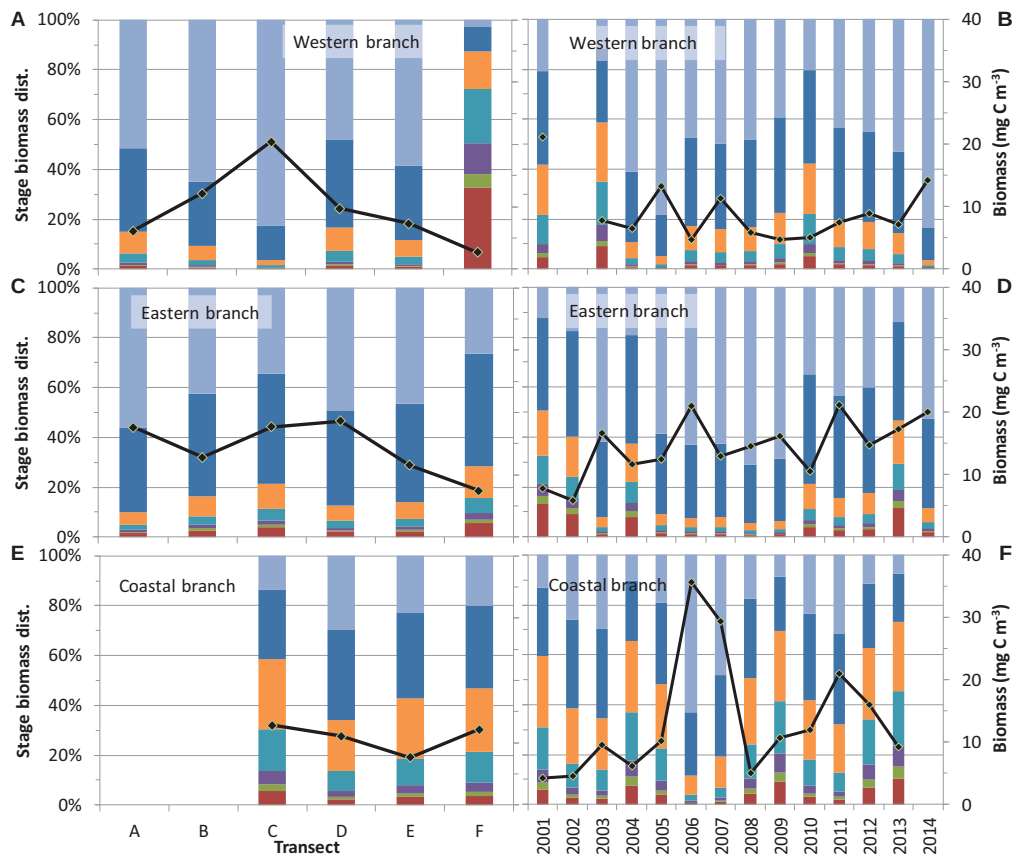


FIGURE 5 | Spatial distribution and temporal trends of *Calanus finmarchicus* stages for the three branches of the West Spitsbergen Current (A,B: western branch, C,D: eastern branch, and E,F: coastal branch). Biomass proportions were modeled using Eq. 2. For comparison the mean biomass of *C. finmarchicus* is plotted for the different transects.

However, systematic temporal trends were observed only for *C. finmarchicus*, increasing from ~40 to ~60% (Figure 4B), *C. glacialis*, increasing from almost 0 to ~3% (Figure 2E), and *A. digitale*, decreasing from ~2% to almost 0% in recent years (Figure 4Q).

In the coastal branch, none of the dominant species exhibited significant variations among transects or years (Table 2). Moreover, no systematic time trends were observed for the dominant species (Figure 4), and only *C. finmarchicus* showed somewhat consistent tendencies of increasing biomass if the high biomasses in 2006 and 2007 were disregarded. However, it should be noted that the yearly estimates for the coastal branch were relatively uncertain due to the lower number of samples ($n = 39$).

Development of *Calanus finmarchicus*

Calanus finmarchicus copepodid CV and adults made up > 80% of the species biomass in the western and eastern branches, and only 50–60% in the coastal branch suggesting a less mature population over the shelf. Among these older stages, mature individuals (mostly females) constituted approximately 50% of the *C. finmarchicus* biomass in the western and eastern branches, whereas they only constituted 20–30% of the biomass in the coastal branch (Figure 5). An exception from this pattern was

observed on transect F in the western branch. However, the variability in biomass proportions of the different developmental stages was considerable and no significant differences among transects were found (Table 2). For the same reason, interannual variation was only significant for the eastern branch, with about four times as many samples as the two other branches. In the eastern branch, the *C. finmarchicus* population was relatively more mature from 2005 to 2009, compared to years both before and after. Less developed populations were sampled in 2001 and 2003 in the western branch, but these proportion means were based on one observation in 2001 and two in 2003 only. However, there were no systematic trends over time found in relative proportion of *C. finmarchicus* developmental stages in none of the three branches.

DISCUSSION

The data in this study represents one of the longest and most extensive biological time series in the Arctic region. However, clear patterns of spatial and temporal variability did not emerge for all the zooplankton variables, which could be due to that such patterns did not occur or alternatively, that any such

patterns were overridden by even larger random fluctuations. Partitioning variations with the mixed model (Eq. 1) also provides insight into the magnitude of uncertainty present in data. Using the variance estimates from the eastern branch with the most data, we found that uncertainties associated with temperature and salinity were less than 0.5°C and 0.04, respectively (Supplementary Table S1). Thus, transect and annual means were relatively well determined, most precise for the data-richer eastern branch and less precise for the two other branches (Figure 2). However, random variations associated with the zooplankton data were much larger for the biomass of the entire zooplankton community (~50–100%) and even larger for the biomass and proportion of dominant species (data not shown). Consequently, transect and annual means of zooplankton variables were considerably more uncertain than for temperature and salinity, implying that only large spatial and temporal trends were found significant. Nevertheless, despite the large variability in zooplankton data significant changes over time and latitudes were found for some variables.

It should be stressed that our results are limited to a narrow seasonal window from late June to mid July. Unfortunately, seasonal studies of the zooplankton community are rare for the Arctic region, and for practical reasons only coastal areas have been studied seasonally. Only recently, Basedow et al. (2018) published results on zooplankton variability in Fram Strait and the Nansen Basin of the Arctic Ocean, north of our study area. They showed that high abundances of carbon-rich copepods were present in the AW inflow during all seasons (January, May, and August); however, that there was also variability in zooplankton transport between seasons, most likely resulting from the seasonal changes in the vertical distribution of zooplankton. Their study confirmed that the main zooplankton taxa tend to concentrate in the upper layers, particularly in spring and summer; however, they also found patches of unexpectedly high abundances of zooplankton, including *C. finmarchicus*, in winter (January). Seasonal studies are, regrettably, mostly restricted to a single year (e.g., Astthorsson and Gislason, 2003), assuming that particular year to represent the general seasonal variation. At present, multi-annual seasonal studies of open-ocean zooplankton communities are only available for the mid-latitude Atlantic Ocean (Planque et al., 1997; Helaouët and Beaugrand, 2007). Our long-term study demonstrates high interannual variability in the Arctic region and confirms that general inference is not possible with a study period of a single or few years of data.

Similar to our study, long-term studies in the Arctic typically focus on a specific seasonal window related to a specific successional stage of key species, typically *Calanus* species. Espinasse et al. (2017) studied decadal changes in *C. finmarchicus* and *C. hyperboreus* in three coastal locations, but the sampling window changed from May in Northern Iceland, July in Svalbard to October in northern Norway, and therefore the time series represented different phases of these species' life cycle. In the Barents Sea, Tande et al. (2000) studied *C. finmarchicus* in spring (April, May) and summer (June, July) across nine non-consecutive years (1979–1992) and Dvoretzky and Dvoretzky (2013) analyzed the mesozooplankton community

in July–August over a 7-year period (2003–2009). Common to most of the multi-annual studies of zooplankton in the Arctic region is that the sampling time window is chosen to represent the period following the phytoplankton spring bloom, characterized by the highest zooplankton biomass (Søreide et al., 2010). This sampling strategy also applied to our data and our results are likely to represent the zooplankton community at peak biomass in the WSC in the upper part of the ocean.

Key Species Distribution

The number of zooplankton species and taxa of higher rank found in the WSC samples was similar to those reported from other studies. As far as taxonomic affiliation is concerned, the list of identified species includes the majority of those recorded in the study area in previous studies (Hop et al., 2006; Gluchowska et al., 2017a,b). The main differences, both in terms of the number of taxa and individual species present, result primarily from the limitation of this study to the upper 60-m layer. For this reason, it is understandable that only some meso- and bathypelagic species known to occur in the WSC waters were found in the study collection. This can also explain the relatively low frequency of occurrence and the low biomass proportion found for species such as *Metridia longa*, *P. norvegica* or *Microcalanus*. The location of the study in a relatively narrow time window (end of June to mid-July) can explain why the predominant biomass species are *Calanus* copepods, which during this time typically conclude their development and growth in surface waters before migration to greater depths to diapause.

The zooplankton communities of the WSC branches were clearly different, and the observed distribution patterns and community structures can be interpreted in the context of environmental conditions characteristic for the habitats in which the individual communities were observed, in this case limited to temperature and salinity of water masses constituting separate branches of the WSC. In the western branch, the characteristic zooplankton community was made up of *E. hamata*, *C. finmarchicus* and *C. hyperboreus*. Other important species included *O. similis*, *Pseudocalanus* (most likely mainly *P. minutus*), *T. abyssorum*, *C. glacialis*, *Metridia longa*, and *T. libellula*. The high biomass of *C. hyperboreus* in the western branch and the considerable presence of *P. minutus*, *M. longa*, and *T. libellula* is most likely related to low temperature and high salinity of the western branch, which can result from the location of these stations in the Arctic Front zone, separating warmer Atlantic waters of the WSC from colder waters of the Greenland Sea Gyre. These species are generally considered to prefer lower water temperature (Frost, 1989; Auel and Werner, 2003; Daase et al., 2008), and are regarded as main zooplankton components in the Greenland Sea (Conover, 1988; Hirche, 1991; Richter, 1994). However, it is interesting that *C. hyperboreus* was more dominant at the three southernmost transect, as it is an expatriate species of Arctic origin that is transported southward mainly with the East Greenland Current (Conover, 1988). This current was not monitored in our transects, but gyres from this current could recirculate *C. hyperboreus* into the WSC. Thus, the observed higher proportion of *C. hyperboreus* in the south is related to the fact that sampling stations at the southern transects

of the western branch were in closer proximity to the Arctic Front, where mixing of Arctic waters of the Greenland Sea and their fauna, including *C. hyperboreus*, with Atlantic waters of the Norwegian Sea takes place.

In the eastern branch, the zooplankton community was dominated by *C. finmarchicus* and *E. hamata*, but species like *A. digitale*, *C. hyperboreus*, *C. glacialis*, and *O. similis* were also found in most samples with a considerable biomass contribution. The dominance of characteristic boreal species (*C. finmarchicus*, *A. digitale*), as well as a noteworthy share of Euphausiids, is in agreement with warm and saline characteristics of the water masses in this branch; waters possessing a clear Atlantic signature. The eastern branch of the WSC recognized in this study represents undoubtedly the surface water fragment of the WSC core flow (Walczowski et al., 2005; Walczowski et al., 2012). Interestingly, however, there was a declining of *A. digitale* in the eastern branch over the study period (Figure 4Q), despite indications of stronger influence of AW. It is possible that this temporal trend could be associated with changes in the seasonal reproduction and development of *A. digitale*, relative to the time window of the cruises, resulting in younger individuals with less biomass or with deeper distribution of the medusae in recent years (Williams and Conway, 1981). Another explanation of this trend in *A. digitale* could be competition with another predator, *E. hamata*, which biomass was not declining over time. Both the jellyfish *A. digitale* and the chaetognath *E. hamata* are known as copepod predators (Øresland, 1990; Pagés et al., 1996), so maybe, in the instance of increasing population abundance of prey of these predators (i.e., copepods), and changes in phenology of the zooplankton, caused by changes in the environment induced by climate change, the competitive conditions became more in favor for *E. hamata*. Last but not least, the abundance of *A. digitale* could decrease because of increasing pressure of its predators such as scyphozoan medusae *Cyanea capillata* or larvae and juvenile of fish, for example Atlantic mackerel *Scomber scombrus* (Runge et al., 1987; Båmstedt et al., 1997; Purcell, 2003). Increased abundances of pelagic predators have been observed in recent years migrating northward following the Atlantic water pathways (Dalpadado et al., 2012; Renaud et al., 2012).

In the coastal branch, flowing off the Spitsbergen coast along the slope and shelf edge, the most important contribution to the biomass of the zooplankton community was made by *C. finmarchicus* and *C. glacialis*. A high proportion of *C. glacialis*, as well as an important contribution of *P. elegans*, species typically characterized as cold-water, Arctic shelf seas species, matches with the temperature and salinity properties of this branch (Falk-Petersen et al., 1999, 2009; Grigor et al., 2014). The coastal branch had both low temperature and low salinity, which indicates that this water mass is influenced by Arctic water, most likely originating from the Barents Sea. Thus, the physical characteristics and the zooplankton composition, including both Arctic and boreal species, strongly support that the coastal branch is comprised by a mix of Arctic and Atlantic waters.

Conduit or Productive Area

The Arctic Ocean is believed to be net heterotrophic with large inputs of organic material, including zooplankton, from

Atlantic and Pacific waters (Olli et al., 2007). The largest input of zooplankton to the Arctic Ocean enters with the WSC through Fram Strait (Kosobokova and Hirche, 2009; Wassmann et al., 2015), where it supports numerous fish, birds and whales. The extent to which the WSC acts as a simple conduit of zooplankton biomass originating from further south or actually constitutes a productive zone for mesozooplankton, enhancing the northward zooplankton flux has not been investigated yet.

Primary production is restricted in strongly stratified systems, where nutrients are mainly supplied through shear and micro-turbulence (Tremblay and Gagnon, 2009). The western and eastern WSC branches are strongly stratified, which would suggest that these two branches operate mainly as conduits of zooplankton since primary production is expectedly low and unlikely to support zooplankton growth. Both branches displayed decreasing zooplankton biomass in the northward direction (Figures 3A,B). However, there was an increase in zooplankton biomass at transect C for the western branch and transects C and D for the eastern branch. In this area, at the latitude of southern Spitsbergen, the western WSC branch and outflow from the Barents Sea converge with the eastern branch, which follows the shelf break (Walczowski et al., 2012). It is therefore possible that mixing associated with eddies in this area enhances primary production and consequently, zooplankton biomass.

Continuous nutrient supply along the shelf break, on the other hand, supports high levels of primary production (Arrigo and van Dijken, 2015), which can maintain or even enhance zooplankton biomass with the northward flow. Zooplankton biomass in the coastal branch remained constant across latitudes (Figure 3C), supporting this hypothesis. The influence of Barents Sea outflow mixing with the eastern branch was also apparent from the appearance of *C. glacialis* at transect C in the eastern branch. *C. glacialis* is abundant in the Barents Sea, in contrast to Atlantic waters (Falk-Petersen et al., 1999; Wassmann et al., 2015), and its appearance in the eastern branch from transect C and northward is probably caused by mixing with Barents Sea outflow.

Zooplankton biomass in the WSC surface layer is determined by growth and mortality in addition to advective transport and seasonal vertical migration. Loss processes most likely dominated the western and eastern branches along the northward flow, suggesting that these two branches were mainly operating as conduits of zooplankton from south to north. Loss of zooplankton biomass could be due to mortality exceeding growth and descending of key copepods as a part of their seasonal, ontogenetic vertical migration, following the development during the spring (utilizing the spring bloom) and the early summer. The strong dominance of *C. finmarchicus* CV and adults in the eastern and western branches signify a well-matured zooplankton community that may have been ready to descend into greater depths for entering the diapause. Less mature (and therefore of low biomass) *C. finmarchicus* population at transect F may suggest that this is a different population, probably sharing characteristics with the population of coastal branch, which is still in growing stage (Figure 5). At the latitude

of transect F (approximately 79°N) the individual branches of the WSC are most likely strongly mixed with each other, due to confluence of the individual flows primarily because of the local bathymetry (Walczowski, 2013). It is likely that the decrease in zooplankton biomass from south to north at the western and eastern branches is due to seasonal migration or to low food availability that cannot maintain sufficient growth to outbalance mortalities. Alternatively, perhaps the regions more to the north are already border areas of optimal development, primarily for the boreal *C. finmarchicus*, which is responsible for the gross biomass of zooplankton in the studied waters. In both cases, insufficient primary production associated with strong stratification can explain the conduit behavior in the two branches.

The coastal branch behaved differently with a constant biomass and younger *C. finmarchicus* stages across the latitudes. The spring bloom in this branch is expected to start later and last longer due to presence of sea ice (Carstensen et al., 2012). A continuous supply of nutrients associated with upwelling and turbulent mixing at the shelf break further enhances primary production, sustaining a relatively high zooplankton biomass along the Spitsbergen coast. Another possible explanation of higher biomass in the coastal branch, particularly in the northern part of the region, could be associated with physical concentration of zooplankton, as a result of advancement of the eastern branch toward the shallower shelf. In this way, our results support the hypothesis of shelf regions and frontal zones as productivity hot spots (Basedow et al., 2014; Trudnowska et al., 2016).

Potential Effects of Climate Change

The expected poleward movement of enhanced primary production (Arrigo and van Dijken, 2015) may potentially have a large influence on zooplankton distribution and advection into the Arctic Ocean. In a modeling study, Slagstad et al. (2011) estimated a drastic shift in primary productivity from south to north of Svalbard over the 21st century. This change in productivity is likely to sustain high zooplankton biomasses at higher latitudes in the western and eastern WSC branches, assuming spatial patterns of secondary producers follow that of the primary producers, and it will potentially increase the flux of zooplankton into the Arctic Ocean. Our time series did not confirm any significant increase over time in zooplankton biomass within the different WSC branches as a whole (Figure 2F) and we did not observe any particular northwards shifts in zooplankton biomass over the study period (Supplementary Figure S2). Hence, the drastic shift predicted by models could not be confirmed with our relatively long time series. Gluchowska et al. (2017a) reported a small increase over the same period for the D transect, but this trend was small relative to the large interannual variations. Given this large interannual variability, time series of multiple decades are needed to identify systematic time trends in this area.

Although our data could not confirm the expected poleward movement of zooplankton in general, our analyses demonstrated significant changes in the community structure (Figure 4). The increasing proportion of *C. finmarchicus* in the WSC, particularly

the eastern branch, testify to stronger influence of Atlantic zooplankton communities. This finding is consistent with the increasing salinity in the WSC (Figure 2B). Interestingly, the year with the highest *C. finmarchicus* biomass in the coastal branch (2006) was also the warmest year (Figure 2). Whereas the increase in *C. finmarchicus* is expected with increasing influence of Atlantic water, the significant increase in *C. glacialis* biomass over time in the western and eastern branches is more intriguing. The successful life strategy of *C. glacialis* is connected with early spawning, and nauplii and younger copepodid stages feeding on ice algae to better take advantage of the spring production (Falk-Petersen et al., 2009; Søreide et al., 2010; Leu et al., 2011). Retreating sea ice over the study area (Arrigo and van Dijken, 2015) could imply a competitive disadvantage to *C. glacialis* over other species not relying on ice algae, in contrast to the observed temporal trends (Figure 4). Furthermore, the increasing trends in *C. glacialis* were observed in the open-ocean branches that are mostly free of sea ice, whereas no change over time was observed in the coastal branch where sea ice is more prominent. This apparent discrepancy could be explained with increasing outflow from the Barents Sea, which hosts a high concentration of *C. glacialis* (Wassmann et al., 2015). Increasing inflow of Atlantic water has significantly reduced sea ice in the Barents Sea (Årthun et al., 2012), but this “Atlantification” may also have enhanced the general circulation in the Barents Sea and hence, promoted the outflow of Arctic water and *C. glacialis* south of Svalbard and into the WSC. Although the outflow from the Barents Sea is about one of magnitude smaller than the WSC, the effect of an increased outflow could significantly affect biomass in the western and eastern branches, where *C. glacialis* was almost absent in the beginning of the study period. However, longer time series are needed to assess changes in the zooplankton community over time given the large inherent variability of such data and the potential existence of decadal oscillations.

AUTHOR CONTRIBUTIONS

JC led the study design, carried out statistical analyses, and wrote the first draft of the manuscript. AO analyzed the zooplankton samples and contributed to the data discussion. SK contributed to the study design, participated in field sampling, contributed to the sample examination, and discussion and wrote the manuscript.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: <https://www.frontiersin.org/articles/10.3389/fmars.2019.00202/full#supplementary-material>

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Zooplankton Communities Associated With New and Regenerated Primary Production in the Atlantic Inflow North of Svalbard

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The Arctic Ocean is changing rapidly with respect to ice cover extent and volume, growth season duration and biological production. Zooplankton are important components in the arctic marine food web, and tightly coupled to the strong seasonality in primary production. In this study, we investigate zooplankton composition, including microzooplankton, copepod nauplii, as well as small and large copepod taxa, and primary productivity in the dynamic Atlantic water inflow area north of Svalbard in May and August 2014. We focus on seasonal differences in the zooplankton community and in primary productivity regimes. More specifically, we examine how a shift from “new” (nitrate based) spring bloom to a “regenerated” (ammonium based) post bloom primary production is reflected in the diversity, life history adaptations and productivity of the dominant zooplankton. North of Svalbard, the seasonal differences in planktonic communities were significant. In spring, the large copepod *Calanus finmarchicus* dominated, but the estimated production and ingestion rates were low compared to the total primary production. In summer, the zooplankton community was composed of microzooplankton and the small copepod *Oithona similis*. The zooplankton production and ingestion rates were high in summer, and probably depended heavily on the regenerated primary production associated with the microbial loop. There was clear alteration from dominance of calanoid copepod nauplii in spring to *Oithona* spp. nauplii in summer, which indicates different reproductive strategies of the dominating large and small copepod species. Our study confirms the dependence and tight coupling between the new (spring bloom) primary production and reproductive adaptations of *C. glacialis* and *C. hyperboreus*. In contrast, *C. finmarchicus* appears able to take advantage of the regenerated summer primary production, which allows it to reach the overwintering stage within one growth season in this region north of Svalbard. This suggests that *C. finmarchicus* will be able to profit from the predicted increased primary production

in the Arctic, a strategy also recognized in small copepod species such as *O. similis*. We speculate that the ability of the copepod species to utilize the regenerated summer primary production and microbial food web may determine the winners and losers in the future Arctic Ocean.

Keywords: copepods, copepod nauplii, *Calanus* spp., *Oithona similis*, microzooplankton, food web, Arctic

INTRODUCTION

The extreme seasonality of polar marine ecosystems is widely recognized. During winter, the sun is below the horizon (polar night) and the lack of light prevents phytoplankton growth. In seasonally ice-covered regions, the spring bloom of primary producers usually initiates after sea ice melting and lasts only a few weeks, until the surface nitrate is depleted. When nitrate is depleted and stratification prevents new influx of nitrate, phytoplankton will use alternative nitrogen (N) sources, such as ammonium and urea (Kristiansen et al., 1994). The shift from “new” nitrate (NO_3^-) to regenerated forms of N such as ammonium (NH_4^+) is known as the dichotomy of “new” and “regenerated” primary production [*sensu* Dugdale and Goering (1967)], respectively. The fraction of new primary production to total (new and regenerated) primary production is defined by the f-ratio. From the perspective of the grazer communities, the source of nitrogen triggers different autotrophic communities (Shilova et al., 2017). The nutrient replete spring-scenario is typically dominated by large phytoplankton cells (such as diatoms) utilizing nitrate as their N source, and the post bloom phytoplankton community is often dominated by smaller cells that grow efficiently on recycled N and dissolved organic carbon (Paulsen et al., 2018). This transition from spring bloom to post bloom is also associated with a change in phytoplankton lipid composition, with higher contributions of the essential polyunsaturated fatty acids (PUFAs) during spring bloom than during post bloom (Parrish et al., 2005; Leu et al., 2006).

The strong seasonality in food quality and quantity has direct implications for the grazer communities. Most obvious is perhaps the direct effect on the large herbivorous copepods, with life cycles tailored to utilize the short and intense spring bloom for reproduction and lipid synthesis (Falk-Petersen et al., 2009). For example, the large Arctic *Calanus hyperboreus* reproduce in winter, prior to the productive season (Falk-Petersen et al., 2009; Kvile et al., 2018), *C. glacialis* reproduce prior to and during the ice algae bloom (Varpe et al., 2009; Søreide et al., 2010) and *C. finmarchicus* has its main reproductive period during the open water spring bloom (Hirche, 1996; Pedersen et al., 2001). When the large *Calanus* species have built sufficient lipid storages, they enter diapause at depth to survive the long and less productive winter season. When leaving the surface habitat, a niche is created for the smaller copepod species with different life history strategies (Hansen et al., 1999; Svensen et al., 2011). Therefore, the shift in major primary productivity regimes from spring to summer can also be reflected in the grazer communities both with respect to feeding and reproductive strategies.

While a number of studies at high latitudes focus on the zooplankton community composition and life history adaptations during the ice algae- and open water spring bloom (Søreide et al., 2010; Leu et al., 2011; Feng et al., 2016), there has been less focus on links between the zooplankton and microbial food webs at the end of the summer when the large *Calanus* spp. leave the surface waters (Hansen et al., 1999; Svensen et al., 2011). Likewise, small copepod taxa, nauplii and microzooplankton are often not well represented due to predominant use of plankton nets targeting the larger size-fraction of the plankton community. Presently, the Arctic climate is undergoing rapid changes with potential severe effects on the ecosystem. With an already documented earlier sea ice-melt and delayed sea-ice formation in the Barents Sea and Arctic Ocean (Onarheim et al., 2018), the future Arctic Ocean is expected to experience an increase in open water area, increased light transmission to the surface ocean, and a prolonged growing season for phytoplankton (Arrigo and Van Dijken, 2011). A 20% increase of total annual net primary production from 1998–2009 has already been documented (Arrigo and Van Dijken, 2011). However, it is not clear if this increase is based on new or regenerated production. During summer with stratified water masses, a large fraction of the increased production is likely to be fueled by regenerated nutrients (Randelhoff et al., 2016). A direct consequence is a shift from larger to smaller phytoplankton cells (Li et al., 2009), which again will affect the composition of the grazers. The seasonal shift from new to regenerated production and the consequences for zooplankton life history adaptations has not received sufficient attention in Arctic regions.

We investigate seasonal differences in the zooplankton community and in the primary productivity regimes in the Atlantic water inflow area north of Svalbard. Also, we evaluate how a shift from “new” (nitrate based) spring bloom to a “regenerated” (ammonium based) post bloom situation is reflected in the diversity, life history adaptations and productivity of the major zooplankton. We approach this by investigating the composition of the total zooplankton community in the upper 100 m in May and August and by evaluating estimated production and ingestion rates of the main grazers in light of new and regenerated primary production in this area. By applying different zooplankton sampling tools that catches both the large (MultiNet) and small (Go-Flo water samplers) copepods, as well as microzooplankton (Niskin type water samplers), we present a more comprehensive picture of the zooplankton community in spring and summer, taking into account the role of zooplankters representing a wider spectrum of size fractions.

MATERIALS AND METHODS

Study Area and Hydrography

This study was conducted at six “process stations” (where the ship stayed at the station for 30 h to allow rate measurements), located in the Atlantic inflow area north of Svalbard in May (P1, P3, P4) and August (P5, P6, P7) in 2014 (Table 1 and Figure 1). In both study periods, the stations were located along the ice edge, and we aimed for sampling as far north and east as possible without breaking far into the fast ice (Figure 1). Due to adverse ice conditions, only stations P1 and P5 represent one spatial location sampled twice (P1 sampled in May and P5 in August), but in this study we focus more on seasonal than spatial differences. This dynamic area, following the continental slope north and west of Svalbard, is characterized by advection of warm, saline and nutrient-rich Atlantic Water (Randelhoff et al., 2016, 2018; Renner et al., 2018). The strong influx of warm Atlantic water makes this area relatively ice-free. The ice-extent during our study was variable, ranging from 0% at P5 to 90% at P6 in August (Figure 1) and the distribution of drift ice was strongly influenced by wind fields (Randelhoff et al., 2018).

Hydrographic properties of the water column were obtained with a CTD (conductivity, temperature, depth) sensor system (Seabird SBE-911 plus) mounted on a General Oceanics

rosette sampler, equipped with 8-L Niskin bottles and a Seapoint Fluorometer. Physical (temperature, salinity, density, photosynthetically available radiation, PAR) and biochemical properties (inorganic nutrients, fugacity of CO₂), of the water column were obtained for all stations, and are presented elsewhere (Randelhoff et al., 2018). In this paper, to characterize the environment, we present only the temperature within the upper 100 m of the water column where the bulk of the primary production processes take place. In May, stations P1, P3, and P4 were relatively similar with regard to temperature, with surface temperatures (0–10 m) between -1 and 1°C . Warm Atlantic water was found below 10 depth, with temperatures from 2.5 to 3.5°C (Figure 2). In August, the water at station P5 was warm, 6°C , and the water column was mixed within the 0–100 m. At station P6, a layer of cold water $<-1^{\circ}\text{C}$ was found in the upper 50 m, on top of warmer Atlantic water. At station P7, the cold layer was restricted to the upper 10 m (Figure 2).

Particulate Organic Carbon and Chlorophyll *a*

Water samples for particulate organic carbon (POC) and chlorophyll *a* (Chl *a*) were collected with Niskin water bottles from 1, 5, 10, 20, 30, 40, 50, 75, 100, and 200 m depth. Triplicate subsamples of 100–500 mL were filtered onto pre-combusted Whatman GF/F filters for POC, while triplicate subsamples of 5–300 mL were filtered onto Whatman GF/F filters for Chl *a* concentration measurements. The POC and Chl *a* filters were analyzed according to procedures described in Paulsen et al. (2018). For each station, we present the POC and Chl *a* concentration in the upper 100 m as integrated values (by trapezoid integration).

Primary Production

Primary production rates were measured using the ^{14}C method (Steemann Nielsen, 1952). Seawater was sampled at 1, 5, 10, 15, and 30 m to characterize the water mass both within and

TABLE 1 | Overview of process stations in May and August 2014, providing date sampled, latitude, and longitude at the arrival of the station and depth at the start (arrival) and end of the station.

Station	Date (mm/dd)	Lat ($^{\circ}\text{N}$)	Long ($^{\circ}\text{E}$)	Depth (m)
P1	05/18	79 58.05	010 44.30	340–450
P3	05/23	79 43.07	009 27.40	390–490
P4	05/25	79 46.32	006 16.71	1030–970
P5	08/09	79 58.15	010 44.65	340–270
P6	08/11	80 50.96	015 03.07	1290–1140
P7	08/13	80 42.25	015 14.84	1110–300

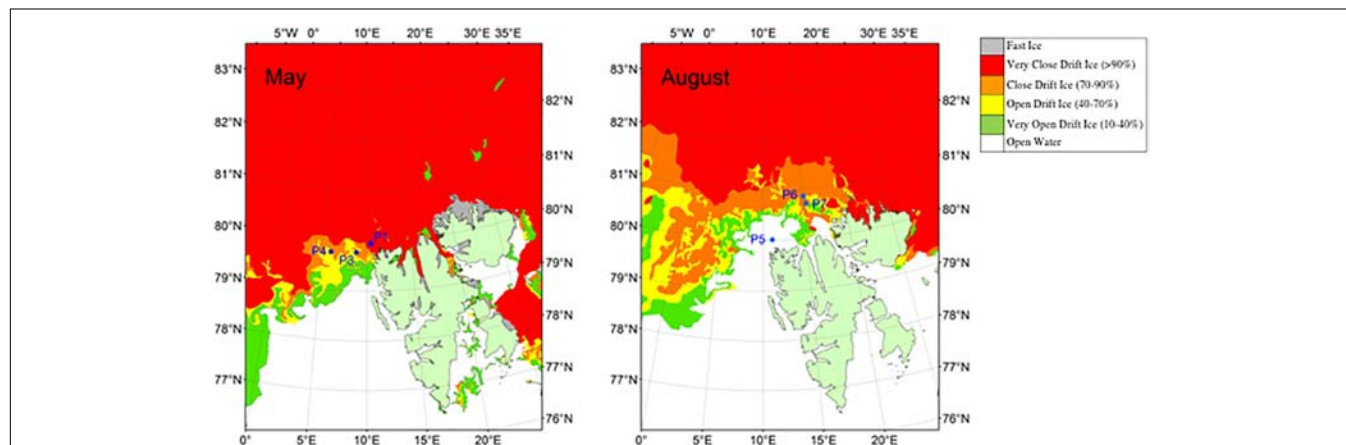
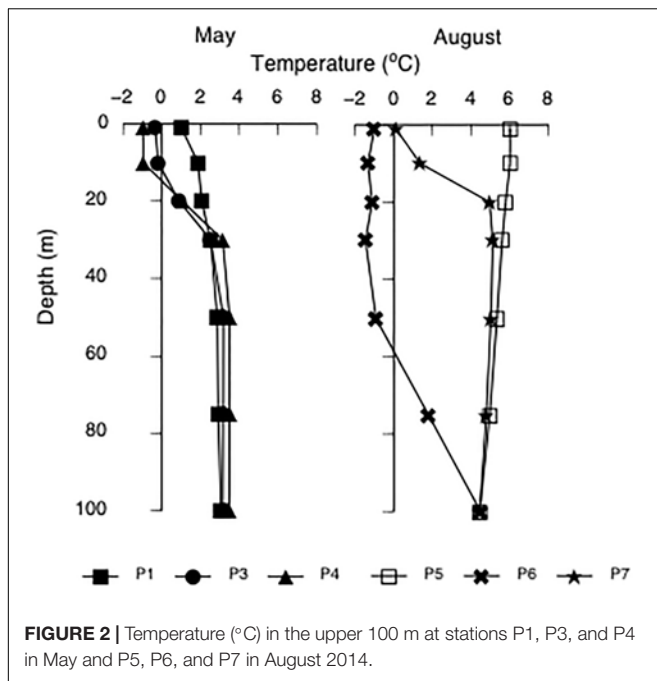


FIGURE 1 | Map of the Atlantic inflow area north of Svalbard, showing the ice extension and sampled stations in May and August. Maps were generated using GSHHG data from the National Oceanic and Atmospheric Administration (US) and ice data were provided by the Norwegian Ice Service (MET Norway) for the dates May 23, 2014 and August 12, 2014. The maps were modified from Wilson et al. (2017).



below the mixed layer (9–15 m) (Randelhoff et al., 2018). Samples were incubated *in situ* by deploying the experimental bottles attached to a line that was anchored to an ice floe. At each depth, two light bottles and one dark bottle were incubated for approximately 22 h. Ten μ Curies of ^{14}C -labelled bicarbonate was dispensed into each bottle, and a Time Zero bottle filtered immediately in order to account for adsorption processes. In addition, for each depth, a 100 μL aliquot was sampled into a 6 mL scintillation vial in order to estimate the initial ^{14}C -bicarbonate concentration by fixing ^{14}C with 0.1 mL 6N NaOH. After the incubation, 200 μL of 20% HCl was dispensed into each scintillation vial containing 2 mL of seawater in order to release any inorganic ^{14}C remaining in the sample. After 24 h, 5 mL of Ultima Gold (Perkin Elmer, United States) was added and the samples stored in the dark until ^{14}C activity was measured with a Perkin Elmer scintillation counter. Primary production was calculated as ^{14}C incorporation into the sample, measured in units of disintegrations per minute (Vernet et al., 1998). Dissolved inorganic carbon was measured in every sample, and 1.05 was used as the discrimination factor between incorporation of ^{14}C and ^{12}C . The ^{14}C incorporation in the light bottle was corrected by subtracting the ^{14}C incorporation in the dark bottle.

New and regenerated primary production was estimated by experimental determination of phytoplankton uptake of nitrate (NO_3^-) and ammonium (NH_4^+), respectively. The uptake measurements were conducted by incubation experiments during both cruises, as described in Randelhoff et al. (2016). From the uptake ratios of nitrate and ammonium, the f-ratio was calculated, defined as the fraction of nitrate (NO_3^-) uptake to the total N uptake ($\text{NO}_3^- + \text{NH}_4^+$). Hence, an f-ratio of 1 means that all the production can be considered as “new” (nitrate-based) while an f-ratio of 0 imply that all the production was “regenerated.”

Microzooplankton

In this study we use the term microzooplankton *sensu lato*, defined as grazers in 15–300 μm size, including phagotrophic ciliates, dinoflagellates, and sarcodines with or without functional chloroplasts. Thus, the functional role of microzooplankton in this study is associated with activity of protists. Microzooplankton were collected within the upper 100 m using 8L Niskin bottles. Samples were preserved in 2% (final concentration) acid Lugol's iodine, stored at 4°C and post-fixed with 1% formaldehyde (final concentration). Additional samples for determination of pigmented microzooplankton were preserved in 1% formaldehyde. In the laboratory, microzooplankton were settled onto Utermöhl chambers (50–100 mL) and enumerated by scanning the entire surface area of the chamber at 200 $\times$. Microzooplankton cells were sized with an eyepiece micrometer at 400–600 $\times$ and converted to carbon based on approximated geometric shapes and volume-carbon conversions (Putt and Stoecker, 1989; Menden-Deuer and Lessard, 2000). All ciliates were included in microzooplankton, whereas dinoflagellates <15 μm in maximum dimension were not. Additionally, microzooplankton cells were examined for chloroplasts in formaldehyde-preserved samples using differential interference contrast and chlorophyll autofluorescence and allocated into heterotrophs and mixotrophs (i.e., pigmented ciliates and dinoflagellates). For details on microzooplankton analysis see Lavrentyev et al. (2019).

Mesozooplankton Abundance and Biomass

Mesozooplankton were sampled at all six stations, with a special focus on the relative contribution of large and small copepods and nauplii. We define mesozooplankton as multicellular heterotrophic organisms, but in this study, we focus on the role of Copepoda. Hence, the fraction mesozooplankton here includes only members of this subclass, ranging from nauplii (lower size approx. 0.09 mm; first nauplii of *Microsetella norvegica*) to adult copepods (upper size 12.0 mm; adult females of *Paraeuchaeta barbata*). Within the group “large copepods,” species with an adult body size > 2 mm are included. This embraces *Calanus finmarchicus*, *C. glacialis*, and *C. hyperboreus*, with their developmental stages from CI to adult. Less common large copepods (mainly *Metridia* spp., *Pseudocalanus* spp., *Paraeuchaeta* spp.) were grouped as “other large.” The group termed “small copepods” includes only *Oithona* spp. (predominantly *Oithona similis*) and the remaining smaller taxa (e.g., *Triconia borealis*, *Microcalanus* spp., and *Microsetella norvegica*) were grouped as “other small.” Copepod nauplii were divided in two groups, calanoid copepod nauplii (predominantly *Calanus* spp.) and *Oithona* spp. nauplii.

To obtain robust data both on smaller and larger size-groups of mesozooplankton (here copepods), we used two different sampling approaches. Large copepods were collected with a MultiNet plankton sampler type Midi (Hydro-Bios, Germany, net aperture area 0.25 m^2), which was equipped with net bags with 180 μm mesh gauze, and was towed vertically

in the depth-intervals 0–20, 20–50, 50–100, 100–200 m and 200–bottom. The content of each cod-end was concentrated on a 180 μm meshed sieve and transferred to polycarbonate bottles. Small copepods and nauplii were collected with Go-Flo water bottles (General Oceanic, volume 30 L) at 1, 10, 20, 30, 50, and 100 m depth. The water samples collected with Go-Flo bottle were emptied with a silicon tube and the content collected on a 20 μm mesh sieve. All mesozooplankton samples were preserved with buffered formaldehyde at 4% final concentration.

The mesozooplankton samples, both collected with MultiNet and Go-Flo bottle, were identified and counted in the laboratory on land, using Olympus stereoscopic microscopes with 7–90 $\times$ magnification, and following standard sub-sampling procedure (Postel et al., 2000). Each sample was first scanned for macrozooplankton (organisms with total length > 0.5 cm), which were picked out, identified and counted in the entire sample. Mesozooplankton was identified and counted in subsamples (2 ml in volume), taken from the fixed sample volume (typically between 100 and 200 ml) using a macropipette (an equivalent of the Stempel pipette), and all organisms in each subsample were identified and counted. The number of subsamples was determined individually to count at least 500 individuals per sample. However, in this paper we focus on the copepods, which were the dominating (in terms of abundance and biomass), component of the mesozooplankton fraction. Representatives of *Calanus* were identified to the species level based on the description given in Kwasniewski et al. (2003). We are aware that distinguishing the species *C. finmarchicus*, *C. glacialis*, and *C. hyperboreus* based on morphology is associated with some uncertainty because prosome lengths of the three species can be overlapping (Choquet et al., 2018).

Copepod contribution to the plankton community was expressed in terms of carbon (biomass), by converting prosome lengths, using individual dry mass data and carbon to dry mass relationships from the literature (Supplementary Table 1).

RESULTS

Primary Production and Productivity Regimes

In May, the integrated (0–50 m) total particulate primary production was generally high, ranging from 0.34 $\text{g C m}^{-2} \text{d}^{-1}$ at P4 to 0.85 $\text{g C m}^{-2} \text{d}^{-1}$ at P1 (Figure 3). In August, the total primary production ranged from 0.19 $\text{g C m}^{-2} \text{d}^{-1}$ at P5 to 0.70 $\text{g C m}^{-2} \text{d}^{-1}$ at P7 (Figure 3). The *f*-ratio, i.e., the fraction of “new” to total (new + regenerated) primary production, ranged from 0.6 to 0.9 in May and was below 0.007 at all stations in August (Figure 3). Hence, the primary production in May was dominated by “new production,” while in August the primary production was predominantly “regenerated.”

The 0–100 m integrated biomass of POC in May was 12, 23, and 17 g C m^{-2} at P1, P3, and P4, respectively (Figure 4). In August it ranged from 8 to 10 g C m^{-2} , and was hence less variable between stations. The ratio of POC to chlorophyll *a*

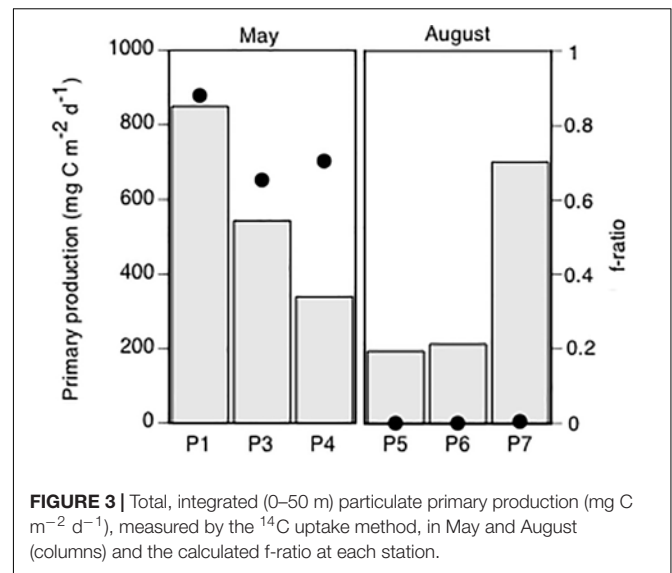


FIGURE 3 | Total, integrated (0–50 m) particulate primary production ($\text{mg C m}^{-2} \text{d}^{-1}$), measured by the ^{14}C uptake method, in May and August (columns) and the calculated *f*-ratio at each station.

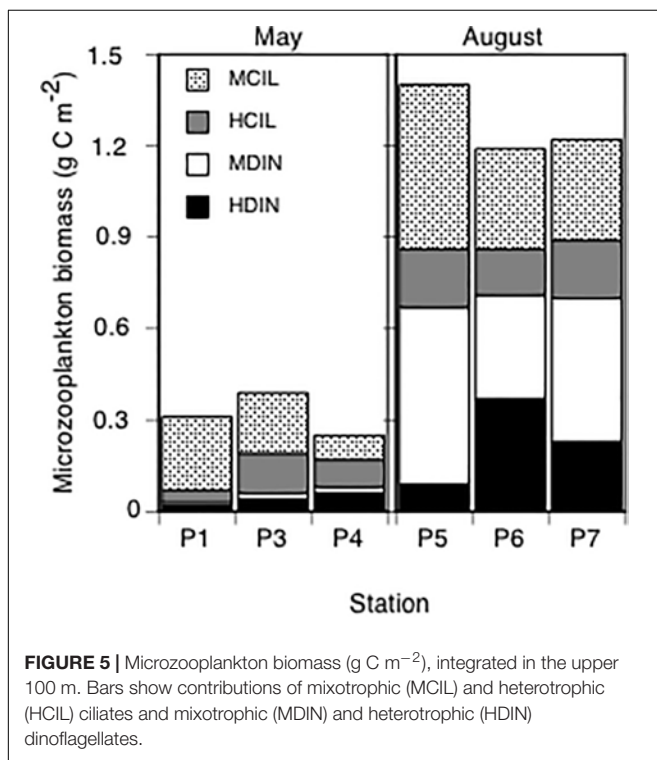
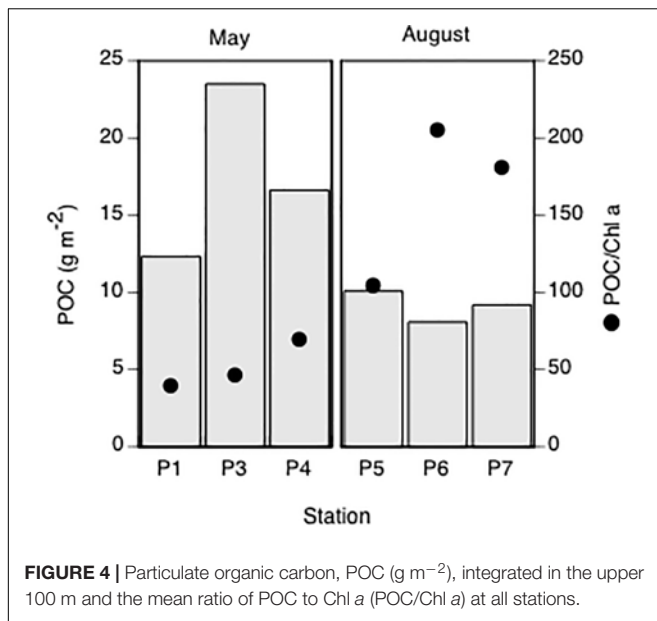
(Chl *a*) increased from 40–70 in May to 100–200 in August (Figure 4), pointing to a more autotrophic community in May than in August.

Microzooplankton Biomass

The integrated (0–100 m) total microzooplankton biomass ranged from 0.25 to 0.39 g C m^{-2} in May. Ciliates, considering both heterotrophic and mixotrophic taxa, represented between 90 and 66% of the total microzooplankton biomass at P1 and P4, respectively (Figure 5). In August, the integrated biomass was significantly higher at all stations (1.2–1.4 g C m^{-2}) and reached the highest value at P5 (Figure 5). Ciliates and dinoflagellates contributed equally to the total microzooplankton biomass representing on average 45 and 55%, respectively. Mixotrophic taxa, including both ciliates and dinoflagellates, contributed between 55 and 82% to the total microzooplankton biomass both seasons. P4 (sampled in May) was the only station where the heterotrophic taxa were dominant (59%). For detailed information on microzooplankton community composition, see Lavrentyev et al. (2019).

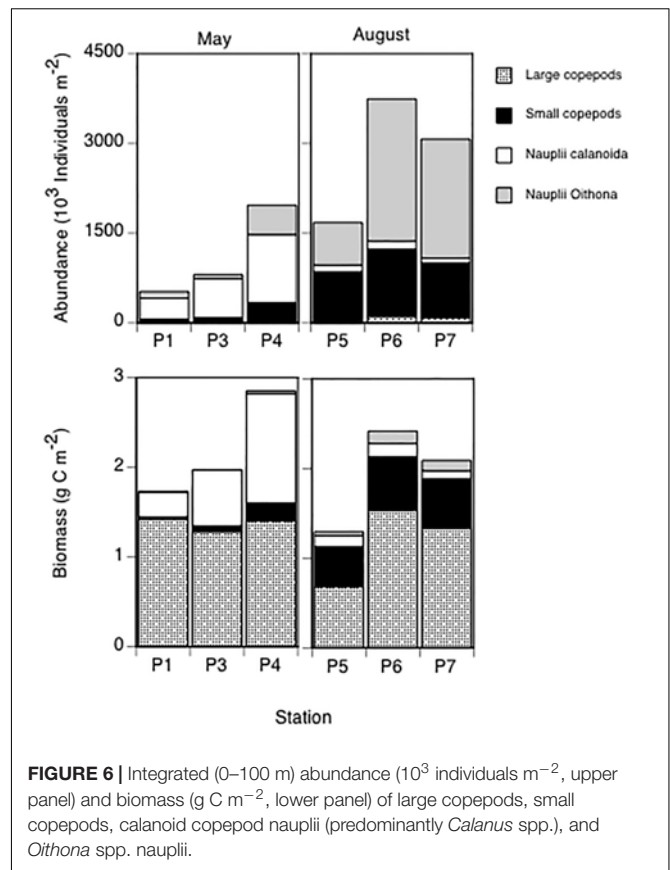
Mesozooplankton (Copepod) Abundance and Biomass

Numerically, the mesozooplankton copepod community in May was dominated by calanoid copepod nauplii (predominantly *Calanus* spp.; Figure 6). In contrast, in August small copepods and *Oithona* spp. nauplii prevailed (Figure 6). The highest total abundances of copepods and nauplii were found at station P6, with almost $4\,000 \times 10^3$ individuals m^{-2} in the 0–100 m depth interval. Compared to the other groups, the abundance of large copepods was negligible in May and August (Figure 6). However, in terms of biomass, the large copepods were important, especially in May. The integrated biomass of the large copepods, small copepods and nauplii ranged from 1.7 to 2.8 g C m^{-2} in May and from 1.3 to 2.4 g C m^{-2} in August (Figure 6). Although the biomass contribution of the



large copepods was overall substantial, calanoid nauplii and small copepods also contributed considerably to the total copepod biomass in May and August, respectively (Figure 6).

In terms of species composition, the large copepods were numerically dominated by *C. finmarchicus* both in May and August (Figure 7). In May, the biomass of *C. hyperboreus* was substantial, but in August *C. finmarchicus* made up the largest fraction of the biomass of the large copepods (Figure 7). At all six



stations, the small copepods were dominated by *O. similis*, both in terms of abundance and biomass (Figure 7).

Vertical Distribution of *Calanus* spp.

The majority of the population of all three *Calanus* species stayed in the upper 100 m in May (Table 2). In August, the majority of the *C. finmarchicus* and *C. glacialis* older copepodids (CV and females) were situated below 100 m, while the young stages CI–CIV were still mostly inhabiting the upper water layers. Except for some CV copepodids in the surface at station P5, the whole population of *C. hyperboreus* was found below 100 m in August (Table 2).

Stage Composition of Dominating Large and Small Copepods

In May, all stages (except males) of *C. finmarchicus* were present, although in low abundances. In August, the population consisted mostly of young stages CI–CIII, and it had increased in abundance nearly four times (except for station P5, Figure 8). The population of *C. glacialis*, which was in general four times less numerous than the population of *C. finmarchicus*, was completely dominated by younger stages CI–CIII in May, with a few females also present. By August, the population was dominated by older developmental stages CIV–CV, and its abundance decreased pronouncedly (Figure 8).

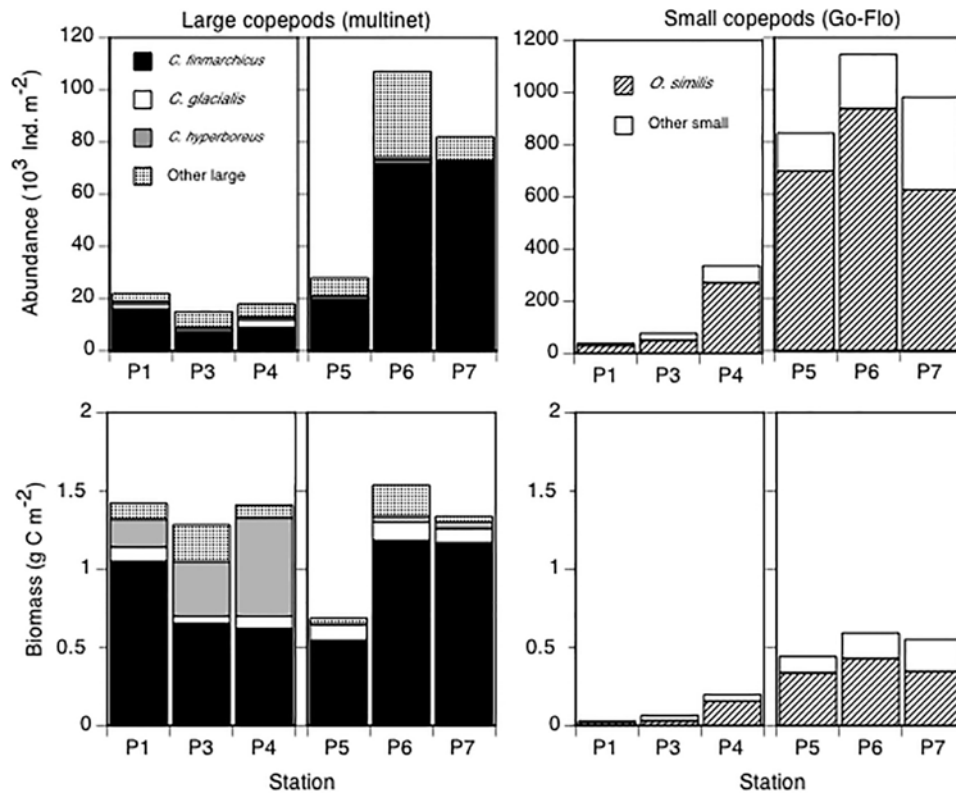


FIGURE 7 | Integrated (0–100 m) abundance (10^3 ind m^{-2} , upper panel) and biomass ($g\ C\ m^{-2}$, lower panel) of large copepods (dominated by *C. finmarchicus*, *C. glacialis*, *C. hyperboreus*) and small copepods (dominated by *O. similis*). The group “other large” consisted mainly of *Pseudocalanus* spp., and the group “other small” consisted mainly of *Triconia borealis*. Note different scales on the y-axes.

Oithona similis was overall the numerically dominating copepod species. In May, the population was dominated by females, although all other copepodid stages were also found. In August, the population size had increased substantially. The younger stages CI–CIII contributed the most, but copepodids CIV, CV and females made up nearly the other half of the population (Figure 8).

The total abundance of copepod nauplii was exceptionally high both in May (500 000–1 500 000 nauplii m^{-2}) and in August (800–2 500 000 nauplii m^{-2}) in the 0–100 m water column. However, in May there was a complete dominance of calanoid copepod nauplii (mostly of *Calanus* spp.), while in August there were few calanoid nauplii and the nauplii stock was totally dominated by *Oithona* spp. nauplii (Figure 8).

DISCUSSION

Productivity Regimes in Spring and Summer

In the Atlantic water inflow area north of Svalbard, the plankton community displayed a strong seasonality during the two investigated periods. Although the mean particulate primary production (as measured by ^{14}C uptake) was high both in May ($578 \pm 257\ mg\ C\ m^{-2}\ d^{-1}$) and in August ($370 \pm 288\ mg\ C$

$m^{-2}\ d^{-1}$), the associated plankton communities were different. In May, we observed an intensive ice-edge spring bloom based on nitrate and with high f-ratio (0.7–0.9) and the dominance of *Phaeocystis pouchetii* and large diatoms (Randelhoff et al., 2016). However, the stations were at different stages of the bloom succession: growing bloom (P1), peak bloom (P3) and decaying bloom (P4) (Paulsen et al., 2018). In August, a post bloom situation was seen at all stations (P5, P6, P7), with low f-ratios (0.001–0.007) and a phytoplankton community dominated by small flagellates. Hence, the two sources of N (nitrate and ammonia) were associated with different microbial communities, which represent different food quality for the grazers. The different pools of N have also different sources and rates of productivity and turnover. While nitrate must be added to surface water through external processes such as upwelling or turbulent diffusion across the pycnocline, ammonia is entering the system through internal biological processes such as regeneration by heterotrophic bacteria, and release by zooplankton (Kristiansen et al., 1994; Legendre and Rassoulzadegan, 1995; Shilova et al., 2017). In a study conducted simultaneously with the present one, Randelhoff et al. (2016) examined seasonal vertical nitrate fluxes in relation to upper ocean stratification at the process stations P1–P7. The authors highlight the importance of turbulent diffusion across the pycnocline as the main pathway for nutrient supply

TABLE 2 | Fraction (%) of the total population present in the upper 100 m depth.

Species	Stage	P1	P3	P4	P5	P6	P7
<i>C. finmarchicus</i>	AM	93	52	84	–	–	–
	AF	98	96	98	62	44	0
	CV	98	92	82	19	23	27
	CIV	98	99	89	41	76	75
	CIII	100	100	100	81	95	98
	CII	98	100	98	99	100	98
	CI	98	100	98	98	99	99
<i>C. glacialis</i>	AM	–	–	–	–	–	–
	AF	100	100	100	60	0	–
	CV	100	100*	77	25	38	51
	CIV	100	–	100	100	23	50
	CIII	–	–	100	–	0	–
	CII	96	100*	100	100	–	–
	CI	97	100	99	–	–	100
<i>C. hyperboreus</i>	AM	–	–	–	–	–	–
	AF	100	74	89	–	0	0
	CV	95	91	85*	100	3	13*
	CIV	100	93	76	0	49	84*
	CIII	–	–	100*	0	31	0
	CII	100	100*	100	–	–	–
	CI	100	100	99	–	–	–

Developmental stage not present is denoted “–” and “0” indicates that all individuals were located below 100 m. Asterisks indicate that the calculations are based on low abundances ($<50 \text{ ind m}^{-2}$).

to a post bloom ocean surface. For our study area, the authors found that upwelling in this area is not very likely during summer, and the upward turbulent nitrate fluxes across the seasonal nitracline are small (Randelhoff et al., 2016). This supports our finding that the relatively high carbon production occurring during post bloom in August was based on regenerated nutrients.

The nutrient dynamics and uptake rates, along with the phytoplankton community composition and primary production rates, both suggest that the grazer communities had to face a strong seasonal shift in their food stock. In the following, we discuss how the seasonal shift at the base of the food web from new production in spring to a post bloom, regenerated production, affect the seasonal patterns of the major grazers. The focus on the dominant copepod species and microzooplankton in the upper 100 m allowed us to link productivity patterns with the active (non-hibernating) part of the planktonic populations.

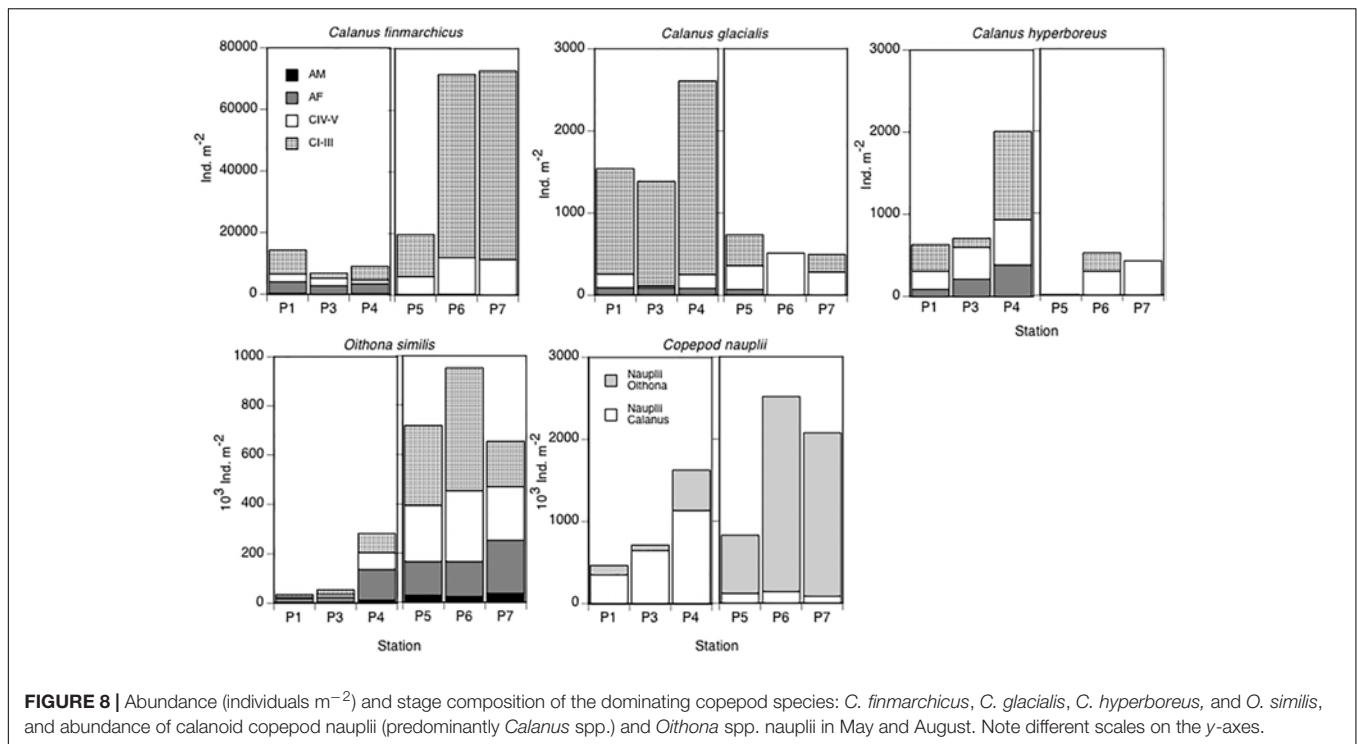
Spring and Summer Grazer Populations

The large copepod species *C. finmarchicus* and *C. hyperboreus* dominated the biomass of the grazer community in May, whereas the copepod nauplii stock, both in terms of abundance (up to $1100 \times 10^3 \text{ ind m}^{-2}$) and biomass (up to 1.2 g C m^{-2}) was represented by calanoid copepod nauplii. On average, the contribution of calanoid copepod nauplii to the total copepod community (sum of the small and large copepods and nauplii) in May was 69% in terms of abundance and 30% in terms of biomass. The exceptionally high nauplii

abundance indicates high reproductive success of *Calanus* in May. In August, on the other hand, the stock of the three *Calanus* species displayed notably different structures, with *C. finmarchicus* predominating in abundance as well as in biomass. This likely reflects different reproductive strategies between the three *Calanus* species, which is also thoroughly documented in previous studies from adjacent areas (Arnkjær et al., 2005; Søreide et al., 2010).

The dominance of *C. glacialis* and *C. hyperboreus* young copepodids CI–CIII in spring indicates that the main reproductive period for these species happened before our investigation, and hence prior to the onset of the spring bloom. By reproducing prior to the (open water) spring bloom, the new cohorts are ready to feed and grow during the short and intensive pelagic bloom, and have a chance to reach the overwintering stage later during the growth period. This reproductive strategy is referred to as capital breeding and is an adaptation to strong seasonality (Varpe et al., 2009). In addition, because the developmental time and survival of *C. glacialis* nauplii are sensitive to food quality, the chances to survive are higher when feeding on algae with high proportions of PUFAs (Daase et al., 2011). Due to efficient lipid synthesis and storage, both species can overwinter relatively young; *C. glacialis* mainly as CIII–CIV (Madsen et al., 2001; Søreide et al., 2010) and *C. hyperboreus* already as CIII (Kvile et al., 2018). The early egg laying, and the accessibility to high-quality and lipid-rich phytoplankton such as diatoms for the developing nauplii and young copepodids, allows these species to reach the overwintering stage within the first year. However, they may use two or more years to reach the reproductive stage (Diel, 1991). We suggest that *C. glacialis* and *C. hyperboreus* populations in the Atlantic inflow areas north of Spitsbergen depend to a large extent on the new production (nitrate-fueled) for the recruiting generation to reach the first overwintering stage. This is also in agreement with previous investigations of *Calanus* spp. feeding preferences (Levensen et al., 2000b; Søreide et al., 2008).

Calanus finmarchicus abundance and biomass were higher in August than in May, in contrast to what was observed for *C. glacialis* and *C. hyperboreus*. The *C. finmarchicus* population found during this study in August was still largely composed of younger stages CI–CIII, with only a few older stage CIV–CV (Figure 8). For the younger developmental stages CI–CIII to continue development and reach the overwintering stages CIV–CV, *C. finmarchicus* needs access to a stable food source, also after the short spring bloom period. In our study, this condition was met by a high rate of regenerated production, and possibly also the large availability of heterotrophic and mixotrophic microzooplankton in August. Madsen et al. (2001) made similar observations, showing that nauplii and protists may form a substantial part of the diet of the *Calanus* community in the post bloom period in Disco Bay, western Greenland. Our findings support the existing knowledge on the reproductive strategy of *C. finmarchicus*. This species is defined as an income breeder (Varpe et al., 2009), whose females need to feed on the open water spring bloom to produce eggs. The new cohorts develops from egg to young copepodid during



the spring bloom (Arnkjær et al., 2005). However, we stress that the new production is important during the early phase of the life cycle (fueling egg production in the females, and the development from eggs to CIII copepodids) whereas the regenerated production appears essential for *C. finmarchicus* to reach the hibernating stage (CIV–CV) within the same growth year in our study area.

Among the small copepods, *O. similis* was the most abundant species both in spring and summer, but the population size was significantly larger in August than in May. Nauplii of *Oithona* spp. were found at all stations and occurred in extreme abundances in August (exceeding 2000×10^3 ind m^{-2} at P6). The high contribution of copepod nauplii to the total copepod community at all stations was notable, and the clear shift from dominance of *Calanus* spp. nauplii in May to *Oithona* spp. nauplii in August reflects differences in reproductive strategies between the two copepod genera. The life history strategy of the cyclopoid copepod *O. similis* is in strong contrast to the strategy of calanoid copepod *Calanus* spp. (Svensen et al., 2011). *O. similis* does not overwinter at great depths and it can reproduce year-round, except in mid-winter (Madsen et al., 2001, 2008). At high latitudes, main reproductive periods are suggested to occur in May and September (Lischka and Hagen, 2005; Madsen et al., 2008; Narcy et al., 2009). *O. similis* is a strict ambush feeder with a preference for ciliates and dinoflagellates (Svensen and Kiørboe, 2000). Analyses of fatty acid of *O. similis* in the Arctic Kongsfjorden (Svalbard) demonstrated high abundance of the 18:1 ($n - 9$) fatty acid in all stages and seasons, which indicates an omnivorous diet that does not change notably with season (Lischka and Hagen, 2007). Since it is not directly dependent on the spring bloom to

reproduce or to complete its life cycle, *O. similis* can instead take advantage of the post bloom regenerated production in summer to support its mass reproduction and successful population growth. In turn, through sloppy feeding, *Oithona* can release dissolved organic carbon (Svensen and Vernet, 2016) fueling the microbial loop, bacterial growth and eventually a buildup of the microzooplankton.

The biomass of microzooplankton was more than three times higher in August than in May. This could reflect both better feeding conditions and decreased copepod predation in August compared to May. In August, the predominance of nanophytoplankton and the increase in *Synechococcus* abundance (Paulsen et al., 2016) could have supported the higher and more diverse microzooplankton biomass (Lavrentyev et al., 2019). In fact, although low temperature can affect microzooplankton physiology, when adapted to cold environment, Arctic microzooplankton can grow (Franzè and Lavrentyev, 2014, 2017; Menden-Deuer et al., 2018) and graze phytoplankton (Franzè and Lavrentyev, 2017; Lavrentyev et al., 2019) at rates comparable to their temperate counterparts. Microzooplankton can respond quickly to changes in primary production by increasing their biomass (Levinson et al., 2000a) and ingestion rates (Calbet, 2001). At the same time, microzooplankton are preferred prey of copepods (Campbell et al., 2009), and their biomass can be suppressed by copepod grazers. In our study, the older developmental stages of *C. finmarchicus* and *C. glacialis* were located mostly below 100 m in August, and this may have reduced the grazing pressure on the microzooplankton, which were distributed above 100 m. A comparable scenario has also been reported in other Arctic areas in summer (Levinson et al., 1999, 2000b).

TABLE 3 | Daily production to biomass (P/B) ratios (literature values), integrated biomass (mg C m⁻², seasonal mean ± SD), and estimated production and ingestion rates (mg C m⁻² d⁻¹) for microzooplankton and the dominating copepod species in the upper 100 m.

	P/B	Biomass		Production		Ingestion	
		May	August	May	August	May	August
Microzooplankton	0.23 ¹	304 ± 61	1032 ± 50	70 ± 14	237 ± 23	233 ± 47	791 ± 77
<i>O. similis</i>	0.08 ²	66 ± 77	369 ± 50	5 ± 6	30 ± 4	18 ± 20	99 ± 13
<i>C. finmarchicus</i>	0.01 ³	773 ± 239	965 ± 363	8 ± 2	10 ± 4	46 ± 14	58 ± 22
<i>C. glacialis</i>	0.01 ³	73 ± 23	103 ± 14	1 ± 0.2	1 ± 0.1	2 ± 1	1 ± 1
<i>C. hyperboreus</i>	0.008 ²	385 ± 228	26 ± 21	1 ± 3	0.2 ± 0.2	10 ± 6	1 ± 0.6

Ingestion rates (mg C m⁻² d⁻¹) were calculated assuming a production/ingestion ratio of 30% (Omori and Ikeda, 1984; Straile, 1997). ¹Lavrentyev et al. (2019). ²Tremblay and Roff (1983). ³Diel and Tande (1992).

Estimated Production and Ingestion Rates of Dominating Copepods and the Microzooplankton

The biomass of microzooplankton and *O. similis* increased significantly from May to August (Table 3). While the biomass of *C. hyperboreus* decreased from May to August, the total biomass of *C. finmarchicus* and *C. glacialis* was relatively similar in the two sampling periods (Table 3). How well were the different grazer groups supported by the new and regenerated autotrophic production during the two seasons? We calculated production rates of the microzooplankton and the dominating copepod species (*C. finmarchicus*, *C. glacialis*, *C. hyperboreus*, and *O. similis*) in the upper 100 m, based on published production/biomass (P/B) ratios (Table 3) and ingestion rates by assuming a gross growth efficiency of 30% (Omori and Ikeda, 1984; Straile, 1997). These estimations, although somewhat crude, provide the possibility to evaluate the energy demand of the zooplankton communities in relation to spring and summer productivity state.

The estimated production rates in May were high for the microzooplankton community (70 ± 14 mg C m⁻² d⁻¹), and generally low for the dominating copepod species (Table 3). Furthermore, the estimated ingestion rates in May were well below the measured total primary production rate (Table 4) and did not exceed the total estimated new production for this time (Table 4). Hence, based on these rough calculations, we can assume that both the microzooplankton and the *Calanus* spp. populations were sufficiently supported by the new primary production resulting from the activity of the dominating phytoplankton community

in May. Similar findings are available from a study in Disko Bay (Greenland), where during the early phase of the bloom, *C. finmarchicus* were predominantly herbivorous with a very small contribution of microzooplankton to their diet (Levinsen et al., 2000b).

In August, the total zooplankton production was dominated by microzooplankton (237 ± 47 mg C m⁻² d⁻¹) and *O. similis* (30 ± 4 mg C m⁻² d⁻¹), followed by *C. finmarchicus* (10 ± 4 mg C m⁻² d⁻¹) (Table 3). The estimated ingestion rates of this grazer community was 948 mg C m⁻² d⁻¹ (Table 3) and exceeded the measured total primary production in August (Table 4). The apparent discrepancy between the total primary production and the estimated ingestion rates of the main zooplankton could indicate that there were additional food sources than autotrophic phytoplankton available during the post bloom period. Paulsen et al. (2018) found that dissolved organic nitrate (DON) accumulated during summer, resulting from microbial activity. The bacteria biomass and production rates at the investigated stations were also higher in August than in May (Paulsen et al., 2018). The bacteria were likely grazed by picophytoplankton and heterotrophic flagellates (Paulsen et al., 2018), which are important food sources for microzooplankton (Franzè and Lavrentyev, 2017). This could explain the high standing stock of microzooplankton found in August. Consequently, the carbon-demands of *O. similis*, *C. finmarchicus* and other copepods present were probably met through a diet consisting mainly of microzooplankton during this time, pointing to the importance of the post bloom microbial food webs in this season and area. A similar structure of the grazer food chain in summer has also been reported in other Arctic ecosystems (Levinsen et al., 2000b).

TABLE 4 | Total (monthly mean ± SD) particulate primary production (PP, mg C m⁻² d⁻¹) based on integrated values 0–50 m depth and f-ratio (at the depth of highest PP).

Primary production	Mean May	Mean August
PP total	578 ± 257	370 ± 288
f-ratio	0.7 ± 0.1	0.003 ± 0.003
PP new	448 ± 268	2 ± 3
PP regenerated	130 ± 51	368 ± 286

New PP and regenerated PP were calculated from the f-ratio.

Synthesis and Outlook

The Arctic is undoubtedly changing. A main driver of these changes is the rapid loss of sea ice, causing a longer productive period and increased primary production due to increased light penetration in open versus ice covered water (Arrigo and Van Dijken, 2015). However, there is little knowledge on the changes in nutrient dynamics in the future Arctic scenarios, making it difficult to foresee if the increased production will be “new” or “regenerated.” Our study was limited geographically to the

Atlantic inflow area north of Svalbard, representing a region of the Arctic that is seasonally ice covered and strongly influenced by Atlantic water masses. Historically, few studies have focused on the food web implications of new and regenerated production in this area. Our investigation may not be extrapolated to all parts of the Arctic, since the different Arctic regions are very heterogeneous with respect to nutrient dynamics over the productive season. However, the scenario encountered in our study is still relevant for large parts of seasonally ice covered areas in the Arctic.

For an increase in new production, nitrate must be added to the productive surface waters from deep water reservoirs through processes such as upwelling and diffusion across the pycnocline (Randelhoff et al., 2016; Randelhoff and Sundfjord, 2018). In the investigated area north of Svalbard, a summer upwelling event has been considered rather unlikely (Randelhoff and Sundfjord, 2018), and an oligotrophic post bloom situation may be the governing situation after the spring bloom decline. In oligotrophic areas, regenerated production supported by recycled N accounts for 90% of the gross primary production (Eppley and Peterson, 1979). It therefore appears reasonable to assume that a large fraction of the increased primary production in this part of the Arctic in summer will be based on recycled N (or e.g., dissolved organic carbon). This is in accordance with Randelhoff et al. (2015), who found that the summer primary production was nutrient limited, and concluded that the potential for an increase in new production in a scenario with less sea ice is limited in the area north-east of Svalbard.

The question is, if the magnitude of the new production remains the same due to nitrate limitation (provided the net influx of nitrate will not change), who will benefit from an increased regenerated production in a future Arctic characterized by decreased seasonal ice cover and an increased productive season? A short growth season favors large bodied capital breeders because the adults have large storage capacity for lipids that increases their fecundity, and the new generation appearing prior to the bloom can utilize the pulsed production (Varpe et al., 2009; Sainmont et al., 2014). We argue that an extension of the growth season by a prolonged period of regenerated production may favor small bodied copepods with short generation times, low lipid storage capacity, low metabolic rates and low fecundity. The regenerated production can be sustained on reduced form of inorganic N (such as ammonium), but also on dissolved organic carbon (DOC) and nitrogen (DON) (Paulsen et al., 2018). We argue that an active microbial food web, fueled by DOC and DON, may support a large heterotrophic community and high secondary production after the sources of inorganic N have been used up.

Our study confirms the dependence and tight coupling between the early spring bloom and life history adaptations (large lipid storage capacity, early start of diapause) of *C. glacialis* and *C. hyperboreus*. Although the remaining surface-active populations of *C. glacialis* and *C. hyperboreus* graze the microzooplankton in summer (Levinsen et al., 2000b), it seems that it is the diatom-dominated spring bloom that is the

most important food source for the new cohort to reach the overwintering stage (Søreide et al., 2008). In contrast, the younger fraction of the *C. finmarchicus* population may remain in the surface waters for a longer time (Hansen et al., 1999) and may use the post bloom regenerated production and microbial food web to reach the overwintering stage within one growth season. This indicates that *C. finmarchicus* may be able to profit from an increased primary production in the Arctic, even if the primary production is based on regenerated nutrients. This practice could support a northward extension of this species' habitat range. This is also a likely strategy for dominating small copepod species such as *O. similis*, that could most likely fulfill its full life cycle on regenerated production only. We suggest that the degree of coupling to the regenerated production and microbial food web may be of crucial importance for the success of the heterotrophic planktonic grazers in the future Arctic Ocean.

AUTHOR CONTRIBUTIONS

CS analyzed the data and wrote the manuscript. CS and EH sampled the zooplankton. MV conducted the primary production measurements. GF and PL collected and analyzed the microzooplankton samples. KD and SK were responsible for analyzing the mesozooplankton samples. All authors contributed to the interpretation of data and commented on the text.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: <https://www.frontiersin.org/articles/10.3389/fmars.2019.00293/full#supplementary-material>

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Advection of Mesozooplankton Into the Northern Svalbard Shelf Region

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The northern Svalbard shelf region is part of the Atlantic advective contiguous domain along which nutrients, phyto- and mesozooplankton are advected with Atlantic Water from the Norwegian Sea along the Norwegian shelf break and into the Arctic Ocean. By applying the SINMOD model, we investigated how much mesozooplankton may be advected into the northern Svalbard shelf region. We also compared this supply with the local mesozooplankton production. To achieve this, we selected a box north of Svalbard and calculated the in- and outflux of Atlantic *Calanus finmarchicus* and Arctic *Calanus glacialis*. The average biomass inside the box ranged between 0.5 and 3.0 g C month⁻² in March and August, respectively. Annually, 18.8 g C month⁻² of advected (and locally produced) mesozooplankton would be available for predators inside the box before it is advected out. The advection of mesozooplankton reached 12 times more than the average biomass within the box. The model projects significance variability in mesozooplankton advection which may be explained by the hitherto non-quantified recirculation in the northern Fram Strait and differences in the geographic origin of the mesozooplankton source population. The results imply that grazing upon mesozooplankton in the Atlantic advective contiguous domain north of Svalbard is greatly advantageous for pelagic predators. It could represent an important food source for fish, birds, and whales. It is suggested that mesozooplankton encountered on the shelf north of Svalbard may derive from populations along the North Norwegian shelf break, in some years as far south as the Lofoten/Vesterålen region. This illustrates the extent and significance of the Atlantic advective contiguous domain for the European shelf of the Arctic Ocean which apparently depends on significant food supply through expatriates. Primary production on the shelf is lower than C consumption and thus the European shelf of the AO is presumably net-heterotrophic.

Keywords: Arctic Ocean, zooplankton, *Calanus finmarchicus*, advection, contiguous domains, harvestable production

INTRODUCTION

The North Atlantic Current transports large amounts of phytoplankton and nutrients along the slope off and on the Northern-Norwegian shelf. For the connection between subarctic regions and the Arctic Ocean (AO), the transport of long-lived mesozooplankton from the eastern realms of the Norwegian Sea northward is of particular interest (Wassmann et al., 2015). For the most part, the mesozooplankton biomass is comprised by the copepod *Calanus finmarchicus*

(Tande, 1991; Slagstad et al., 1999) and modeled estimates suggest that about 1.5 million t C year⁻¹ of *C. finmarchicus* leave the shelf off northern Norway. One branch enters the southern and central Barents Sea while the main flux is directed along the eastern Fram Strait and the slope and shelf of western Svalbard (Gluchowska et al., 2017; **Figure 1**). North of Svalbard, Atlantic Water and its mesozooplankton biomass is diverted into two branches (Basedow et al., 2018). One transports mesozooplankton biomass toward the western Fram Strait, Greenland, and partly back toward the Norwegian Sea. The other branch moves mesozooplankton biomass eastward along the shelf of northern Svalbard (Basedow et al., 2018) and along the central AO slope toward the Lomonosov Ridge (Hirche and Kosobokova, 2007; **Figure 1**). The transport is part of the Atlantic contiguous advective domain (Wassmann et al., 2015; Hunt et al., 2016) that connects the boreal zone off the Lofoten/Vesterålen region with the European Arctic Corridor (northeastern Greenland to the Eastern Kara Sea), comprising the hydrographically most active sector of the central AO (Rudels et al., 2004; Polyakov et al., 2017). The Atlantic contiguous advective domain is joined by the Arctic contiguous advective domain east of Franz Josefs Land (transporting *C. glacialis* from the northern Barents Sea) and from there, both domains carry on in concert toward the origin of the Lomonosov Ridge (**Figure 2**).

However, because this transport has not yet been adequately quantified based on observational data (but see Basedow et al., 2018), mesozooplankton contribution to the AO is poorly defined (Wassmann et al., 2015), and future changes in Arctic zooplankton communities are difficult to appraise, let alone to observe and project. We applied the coupled physical-chemical-biological -models system SINMOD (Slagstad and McClimans, 2005; Wassmann et al., 2006) to investigate the transport of the Atlantic *C. finmarchicus* toward and along the northern shelf of Svalbard (Slagstad et al., 2011, 2015). In addition, we investigated the transport of the Arctic copepod *C. glacialis* that dominates in the arctic waters east of the Svalbard Archipelago. *C. glacialis* is transported along the Svalbard shelf by cold water masses through the Svalbard Coastal Current toward northern Svalbard (**Figure 2**). We ask (a) how much mesozooplankton biomass is transported along the Northern Svalbard region, (b) to what extent this advective transport is connected to the Norwegian shelf, and (c) what are the consequences of advection of mesozooplankton for planktonic composition at the edge of the AO (Nansen Basin).

MATERIALS AND METHODS

The model (SINMOD) applied in this work is a coupled hydrodynamic and ecological model system with a particle tracking module that takes current velocities from the hydrodynamic model. A comprehensive description of the physical and ecosystem and food web model is found in Slagstad and McClimans (2005) and Wassmann et al. (2006). A short description, including recent deviations, is given here, but more information can be found in references given. The hydrodynamic

model is based on the primitive Navier–Stokes equations and is established on a z-grid (Slagstad and McClimans, 2005; Slagstad et al., 2015).

The model structure was created for the Barents Sea ecosystem. State variables include nitrate, ammonium, silicate, diatoms, autotrophic, flagellates, bacteria, heterotrophic nanoflagellates, microzooplankton and two mesozooplankters: the Atlantic *Calanus finmarchicus* and the arctic *C. glacialis*. Parameter values were set for modeling the carbon flux in this region. SINMOD calculates Gross Primary Production (GPP), new production (NP), the f ratio (NP/GPP), and secondary production of two key mesozooplankton species. The secondary production is calculated from grazed phytoplankton, minus egestion, and respiration losses. For details of the biological model, see Wassmann et al. (2006). The model contains additional compartments for sinking detritus (fast and slow), dissolved organic carbon and the sediment. The model uses constant stoichiometry [C:N ratio equal 7.6 was used, average data from the Barents Sea (Reigstad et al., 2002)].

The particle tracking module advect particles using a Runge–Kutta 4th order computational scheme. Most of the Atlantic Water deeper than 500 m in the model domain (e.g., Norwegian Sea) was populated with particles. Advection of the particles started April 1st each year. These state variables are calculated as a product of water flux and concentration through the selected boundaries. The time step was 1800 s.

The model set-up encompassed the Nordic Seas (located north of Iceland and south of Svalbard), the central AO and the Eurasian shelf (see Slagstad et al., 2015) and uses a horizontal grid point distance of 20 km. The model has 25 vertical levels. The vertical level thickness increases from 5 to 10 m near the surface to 500 m below 100 m. A total of 8 tidal components were imposed by specifying these (elevation and currents) at the open boundaries. Data were taken from TPXO 7.1 model of global ocean tides¹. The ERA INTERIM reanalysis (Dee et al., 2011)² data (wind, sea level air pressure, air temperature, cloud cover, and humidity) were used to force SINMOD.

Data on freshwater discharges from rivers and land along the Norwegian coast and Svalbard were collected from simulations by the Norwegian Water Resources and Energy Directorate³. The simulations were performed using a version of the HBV-model in 1 km horizontal resolution (Beldring et al., 2003). For Arctic Rivers, data were obtained from R-ArcticNet (Vörösmarty et al., 1996, 1998) available through <http://www.r-arcticnet.sr.unh.edu/v4.0/main.html>.

Initial values of temperature and salinity were taken from World Ocean Circulation Experiment (WOCE) Global Data Resource Version 3.0⁴ using a spin-up phase of 26 years prior to the start of the simulation in this work. A comprehensive description of the WOCE data system can be found in Lindstrom (2001).

¹<http://www.coas.oregonstate.edu/research/po/research/tide/global.html>

²www.ecmwf.int

³www.nve.no

⁴<http://www.nodc.noaa.gov>

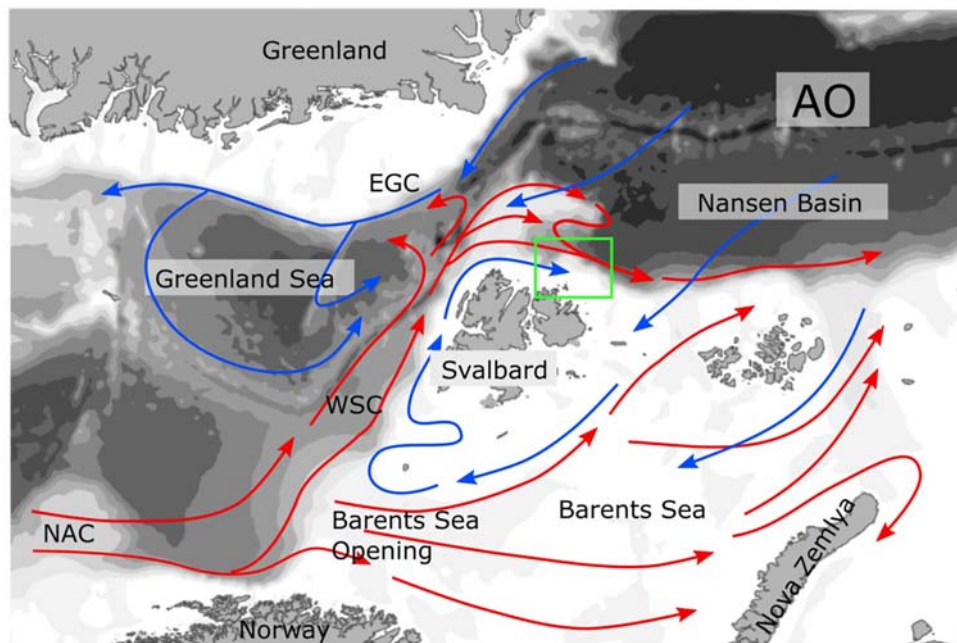


FIGURE 1 | Currents in the Northern Norway, Fram Strait, Barents Sea, and Arctic Ocean (AO) region. The warm currents dominated by Atlantic Water are marked in red, for example the North Atlantic Current (NAC), and West Spitsbergen Current (WSC). The cold Arctic Water currents are in blue, for example the East Greenland Current (EGC). In the Lofoten/Vesterålen region the NAC touches the North Norwegian shelf and forms a strong slope current.

The model calculates the transport of the two calanoid copepods into and out of as well as their production and respiration inside the box (**Figure 1**). In backtracking mode SINMOD also tried to approximate the drift pathways of *C. finmarchicus* type particles until April, the main reproductive period.

RESULTS

The modeled biomass of *C. finmarchicus* and *C. glacialis* for the months June and September showed widely different distribution and advection patterns for the two species (**Figure 3**). In June *C. finmarchicus* had recruited a large biomass in the eastern Norwegian Sea and north of the Norwegian shelf while late arrivals of the advected local *C. finmarchicus* are found west and north of Svalbard (**Figure 3**, upper left). In September the advection of *C. finmarchicus* from northern Norway to the Barents Sea and further along Svalbard to the AO was clearly detectable, stretching as far as to the Franz-Josefs-Land archipelago (**Figure 3**, lower left). The core population of *C. glacialis* is found in the north-eastern Barents Sea, Kara Sea, and Fram Strait. As compared to June *C. glacialis* had increased its biomass significantly in September (**Figure 3**, right panel). The basic distribution patterns of both copepods suggest that they dominate in different regions. The maximum biomass concentrations of *C. glacialis* and *C. finmarchicus* were similar.

The monthly flux of *C. glacialis* and *C. finmarchicus* over the years 2005 and 2014 was investigated across the western Svalbard shelf (Section A) and across the shelf and slope north

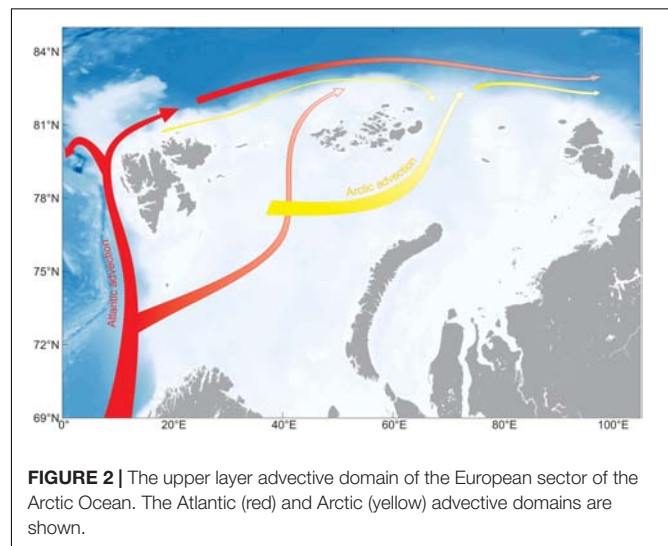


FIGURE 2 | The upper layer advective domain of the European sector of the Arctic Ocean. The Atlantic (red) and Arctic (yellow) advective domains are shown.

of Svalbard (Sections B) (see **Figure 3**). For both species and sections obvious seasonal and interannual variability in flux were detected (**Figure 4**). The flux of *C. finmarchicus* across section A was about twice as high as across section B (**Figure 4**), suggesting that roughly half of the advected biomass was advected west and south in the northern Fram Strait. The flux of *C. glacialis* across section A was negligible (not shown) and that through section B must be based upon recruitment north of Svalbard and the adjacent AO. The flux of *C. glacialis* across section B was an order of magnitude lower than that of *C. finmarchicus* (**Figure 4**).

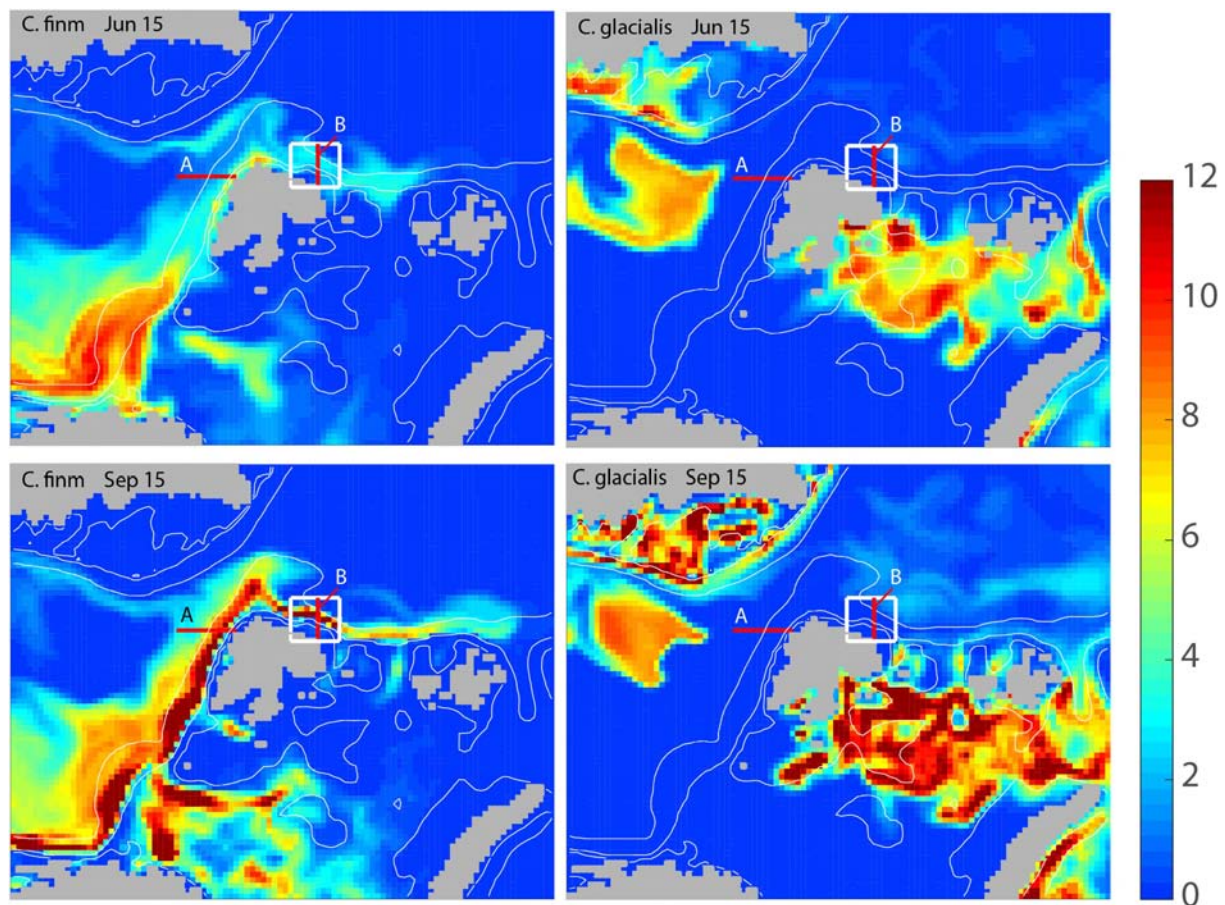


FIGURE 3 | Modeled, integrated biomass of *Calanus finmarchicus* (left column) and *Calanus glacialis* (right column) for the months June (upper panel) and September (lower panel) of 2006 around Svalbard and adjacent arctic waters (g C month⁻²). Locations for sections A and B (red) and the box (white) north of Svalbard for which the advection of mesozooplankton is calculated are also shown.

The flux of *C. glacialis* and *C. finmarchicus* across section B and eastward into the interior of the AO was recurrent (Figure 4).

The biomass, flux, production and mortality of *C. glacialis* and *C. finmarchicus* were estimated for a box (25,600 million month⁻²) on the northern Svalbard shelf and slope (Figure 3 and Table 1). The average monthly biomass of *C. finmarchicus* over the period 2005–2014 declined from about 1.4 to 0.7 g C month⁻² from January to May, increased 3–4 times from May to August (about 3 g C month⁻²) and declined again by May next year (Figure 5). The average biomass of *C. glacialis* over the period 2005–2014 was less than 0.3 g C month⁻², was low in winter, increased in summer and peaked along with that of *C. finmarchicus* in August–September (Figure 5). There was a significant interannual variability in standing stock for both species, in particular for *C. finmarchicus* in summer (Figure 5).

The average annual biomass of *C. finmarchicus* and *C. glacialis* inside the box for the selected period was 38,960 and 3,775 (t C), respectively. Mesozooplankton biomass north of Svalbard is thus dominated by *C. finmarchicus* of North Atlantic origin. The average annual flux into the box of *C. finmarchicus* and

C. glacialis in the period 2005–2014 was 18.8 and 3.6 g C month⁻², respectively. This indicates that significant amounts of *C. finmarchicus* biomass are advected into the region while there is net export of *C. glacialis*. The average production (growth – respiration) of *C. finmarchicus* inside the box was negative: -0.72 g C month⁻² year⁻¹. However, average production of *C. glacialis* inside the box was positive: 0.23 g C month⁻² year⁻¹, contributing to a net export from the box. A similar picture was provided for mortality. Inside the box it was 27,620 and 3,775 t C year⁻¹ for *C. finmarchicus* and *C. glacialis*, respectively.

The flux of *C. finmarchicus* dominated the annual budget for import and export of the two species in and out of the box (Figure 6). Most of the import of *C. finmarchicus* came with the Atlantic Water from the west, with 87% (419,360 t C) being exported annually to the east. Most of the *C. glacialis* import was from the north (Figure 6), although biomass came from the west and south. All export (94,600 t C) was to the east. The export is bigger than then import, caused by production inside the box.

The model in backtracking mode was applied to identify where mesozooplankton-sized particles in September originated from in spring (April). The particles derived from the shelf

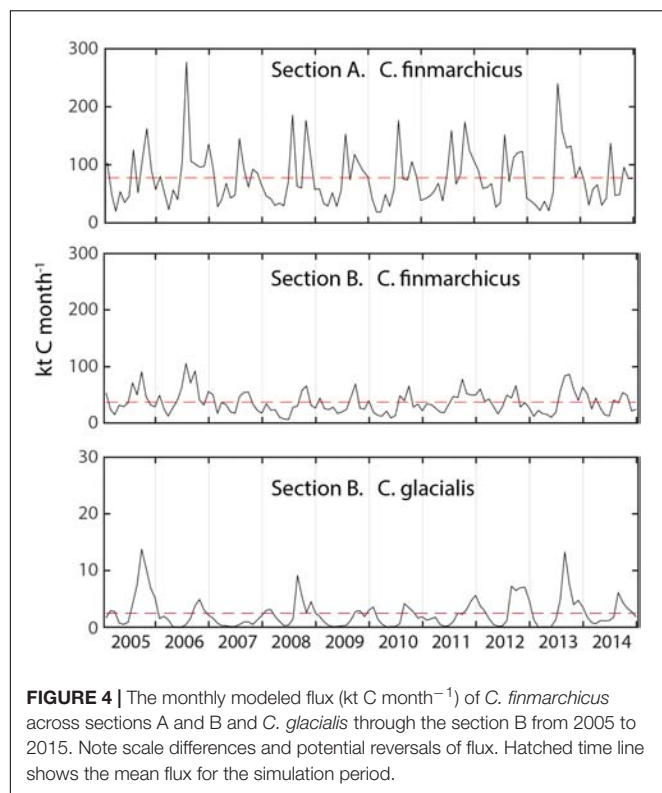


TABLE 1 | Production (growth-respiration), mortality, influx and average biomass of *Calanus finmarchicus* (Cfin) and *Calanus glacialis* (Cgla) in/into the box north of Svalbard (see **Figure 3**). The box area is $25,600 \text{ million month}^{-2}$.

Variable	$\text{g C m}^{-2} \text{ year}^{-1}$	Tons year^{-1}	g C month^{-2}	Tons C
Cfin Production	-0.72	-18432		
Cfin Mortality	1.6	41000		
Cfin flux into the box	18.8	481692		
Average Cfin biomass			1.52	38960
Cgla Prod Production	0.23	5911		
Cgla Mortality	0.08	2000		
Cgla flux into box	3.5	90529		
Average Cgla biomass			0.15	3775

break of western Svalbard, the Barents Sea shelf break toward the Norwegian Sea and the north Norwegian shelf (**Figure 7**). Zooplankton-type particles north of Svalbard (in September) derived from variable recruitment regions in spring (**Figure 8**).

DISCUSSION

The advection of Atlantic Water along the Norwegian shelf and into the Barents Sea and adjacent AO is one of the most significant features of the European Arctic Corridor were by far the greatest water exchanges into and out of the AO take place (e.g., Smedsrud et al., 2013; Polyakov et al., 2017). In the Atlantic Water a considerable amount of nutrients and biogenic matter is advected into the AO (Popova et al., 2013). Biogenic C advection may be 5–50 times bigger than local

primary production along the advective pathway. Along with this advection, large amount of mesozooplankton enter the AO ecosystem that partly depends upon additional food supply. Being partly dependent upon food supply from subarctic regions of a quantification of mesozooplankton advection into the AO, its seasonal features and connection to the North Atlantic are essential to comprehend the regulation of the biota and the dynamics of the AO ecosystem.

Mesozooplankton Transport Along the Northern Svalbard Region

Large amounts of mesozooplankton, for the most part *C. finmarchicus*, are transported along with Atlantic Water from the Norwegian Sea, along northern Norway and the western Fram Strait (Basedow et al., 2018). In the vicinity of the north-western Svalbard region, some of the Atlantic Water is recirculated toward Greenland, so that about half of the advected zooplankton biomass may be retained inside the northern Fram Strait region while the remaining biomass is advected on and along the continental slope of the Nansen Basin toward the Lomonosov Ridge (Hirche and Kosobokova, 2007; Bluhm et al., 2015). This biomass transport is dominated by *C. finmarchicus* north of Spitsbergen (**Figure 3A**), but toward the east more and more of the mesozooplankton biomass becomes dominated by the arctic species *C. glacialis*. This is particularly the case east of the St. Anna Trough (the largest submarine valley of the AO, between the Franz-Josefs-Land archipelago and Novaya Zemlya) where much of the *C. glacialis* production in the northern Barents Sea (**Figure 3B**) was advected eastward into the AO (see **Figure 2**). The mesozooplankton biomass north of Svalbard was lowest in May and highest in August and September (**Figure 5**). The model projected significant variability between years, reflecting both variable reproduction and assumed variation in recirculation in the northern Fram Strait. The seasonal and annual variability of mesozooplankton transport through section A in the eastern Fram Strait was not directly translated to the eastward transport along northern Svalbard through section B (**Figure 4**). The amplitude along section A decreased and not all maxima through section A were found in sector B. In general, recirculation in the Fram Strait is inadequately known (e.g., Marnela et al., 2013; Hattermann et al., 2016; Wekerle et al., 2017). Thus, also the advection of mesozooplankton into the Fram Strait and, particularly, how much of this biomass enters the adjacent AO is challenging. The application of a model seemed a fruitful first step before more precise estimates may be provided. According to the SINMOD model about 50% of the advected mesozooplankton biomass through sector A of the eastern Fram Strait entered the central AO through section B (**Figure 4**). The model further suggests that the flux of *C. glacialis* through section B reflected the low local production on the north-western Svalbard shelf with its strong Atlantic Water inflow.

On average, about 480,000 t C of *C. finmarchicus* were transported into of the box from the east and north per year, respectively (**Figure 6**). The inflow of *C. finmarchicus*

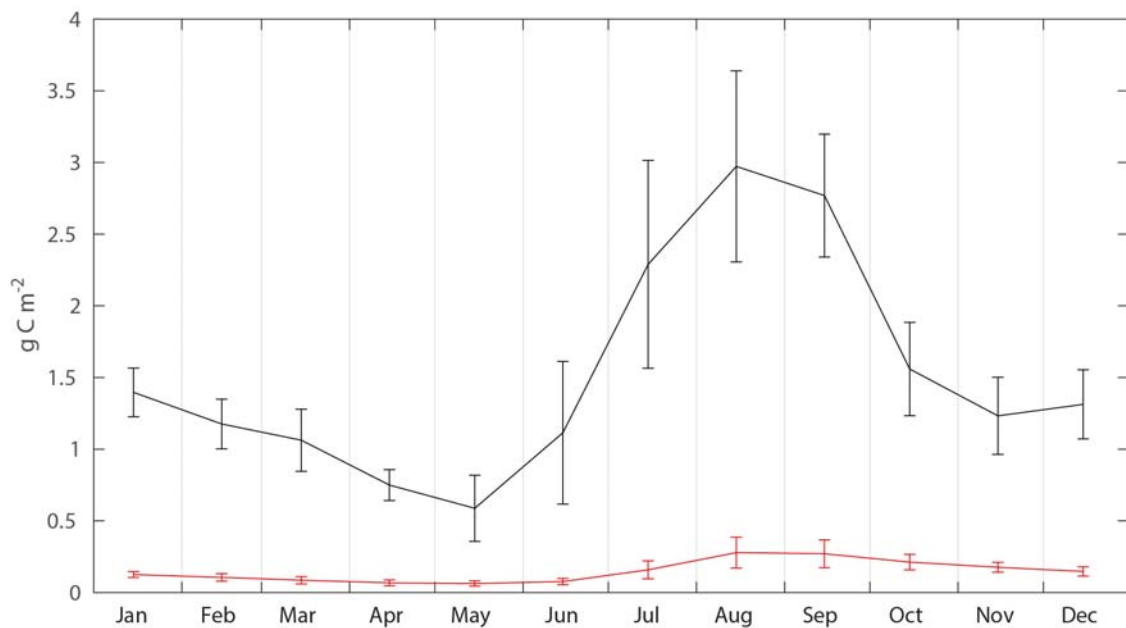


FIGURE 5 | Average seasonal (2005–2015) *C. finmarchicus* (black) and *C. glacialis* (red) biomass (g C month⁻²) in the box, with monthly standard deviations.

with Atlantic Water to northern Svalbard estimated from Laser Optical Plankton Counter and Multinett samples (Basedow et al., 2018) was on the order of 500,000 t C year⁻¹, which compares well to our modeled estimates. This considerable biomass will support ecosystems along the European shelf edge to the AO. It implies that Atlantic mesozooplankton, advected from outside the AO, plays a significant role as an allochthonous food source for polar marine ecosystems from the Eurasian shelf break. The strength of this supply decreases toward the Lomonosov Ridge, while advection of arctic mesozooplankton from the northern Barents Sea and local production plays an increasingly important role along the Eurasian shelf (Hirche and Kosobokova,

2007). The advection of *C. finmarchicus* into the Eurasian AO shelves is unidirectional, since *C. finmarchicus* cannot reproduce successfully and the advection has been characterized as a death trail (Wassmann et al., 2015). Once *C. finmarchicus* enters the AO they persist until grazed or die. Because of the high advected biomass the grazing capacity of the expatriated mesozooplankton population will match the reduced primary production toward the second part of the annual cycle, diminishing the likelihood of algal blooms. However, climate change and the loss of sea ice (Overland and Wang, 2013; Onarheim et al., 2014) will support significant future increases in primary production along the Eurasian shelves (Wassmann et al., 2010; Slagstad et al., 2011; Ivanov et al., 2012) and more allochthonous zooplankton production may be expected. This scenario is true for both *C. finmarchicus* [caused by increased Atlantification (warming and increased primary production), Polyakov et al., 2017] and *C. glacialis* (increased primary and secondary production, Slagstad et al., 2015).

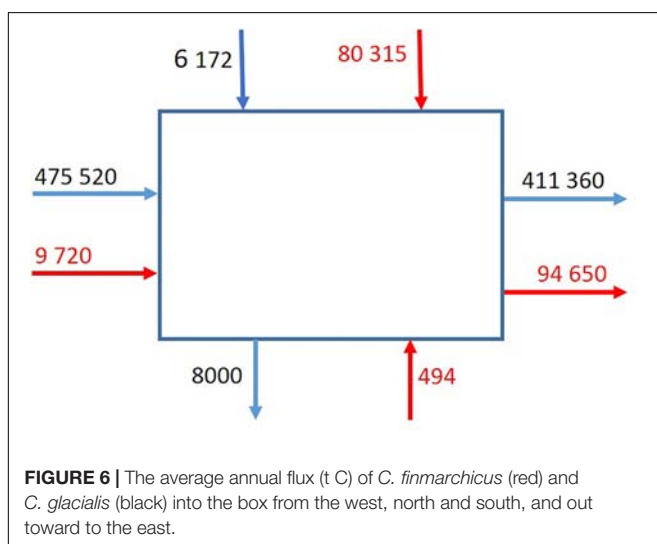
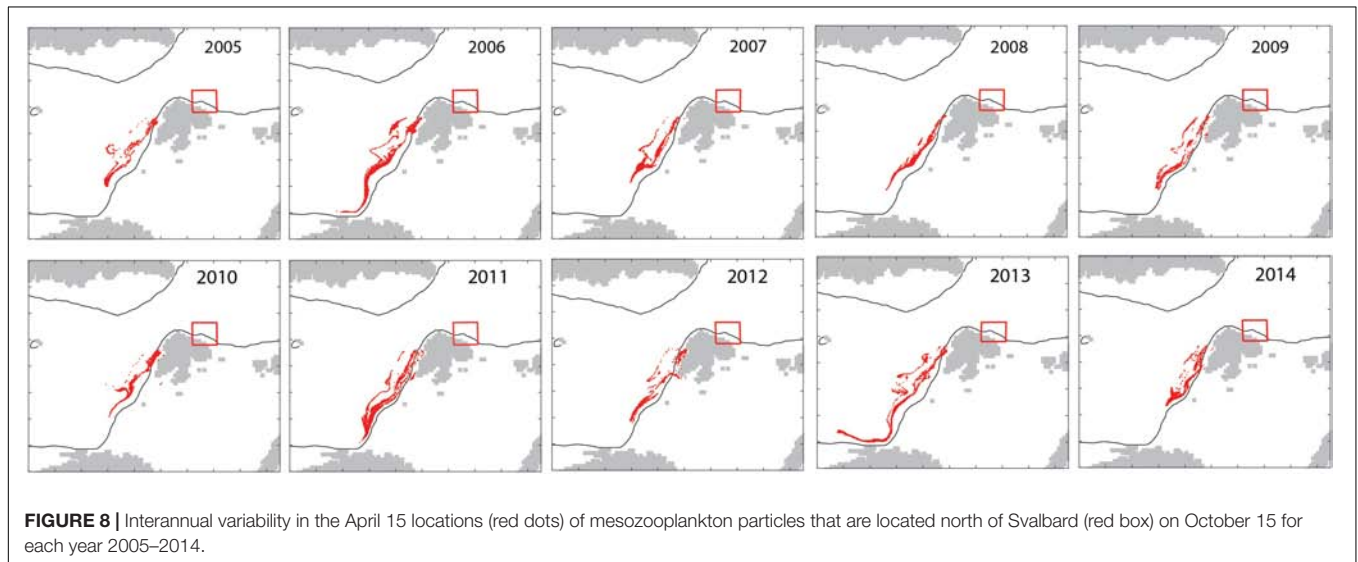
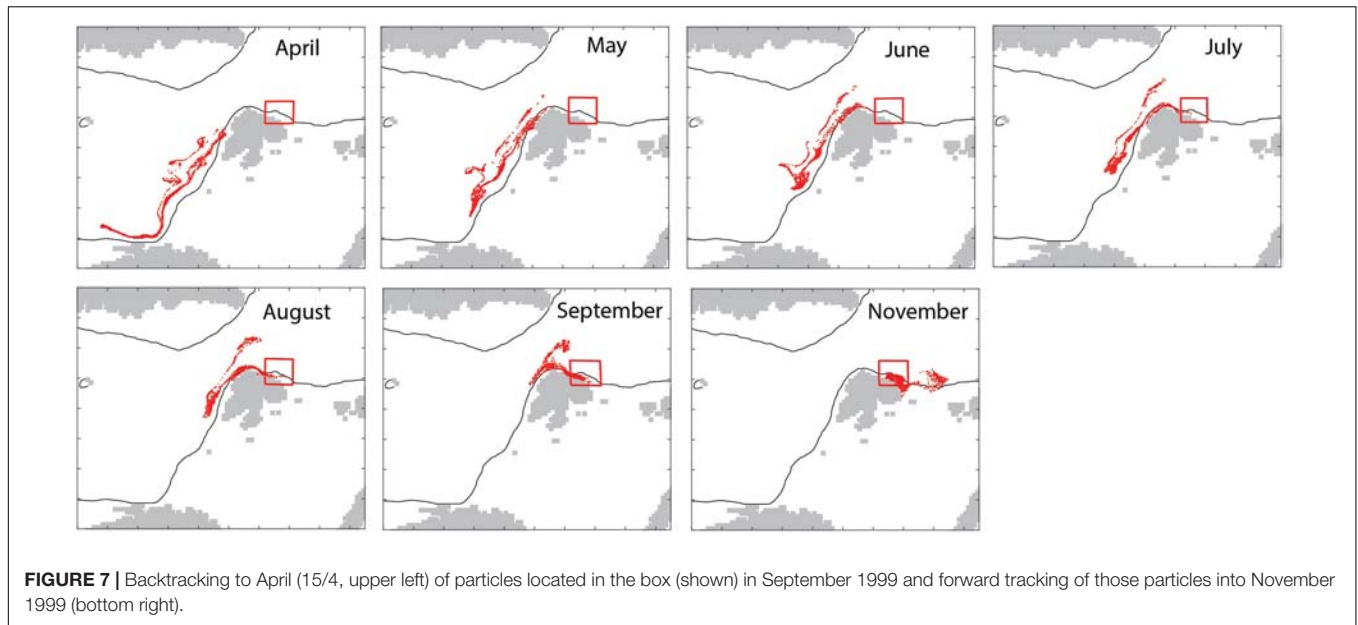


FIGURE 6 | The average annual flux (t C) of *C. finmarchicus* (red) and *C. glacialis* (black) into the box from the west, north and south, and out toward the east.

Advective Zooplankton Transport North of Svalbard Is Connected to the Norwegian Shelf

The simulated seasonal variability of mesozooplankton north of Svalbard showed a wide maximum in August and September, i.e., several months after the spring bloom. As *C. finmarchicus* reproduces in spring the cause must be allochthonous. To figure out the source of the advected mesozooplankton we applied the model in backtracking mode to identify where mesozooplankton-sized particles in September originated from in spring (April). The results indicated that the particles derived from the shelf break of western Svalbard, the Barents Sea opening (Figure 7).



April is an important month for the spawning and recruitment of *C. finmarchicus* and the new recruits from these regions have drifted to northern Svalbard by early autumn. This finding demonstrates that northern Svalbard and the Eurasian rim of the AO are directly connected to the Norwegian Sea and the strong North Atlantic Current that follows the continental shelf northward. Static regions are linked to geography, but they may be linked by contiguous domains of shared function that facilitate material transports and share key ecological features. In general, such features are termed contiguous domains (Carmack and Wassmann, 2006). All contiguous domains have lengths of several thousand km and pass often through multiple biogeographic regions. Their components share (i) a common boundary or set of properties and (ii) are connected, over defined scales, in time and space. The Lofoten/Vesterålen region of

northern Norway and the Eurasian rim of the AO thus form the Atlantic advective contiguous domain that supports the AO with nutrients, phytoplankton biomass and, particularly, long-lived zooplankton (Wassmann et al., 2015). As such, the northern Svalbard shelf is part of the Arctic inflow shelves which play an important role for the transfer of water masses of Atlantic origin (Smedsrud et al., 2013), with the nutrient availability and primary production (Randelhoff et al., 2018) as well as the advection of pelagic organisms (Wassmann et al., 2015). The Atlantic contiguous advective domain is not a constant, but rather dynamic feature that continuously exports and imports biogenic compounds and planktonic organism on its pathway toward the AO. The Atlantic advective contiguous domain may be one of the most dynamic features of the AO with significant biogeochemical cycling along its pathway.

The advection of mesozooplankton toward the northern Svalbard shelf region is an annually recurrent phenomenon. The model suggested that the influx was characterized by significant annual variability (Figures 4, 5). The cause for the interannual variability is unknown. It appears to reflect variable recirculation patterns in the northern Fram Strait, but could also be caused by variable recruitment, advective supply from the North Norwegian shelf, influx into the Barents Sea and grazing along the advective pathway. Over the course of years, zooplankton-type particles north of Svalbard (in September) may derive from variable recruitment regions in spring and advection drives this variability. In some years, they may be derived from the boundary between the Barents Sea and the Norwegian Sea (2005, 2008, and 2012), while in other years (2006, 2011, and 2013), they may be derived from the region south-east of the Lofoten Islands (Figure 8). Together these regions form the > 3000 km long Atlantic advective contiguous domain through which advection crosses several biogeographic regions, light regimes and productive regions during the year. Certain sections of the sub-boreal, sub-arctic, and arctic regions can thus not be understood and managed separately, but must be considered as functional units of the contiguous domain. The central Norwegian Sea is considered the “home region” of *C. finmarchicus* and the recirculation in northern Fram Strait moves expatriates back into the source region of the species. Expatriates that enter the shelf of northern Svalbard are, however, lost for good and represent a food supply for the AO that is lost from the Atlantic Ocean.

Significance of Mesozooplankton Advection for the Pelagic

The increase in mesozooplankton biomass north of Svalbard in August and September reflects, for the most, growth and production of cohorts that spawned along the southern section of the Atlantic contiguous advective domain. This cohort commences in spring and is particularly strong in the Lofoten/Vesterålen region. While the cohort from the previous year is exported or lost from the region of northern Svalbard, as reflected declining biomass (October to May, Figure 5) in spring a new cohort is advected northward, arriving there for full in August and September. Despite these cohorts, Figure 5. Suggests that the advective supply of mesozooplankton to the northern Svalbard shelf is continuous as verified by Basedow et al. (2018). This advection of zooplankton fuels pelagic life, also during winter (Daase et al., 2014; Falk-Petersen et al., 2014; Berge et al., 2015; Blachowiak-Samolyk et al., 2015). The Atlantic contiguous advective domain is thus characterized by pulsing *C. finmarchicus* cohorts. The advent of the spring pulse has a strong grazing impact on the phytoplankton bloom north of Svalbard that takes place in late summer. Also, along this pulse (for details of the highly variable biogeochemical processes along the drift) the grazing impact is continuously strong. The grazing impact in the southern section of the Atlantic contiguous advective domain was reported to be so strong that diatoms blooms do not

occur, despite strong silicate depletion that suggests a diatom production rate of close to $100 \text{ g C month}^{-2}$ (Ratkova et al., 1999; Slagstad et al., 1999). Consequently, chlorophyll concentrations may stay low throughout the productive season along the North-Norwegian shelf break and toward northern Svalbard (Wassmann et al., 1999). The spring bloom north of Svalbard takes place in May/June, i.e., when the model predicted that the mesozooplankton biomass was lowest, consistent with the findings of Søreide et al. (2010). This suggests that a potential for strong pelagic-benthic coupling and strong benthic production exists in the early stages of the productive season. The post bloom period north of Svalbard is thus characterized by heavy grazing, executed by the new approaching mesozooplankton cohorts and thus chlorophyll concentrations stay low. The Arctic contiguous advective domain, dominated for the most of *C. glacialis*, appears to be less pulsed and more continuous (*C. glacialis* has a 2- to 3-year life cycle, Kosobokova, 1999), with the population of *C. glacialis* in the northern Barents and Kara seas as the main source.

Annually $18.8 \text{ g C month}^{-2}$ of advected (and locally produced) mesozooplankton could be available for mesozooplankton predators before advected out again, implying that far greater amounts of feed are available along the Atlantic contiguous advective domain than outside the domain. Zooplankton predators inside the box experience, on average, $1.4 \text{ g C month}^{-2}$ of prey biomass during the year. However, the advection of mesozooplankton is about 12 times bigger than the average concentration, implying that mesozooplankton in the Atlantic advective contiguous domain represents an important food source. It could represent a continuous replenished food source for pelagic fish, birds and marine mammals. Feeding in a stream of food or utilizing accumulation of feed in regions where eddies are prominent is a well-known phenomenon in coastal regions of northern Alaska. Here about 1/3 of the zooplankton biomass advected through Bering Strait seem to be grazed by bowhead whales see, calculations in Wassmann et al. (2015) and Moore et al. (2018). Similar scenarios may also exist north of Svalbard, but the feeding impact of marine mammals there is not yet available. For the increasing population of young cod recently reported from the region (e.g., Fosheim et al., 2015), the feeding conditions north of Svalbard are good, if not excellent. Their availability is not so much based upon the feed concentration, but on the flux of feed through the area that consistently replenishes the feeding concentration. Along advective contiguous domains feeding on the flux of advected food is thus an excellent feeding strategy. Thus, large amounts of mesozooplankton prey may sustain fish, birds and marine mammals at the western Eurasian perimeter of the AO basins.

Outlook

The advection of Atlantic Water, including its nutrients, phyto- and zooplankton, plays a significant role for the ecosystem function of the AO that needs obviously dedicated investigations. The SINMOD model projects advection mesozooplankton biomass that contributes to the heterotrophic nature of the

Eurasian rim of the AO. However, the model has shortcomings that should be kept in mind. Its hydrodynamic model has a set-up using 20 km horizontal grid point distance. This is a rather coarse resolution in the complex hydrographical region of the Fram Strait. The horizontal (and vertical) resolution is probably the most important factor for improving the model's ability to improve the flow field. Further, the mortality of the mesozooplankton is difficult to assess. In lack of other alternatives, we assumed this parameter as a constant, but it will certainly vary through the season, with the variable presence of pelagic feeders (such as young cod) and from year to year.

The principle situation along the European Arctic Corridor is not unique. On the opposite Pacific side of the AO, a similar advective contiguous domain is found (Wassmann et al., 2015). Moore et al. (2018) described how zooplankton-rich water of Pacific origin flows through Bering Strait in the southern Chukchi Sea and along the shelf of northern Alaska, supporting the good feeding condition for whales. The pelagic-benthic coupling in the region is tied to the Pacific through flow because of continuous feed supply from the south. The "Arctic Pulses" model of Moore et al. (2018) and the "Advective" model of Grebmeier et al. (2015) for the Pacific opening of the AO have been launched. The results of the present investigation also illustrate the significance of the advective contiguous domain

concept for the productivity, phenology, and food supply of the perimeter of the central AO. As climate change causes changes in the atlantification (Polyakov et al., 2005) and "pacification," major changes in the food availability along the AO shelf breaks may be expected. Similar scenarios for food supply for pelagic carnivores, birds and marine mammals seem to exist for Arctic inflow shelves. However, the comparatively shallow environments on the Pacific side results in larger share of the food consumed by benthos.

AUTHOR CONTRIBUTIONS

PW initiated the research, interpreted the results, and wrote the manuscript. DS and IE stood for the modeling work.

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Pelagic Amphipods in the Eastern Fram Strait With Continuing Presence of *Themisto compressa* Based on Sediment Trap Time Series

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Pelagic amphipods represent a large fraction of organisms entering sediment traps as so-called “swimmers.” These swimmers were sampled with sediment traps (~200–300 m water depth) with two mooring arrays deployed at two different positions in the Long-Term Ecological Research observatory HAUSGARTEN in the northeastern Fram Strait. This sampling allowed us to investigate amphipod year-round abundances and inter-annual trends from 2000 onward. In this study, newly analyzed data from a 3-years period (August 2011–June 2014) are presented, extending this long-term investigation. In our results, the species *Themisto abyssorum*, *T. libellula*, and *T. compressa* dominated the swimmer biomass, corroborating previous studies. The observed increase of amphipod abundances persisted in all three species, additionally implying that *Themisto compressa* maintained its population off Svalbard, which appeared for the first time here after a warm anomaly in 2004–2007. This study provides evidence for changes in amphipod community patterns that can mainly be attributed to growing abundances of *T. compressa*. Similarly, another hyperiid, *Lanceola clausii*, also increased in abundance over the investigated period. For *T. libellula*, almost no juvenile individuals were recorded in the sampling period 2013/14, even though juveniles of this species were common in earlier records. The three more years of observations clearly suggest that recently documented environmental shifts persist in the eastern Fram Strait. They also highlight the merit of using sediment trap time series to obtain year-round data sets needed to reveal processes and range shift dynamics in the pelagic system on a long-term basis.

Keywords: sediment traps, hyperiids – pelagic amphipods, Arctic marine ecology, biodiversity, range shifts

INTRODUCTION

The Arctic environment is in rapid transition and is severely impacted by climate change (Schiermeier, 2007; Beaugrand, 2009). The sea ice is thinning (Hansen et al., 2013; Renner et al., 2014; Krumpen et al., 2015), and its extent is shrinking, with predictions of nearly ice-free summers in the Arctic within the next 25 years (Nghiem et al., 2007; Wang and Overland, 2012;

Liu et al., 2013). Decreasing sea ice in the high Arctic impacts the prevailing ice situation in the Fram Strait where sea ice, transported via the Transpolar Drift, leaves the Arctic Ocean. In addition, oceanographic surveys reveal an increase in warm water anomalies throughout the Arctic (Polyakov et al., 2005) that are largely transported via the Fram Strait. The Fram Strait is considered the main gateway to the Arctic Ocean: in its western part, the East Greenland Current transports polar water southward; in its eastern part, relatively warm water flows northward with the West Spitsbergen Current (WSC). Mixing, eddies, and recirculating water of the warm WSC add to the hydrographic complexity observed in the strait (e.g., Gascard et al., 1988; Walczowski, 2013; Von Appen et al., 2015). In the eastern part, both increasing water temperature and heat flux have been observed over the last two decades (Schauer et al., 2004, 2008; Piechura and Walczowski, 2009; Walczowski, 2013; Walczowski et al., 2017). Hence, the increasing influence of Atlantic waters in the Arctic domain, termed “Atlantification,” is extending its area of impact to a great extent through the eastern Fram Strait northward into the Arctic (Piechura and Walczowski, 2009; Beszczynska-Möller et al., 2012; Polyakov et al., 2017).

In general, alterations of environmental parameters have been shown to change plankton communities by impacting species distributions (e.g., Beaugrand, 2009) and life cycles/development (Weydmann et al., 2018). This is particularly true for the Arctic. The observed occasional warm water peaks in the eastern Fram Strait (Beszczynska-Möller et al., 2012) were accompanied by changes in phytoplankton biomass and particle flux (Bauerfeind et al., 2009; Nöthig et al., 2015; Soltwedel et al., 2016). Biogeographical shifts are also occurring in higher trophic levels, e.g., copepods in the WSC (Weydmann et al., 2014; Gluchowska et al., 2017), krill around Svalbard (Buchholz et al., 2010; Dalpadado et al., 2016), Atlantic cod in the western Greenland Sea (Christiansen et al., 2016), pteropods (Busch et al., 2015), and amphipods (Kraft et al., 2013; Dalpadado et al., 2016) in the Fram Strait. These changes consequently propagate through the Arctic food web, affecting predators such as seabirds and fish (Stempniewicz et al., 2007; Kwasniewski et al., 2012; Kortsch et al., 2015; Dalpadado et al., 2016).

Due to their abundance and their being a major prey for higher trophic levels, the three dominating pelagic amphipod species play a key role in the Arctic pelagic food web (Koszteyn et al., 1995; Dalpadado et al., 2001, 2008a,b; Auel and Werner, 2003; Melle et al., 2004). The three dominant amphipod species found in Arctic waters belong to the genus *Themisto*, namely the Arctic *T. libellula*, the Arctic-boreal *T. abyssorum* (both natives to the eastern Fram Strait), and the North Atlantic species *T. compressa* (Klekowski and Węśławski, 1991; Weigmann-Haass, 1997; Dalpadado et al., 2001; Dalpadado, 2002). *Themisto abyssorum* co-exists with *T. libellula* throughout the Arctic (Klekowski and Węśławski, 1991; Weigmann-Haass, 1997; Dalpadado et al., 2001; Dalpadado, 2002); however, *T. abyssorum* is thought to be more abundant in waters of Atlantic origin and therefore displays a greater tolerance of fluctuations in water temperature (Dalpadado, 2002). The distribution center of *T. compressa* is temperate, North Atlantic waters. It is seldom found, and only in low abundances, in the Arctic marginal seas such as the

Barents Sea off Svalbard (Dalpadado, 2002) and the Greenland Sea (Weigmann-Haass, 1997) and was recorded for the first time in the eastern Fram Strait in 2004 (Kraft et al., 2013). After its establishment in the Fram Strait, abundances of *T. compressa* have been increasing between 2005 and 2008 (Kraft et al., 2011, 2013); this was attributed to a warm surface water anomaly in the area (Soltwedel et al., 2016).

As warmer waters of Atlantic origin have been entering the Arctic Ocean via the WSC during the last 20 years, the amphipod community composition was expected to change accordingly. Set up in 1999, the Long-Term Ecological Research (LTER) observatory HAUSGARTEN (79°N, 4°, **Figure 1**) has provided data to detect environmental and biological changes in the Fram Strait. Since pelagic amphipods are good indicators of the presence of distinct water masses and therefore suitable for monitoring the effect of environmental change, this study aimed to assess the temporal and spatial differences in amphipod composition in the gateway to the Arctic. We investigated swimmer time series from the LTER sediment traps during the years 2011–2014, including and building on time series previously analyzed by Kraft et al. (2011, 2013) to assess trends in the prevailing pelagic amphipod population.

MATERIALS AND METHODS

All samples were collected using automatic Kiel sediment traps (K/MT 234; K.U.M. Umwelt- und Meerestechnik Kiel GmbH) with an opening of 0.5 m² and 20 collection cups. Two different localities were sampled over the period from September 2000 to July 2014 (**Figure 1**); sampling intervals lasted from summer to the following summer. The moorings were located at approximately 79°00' N, 04°19' E and 79°44' N 04°30' E. The sampling depth of the upper traps that were used for the present analysis were located between 190 and 280 m water depth. Traps were retrieved during 16 expeditions to the Arctic LTER observatory HAUSGARTEN located the eastern Fram Strait. Details of positions and traps for each year are found in **Table 1**. Collector cups of the sediment traps were filled with filtered, sterile North Sea water at an adjusted salinity of 40 psu and poisoned with HgCl₂ (0.14% final solution). Automatic sampling was set to rotate to new collectors every 7–26 days during times of high primary and secondary production (May–September), with longer sampling intervals (up to 32 days) during other months (see **Supplementary Table S1** for more details of sampling intervals).

Collected amphipods were removed and rinsed under a dissecting microscope (Olympus SZX10, magnification 20–50×). They were identified to species level and life stage and counted. For *T. abyssorum* and *T. compressa*, specimens <8 mm were considered as juveniles, whereas for *T. libellula*, the range <11 mm was chosen (lower size-limit: 2 mm, respectively), based on Kraft et al. (2011). In addition, numbers of *Lanceola clausii* were evaluated, because it was the most abundant amphipod after the three *Themisto* species.

We observed erratic peaks in amphipod abundances, especially in *T. abyssorum* (see also results **Figure 3**), suggesting

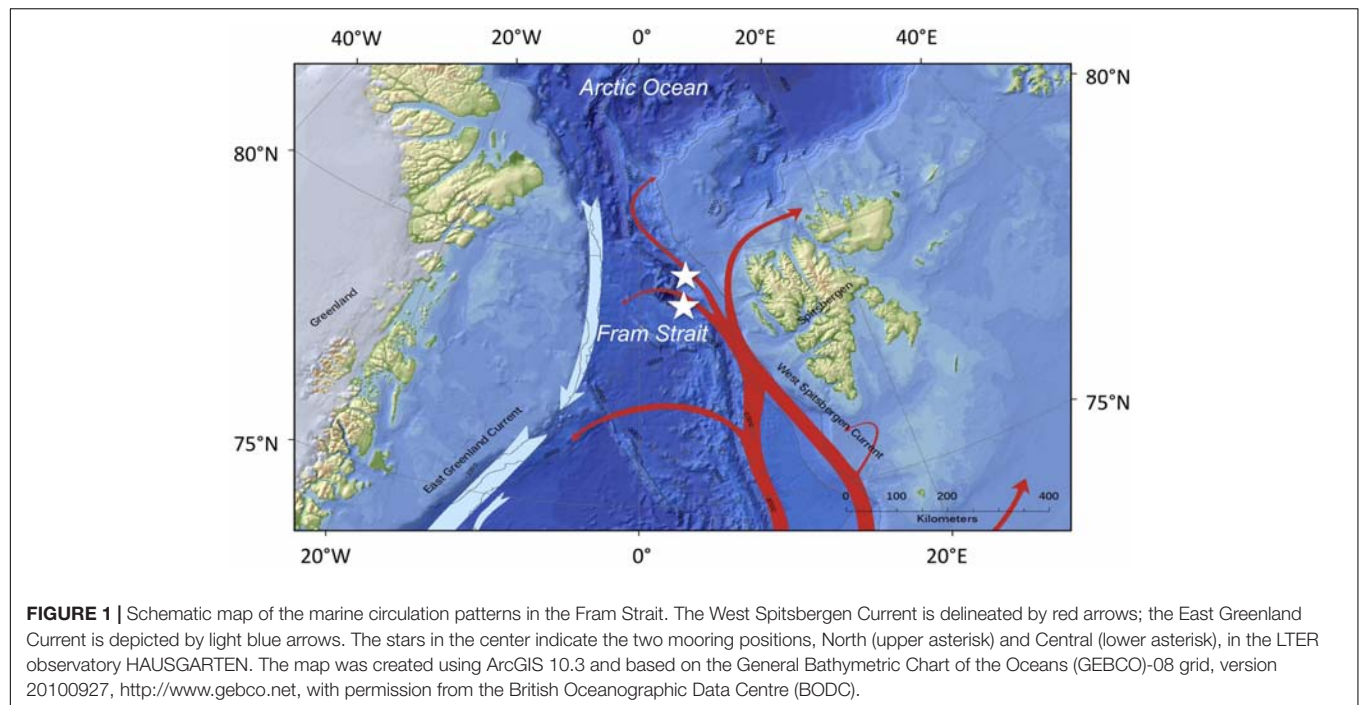


TABLE 1 | Location, sampling time, water depth, and trap depth of moored sediment traps in the HAUSGARTEN and Greenland Sea analyzed for their amphipod composition with multivariate analyses.

Mooring period in years	Lat. N	Long. E	Water depth	Trap depth (m)	Number of samples	Remarks
2000–2001						
31.08.2000–14.08.2001	79°01.70′	04°20.86′	2456	280	18	Last two cups did not run
2004–2005						
15.07.2004–19.08.2005	79°35.98′	05°09.86′	2784	280	20	
15.07.2004–21.08.2005	79°00.99′	04°20.62′	2584	280	18	Last two cups did not run
2006–2007						
07.09.2006–20.06.2007	79°36.07′	05°09.87′	2739	190	20	
25.08.2006–20.06.2007	79°00.82′	04°20.50′	2540	230	20	
2007–2008						
21.07.2007–15.07.2008	79°00.82′	04°20.62′	2589	190	20	
2008–2009						
17.07.2008–18.07.2009	79°00.40′	04°20.00′	2557	201	20	
2011–2012						
01.08.2011–15.07.2012	79°44.38′	04°30.37′	2690	200	20	
01.08.2011–15.07.2012	79°00.42′	04°19.90′	2605	200	19	One cup degraded
2012–2013						
27.07.2012–30.06.2013	79°44.38′	04°30.37′	2666	205	20	
29.07.2013–30.06.2013	79°00.42′	04°19.90′	2554	205	19	One cup degraded
2013–2014						
05.07.2013–15.06.2014	79°44.34′	04°30.24′	2675	205	16	Four cups degraded
10.07.2013–15.06.2014	79°03.76′	04°1.81′	2567	205	17	Three cups degraded

If deviations from the routine occurred, the respective information is given in the last column. A complete sample set consisted of 20 cups (Bold shows moored traps at the northern position, normal font represents the central HAUSGARTEN site, see also **Figure 1**). Degraded: Most of the sedimented material had disintegrated and was impossible to identify.

an underestimation of individuals in some of the samples. Reasons for this are discussed below.

Incorporating data obtained in the study period 2000–2009, multivariate analysis was carried out using PRIMER

6 (Plymouth Marine Laboratory, United Kingdom) (Clarke and Gorley, 2005) to visualize the similarity between the abundances of the different *Themisto* species obtained in every sample for the different sampling periods and sites.

The averaged amphipod flux data (including rare species) were standardized and square root transformed to avoid large values (abundant species) overwhelming the analysis. Nevertheless, the rare species only marginally contributed to the clustering. Thereafter, similarities between the groups of sample sets were checked. Comparing these sample sets, a resemblance matrix was generated applying the Bray-Curtis measure, because this measure was shown to apply best to marine data (Field et al., 1982). Based on the resemblance matrix, a multidimensional scaling (MDS) plot was generated for the established spatial and temporal criteria (Field et al., 1982; Clarke and Gorley, 2005). Similarity Percentage (SIMPER) routines were applied to highlight the species mainly responsible for the differences between the sample clusters (Clarke and Gorley, 2005).

RESULTS

Amphipod Swimmer Composition in Traps 2011–2014

Analyzing six sediment traps of three consecutive years, a total of 10,906 specimens comprising seven different amphipod species were found in the traps – in order of decreasing abundance: *T. abyssorum*, *T. libellula*, *T. compressa* (Figure 2), *L. clausii*, *Eusirus holmii*, *Hyperia medusarum*, and *Gammarus wilkitzkii*, representing four different families (Hyperidae, Lanceolidae, Eusiridae, and Gammaridae) (see Supplementary Table S1 for all and Supplementary Table S2 for rare species abundances).

The hyperiid genus *Themisto* dominated the epipelagic amphipod counts by >97%. The three dominating pelagic *Themisto* spp. showed significant seasonal, inter-annual and spatial variability over the studied period 2011–2014 (Figure 3), with high abundances in summer and lower numbers in winter. The highest peaks of *T. libellula* were observed at the end of summer (August–September), at both sites, in most cases with maximal abundances in periods of maximum ice cover. Monthly abundances of *T. abyssorum* were more variable regionally; for the northern HAUSGARTEN site they were highest in August, whereas in the central site they were highest in June for 2012 and in September for 2013, coinciding with ice-free periods. Overall, *T. abyssorum* dominated the amphipod community by >50%. However, in 2012/13, *T. abyssorum* and *T. libellula* were present in nearly equal proportions (~40%, respectively), over the entire year at both HAUSGARTEN sites. Whereas the two native *Themisto* species were present and dominating throughout the year, *T. compressa* was absent in the trap samples over long periods in winter (November–February), reappearing in spring. Abundances of this North Atlantic species remained elevated compared to the mid-2000s, with noteworthy counts in late summer 2011. *L. clausii* was the most abundant amphipod species after the three *Themisto* spp. with 19 specimens collected between 2011 and 2014. Previously, this species was absent, but, similarly to *T. compressa* – it became more abundant although to a much lower degree.

Population Structures (2011–2014), Sex Ratio and Life Stages of *Themisto* spp.

Examination of the occurrences of the different life stages (Figure 4) showed noteworthy proportions of juveniles of *T. abyssorum* (up to 8% of the total specimens). These were found at each site both in winter and summer, with higher proportions in winter. Focusing on the sample sites, higher proportions of juvenile *T. abyssorum* were observed at the northern HAUSGARTEN site compared to the central location. For *T. libellula*, juveniles did not reach more than 1% of the total individuals. Not a single juvenile specimen of *T. compressa* was recorded in this study during winter, and only very few occurred in summer (max. 1% of the total individuals). Females were always dominant for all three species, with a maximum value of 96% in *T. libellula*. For both *T. abyssorum* and *T. libellula*, the sex ratio was even more skewed toward female dominance in summer than in winter at both sites. The opposite was true for *T. compressa*, where the largest proportions of females occurred in winter at both sites.

Trends in *Themisto* spp. Abundances Over the Entire Sampling Period (2000–2014)

We combined our abundance data from the different years of observations (2011–2014) with the data (2000–2011) of Kraft's (2010) Ph.D. thesis and detected a compositional dissimilarity of the amphipod community between different sampling periods. A separation of earlier samples from those collected for this study is apparent (Figure 5). Altogether, the ordination plot suggests three different clusters: the 2000/01 sample, both 2012/13 samples, and the remaining samples. SIMPER analysis (Supplementary Table S3) showed a clear trend of increased contributions of high *Themisto compressa* abundances toward the right domain of the ordination chart (Figure 5). Furthermore, a tendency of increasing *T. libellula* abundances toward the upper domain of the chart could be identified, and vice versa for *T. abyssorum*. The exclusive position of the sample on the very left in the MDS-plot (2000/01 in Figure 5) was mainly due to the absence of *T. compressa* in that sampling period. The joint isolated positions of the 2012/13 samples were caused by increased abundances of *T. compressa* and *T. libellula*, as well as by relatively low abundances of *T. abyssorum*, compared to other years.

DISCUSSION

General Long-Term Trends of *Themisto* spp. at LTER HAUSGARTEN in the Eastern Fram Strait

The focus of this study was to verify the trends in dominating pelagic amphipod swimmer abundances recorded by Kraft et al. (2011, 2013) by investigating three more consecutive years (2011–2014) of amphipod sampling at two locations within the LTER observatory HAUSGARTEN. As amphipod species are more abundant in particular water masses

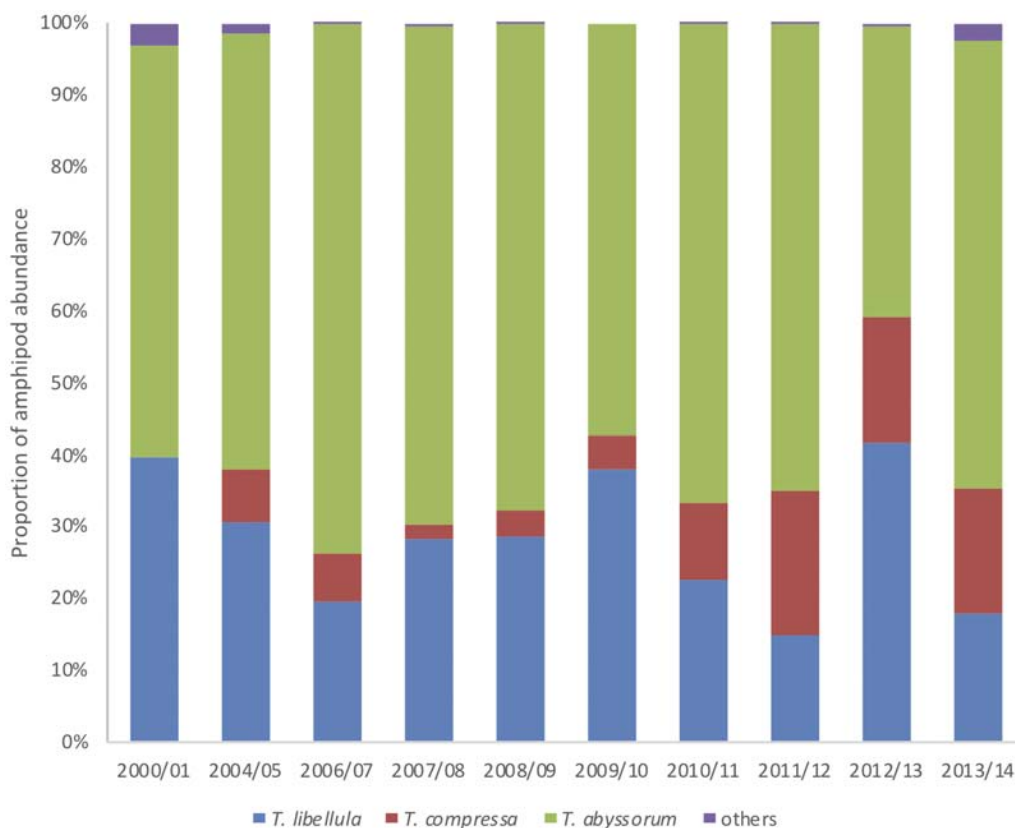


FIGURE 2 | Proportion of amphipod abundances (%) at HAUSGARTEN Central Station per sampling period. Details for the years 2009/10 and 2010/11 can be found in the **Supplementary Material**.

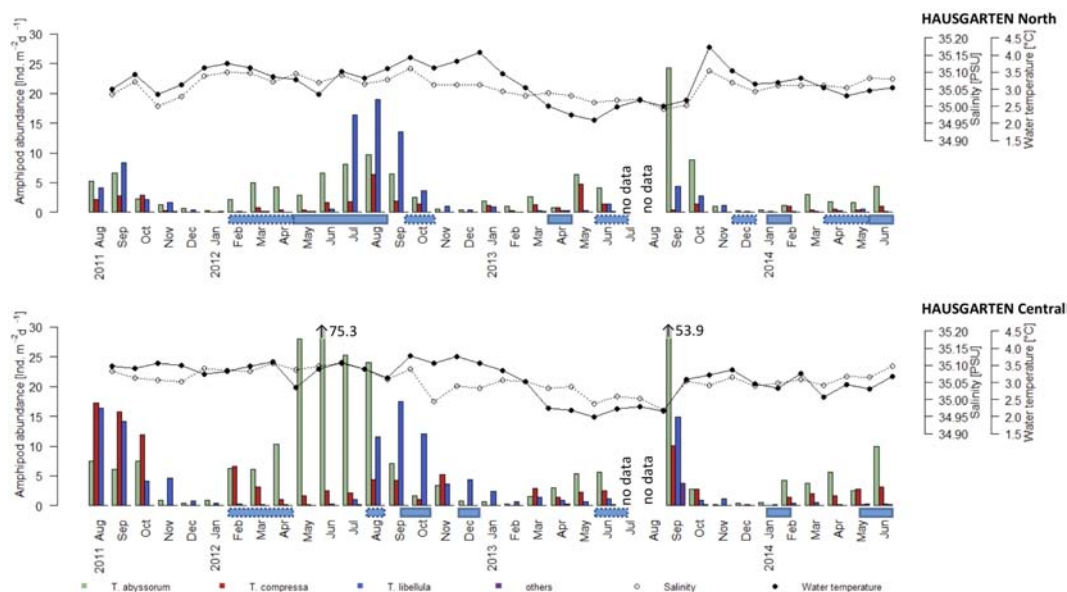


FIGURE 3 | Progression of mean monthly amphipod abundance (Ind.m⁻².d⁻¹) in HAUSGARTEN sediment traps along a latitudinal gradient: northern (upper panel) and central position (lower panel). Note the off-scale values of *Themisto abyssorum* in the lower panel (dashed boxes = periods of occasional ice cover, solid boxes = permanent ice cover). Connected dots represent the salinity (open circles) and temperature (filled circles) values across the years (for amphipod species color codes, see **Figure 2**).

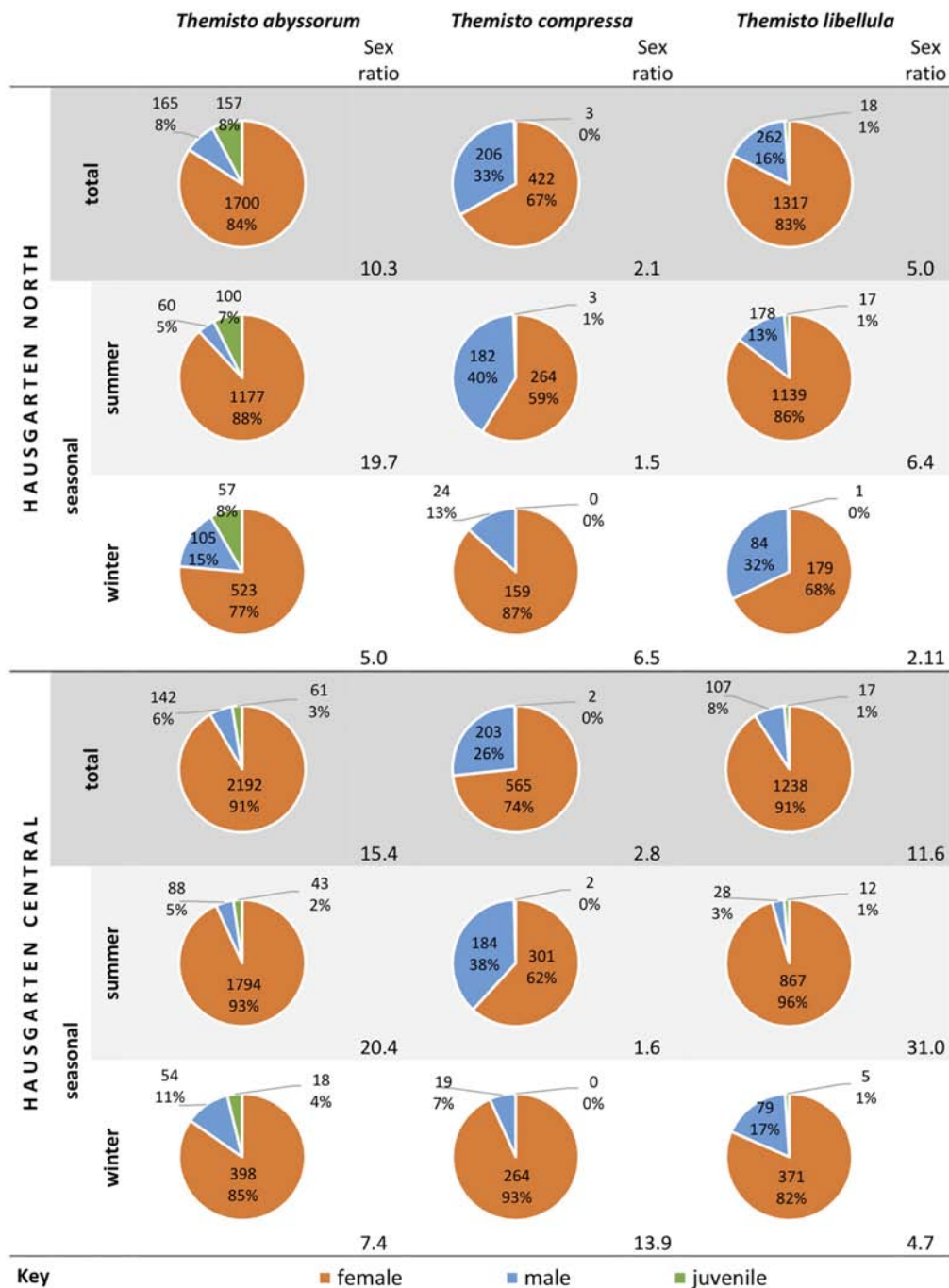
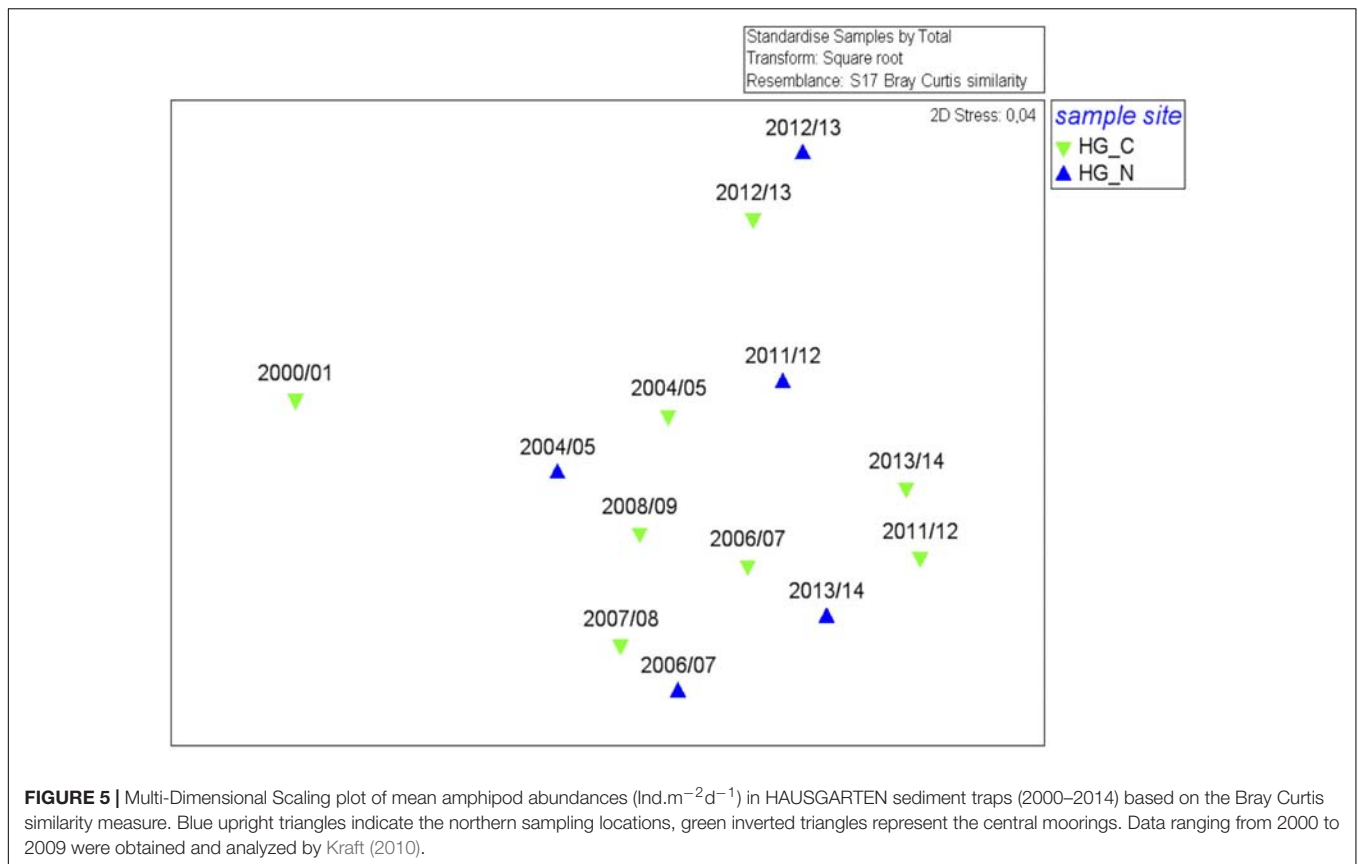


FIGURE 4 | Total and seasonal percentages of gender and maturity of the *Themisto* species between 2011 and 2014; absolute numbers are counts, relative numbers are proportions of total counts. Sex ratios = female counts/male counts. Missing data were replaced with comparative means of the respective month.

(Dalpadado et al., 2001), they may serve as sentinel species to detect changes in the pelagic environment. With this new dataset, we also analyzed the population structure of the three dominating amphipod species.

The trends of respective abundances of the two native *Themisto* species – the boreal *T. abyssorum* and the Arctic *T. libellula* – as well of that of the intruding *T. compressa*,

corroborated the observations from the period 2000–2012 described by Kraft et al. (2013). In the period 2000–2012, total amphipod counts increased by a factor of 14 during and after a warm anomaly (**Supplementary Figure S1**) observed in the HAUSGARTEN area, and counts remained equally high until 2014 (**Figures 2, 3**) despite the more stable water temperatures (**Supplementary Figure S1**).



Bottom-up and top-down processes similarly could have caused this tremendous increase in amphipod counts. Soltwedel et al. (2016) reported a slight increase of chlorophyll *a* biomass in the Fram Strait's surface waters as well as in the water column. Hence, they suggested an increase of phytoplankton biomass in the region from 2008 onward (Soltwedel et al., 2016). These findings are complemented by Nöthig et al. (2015) documenting increasing chlorophyll *a* concentrations in the WSC since the 1990s during summer months. This development provided more food for pelagic herbivorous copepods, which in the Fram Strait mainly comprises the genus *Calanus* (Hirche et al., 1994; Mumm et al., 1998; Hop et al., 2006; Hildebrandt et al., 2014). It has been shown that egg production in *Calanus glacialis* was positively correlated to chlorophyll *a* concentration (Hirche et al., 1994). Supporting this, an increase of ~50% in copepod abundances in central HAUSGARTEN sediment taps was evident between 2000 and 2014 (Nöthig et al., unpublished data). It is thus possible that raptorial carnivores, such as amphipods of the genus *Themisto* (Dalpadado et al., 2008b; Kraft et al., 2015), found sufficient prey, which might have caused the continuously increasing amphipod abundances. However, we do not know whether the 50% increase in food availability would have been enough to sustain the very high numbers of amphipods we report. One could speculate that, in addition, amphipods were not so heavily preyed upon by higher trophic levels.

Similarly, a top-down mechanism could have caused increased amphipod abundances. Amphipods are important prey for fish

(e.g., capelin, cod), birds (e.g., little auk), and marine mammals (e.g., ringed seal) (Klekowski and Węśławski, 1991; Dalpadado et al., 2001, 2008b; Auel and Werner, 2003; Melle et al., 2004). For the Barents Sea, Dalpadado et al. (2001) suggested a strong predator-prey interaction between amphipods and fish such as cod and capelin. They further demonstrated that low abundances in predatory fish were accompanied by increased amphipod stocks, and vice versa (Dalpadado et al., 2001). Hence, it is very likely that in this trophic interaction, the release of predation pressure results in the recovery of amphipods preyed upon. Dalpadado et al. (2001) also suggested that this mechanism mainly controls amphipod populations in the Barents Sea. According to the Norwegian Directorate of Fisheries (2015), catches of capelin, haddock, and herring declined between 2010 and 2014, whereas Atlantic cod (*Gadus morhua*) catches increased by ~30% for the same time frame. Given the high commercial value of Atlantic cod and haddock (Norwegian Directorate of Fisheries, 2015), a recently observed northward shift of Atlantic cod (Christiansen et al., 2016) and an enormous increase of fishing vessel sightings near Svalbard (Bergmann and Klages, 2012), the potential fishing pressure may remain high, relieving the amphipods from predation impact.

The three dominant pelagic *Themisto* species showed significant seasonal, inter-annual and spatial variability (Figure 3), with high abundances in summer and lower numbers in winter. Overall, *T. abyssorum* dominated the amphipod community by >50% during the period 2011–2014,

corresponding to Kraft et al. (2011) results. However, in 2012/13, *T. abyssorum* and *T. libellula* were present in nearly equal proportions (~40%, respectively) at both HAUSGARTEN sites. This sampling period was characterized by extraordinary ocean temperatures starting with a warm winter followed by a pronounced temperature drop, with cold water prevailing the entire summer of 2013 (Walczowski et al., 2017). It has been demonstrated that *T. abyssorum* was more abundant than *T. libellula* when warm WSC water predominated (Koszteyn et al., 1995; Dalpadado, 2002; Dalpadado et al., 2008a,b, 2016). Hence, the broad impact of the WSC may explain the observed predominance of *T. abyssorum* at the HAUSGARTEN, potentially coupled with increased reproductive rates and/or less predation mortality as discussed above. High reproductive rates were observed at both sites over the study period as indicated by the high proportions of juveniles compared with the two other species and their ubiquity over both seasons.

Whereas the two common species in the study area were present and dominating throughout the year, *T. compressa* was absent in the trap samples over long periods in winter (November–February). The reappearance of this species in spring may thus indicate an “allochthonous origin” as speculated by Kraft et al. (2013). Abundances of this North Atlantic species remained elevated compared to the mid-2000s, with noteworthy counts in late summer 2011, which may be attributed to inflow of warmer Atlantic water causing higher ocean temperatures in the eastern Fram Strait between 2011 and 2012 (Beszczynska-Möller et al., 2012; Walczowski, 2013; Gluchowska et al., 2017). This warm event has also been shown to be related to a substantial increase in abundances of the Atlantic-associated copepod *Calanus finmarchicus* in the WSC (Gluchowska et al., 2017). Irrespective of its winter absences, *T. compressa* appears to have become a common species in the eastern Fram Strait. To date, however, the species has not yet been recorded in the central Arctic (Kosobokova et al., 2011; Kosobokova, personal communication). *L. clausii* was the most abundant amphipod species after the three *Themisto* spp. with 19 specimens collected between 2011 and 2014. Previously, it was absent, but, – similarly to *T. compressa* in July 2004 – it became more abundant, although on a lower scale.

In this study we observed erratic peaks in amphipod abundances, especially in *T. abyssorum* (see Figure 3). Swarms or high density aggregations of *T. abyssorum*, *T. compressa* and *T. libellula* have previously been recorded both on the seafloor and in the water column (Lampitt et al., 1993; Vinogradov, 1999; Angel and Pugh, 2000). We assume that swarms of *Themisto* spp. were present at the sediment traps no later than the end of July 2013 (Figure 3), accumulating in the instruments' funnels, filling the sample cups to the top, and thus exceeding the poison's capacity to preserve the samples and resulting in degraded samples (Lee et al., 1992). A funnel full of swimmers would also explain the prolonged event lasting until early September 2013, with swimmer material filling up the next sample cup entirely when it was exposed for sampling. Strikingly, degraded samples occurred concurrently at both the central and the northern locations between July and early September 2013, for which similar mechanisms causing the degradation can be assumed.

Furthermore, we suggest that due to degradation, significant numbers of amphipods are not included in the data, possibly leading to an underestimation of the maximum abundances recorded. In this context, the occasional *T. abyssorum* abundance peaks as in June 2012 and September 2013 (75.3 and 53.9 Ind. m⁻²d⁻¹, respectively; Figure 3) were unexpected and can similarly be considered records of swarming events.

Population Structure of *Themisto* spp. in the Eastern Fram Strait During 2011–2014

Noteworthy proportions of juveniles of *T. abyssorum* (up to 8% of the total individuals) were recorded, which is consistent with Kraft et al. (2012). These were higher at the northern HAUSGARTEN site compared to the central location (Figure 4). This difference between sites coincides with a difference of ca. + 0.1°C in mean water temperature between August 2011 and June 2014 at the northern station compared to the central station and differences in sea ice cover. Juveniles were present in both seasons at both sites (contradicting Kraft, 2010), indicating more than one spawning period per year, as discussed by Koszteyn et al. (1995). This outcome contrasts with Kraft (2010), who obtained a seasonal pattern for juvenile *T. abyssorum* abundances, hence suggesting a seasonal migration of juveniles or lower reproductive rates. Not a single juvenile specimen of *T. compressa* was recorded in this study during winter, and only very few occurred in summer (max. 1% of the total specimen count), indicating no or only limited reproduction in the area; this is supported by Kraft et al. (2012). However, the record of Kraft et al. (2013) of brooding females in the traps may indicate that reproduction of *T. compressa* in the area is possible, but still rare. Very low numbers of juvenile *T. libellula* were recorded, irrespective of location and season (max. 1% of the total specimen count), whereas other investigations reported elevated numbers of juveniles between May and June (Percy, 1993; Koszteyn et al., 1995; Dale et al., 2006; Kraft et al., 2012). This may imply unfavorable reproductive conditions for the true Arctic *T. libellula* in a warming environment, as suggested by Dalpadado et al. (2016).

Maturity studies based on net hauls (e.g., Williams and Robins, 1981; Koszteyn et al., 1995; Dalpadado, 2002; Dale et al., 2006; Dalpadado et al., 2016) do not provide year-round data sets as do sediment trap catches (e.g., Kraft et al., 2012). Whereas net catches conducted in the Barents Sea by Dalpadado (2002) between August–September 1993 yielded juvenile proportions of up to 88% for *T. abyssorum* and 80% for *T. libellula*, a maximum percentage of 8% was recorded for *T. abyssorum* herein. Large relative numbers of juveniles have also been found in similar studies in the Greenland and Barents seas (e.g., Koszteyn et al., 1995; Dale et al., 2006). On the other hand, size distributions found herein agree with other sediment trap-approaches, such as Kraft et al. (2012), who generally observed very few juveniles. The different approaches target different depths, and it is known that *Themisto* spp. are often segregated by depth in the water column according to sex and life stage (Williams and Robins, 1981; Węśławski et al., 2006). Varying criteria for classifying life

stages (juveniles, immature adults, mature adults) (Williams and Robins, 1981; Percy, 1993; Węśławski et al., 2006) and seasonal migratory behavior (Percy, 1993; Kraft, 2010) may also account for the large discrepancies in the outcomes.

Community Changes of *Themisto* spp. at LTER HAUSGARTEN in the Eastern Fram Strait

By combining data on pelagic amphipods species from this study (2011–2014) with Kraft (2010) *Themisto* spp. and other pelagic amphipod data sets from her Ph.D. thesis (2000–2011), we obtained a broader view of the amphipod community development between 2000 and 2014. Within this time frame, a separation of older and more recent samples is apparent (Figure 5), indicating a development of the system.

According to the similarity analyses of species composition between the different years and sites, the trend of increased *T. compressa* proportions most probably caused the dissimilarity over years. In general, the system has changed to a state of higher *T. compressa* abundances reflected by an increasing contribution of this species to the observed cluster patterns. Thus, the lack of *T. compressa* in the 2000/01 sample resulted in its strong dissimilarity with other samples. Furthermore, increased *T. libellula* abundances mainly contributed to the vertical separation of the samples with increasing numbers in the upper domain. Similarly, high *T. abyssorum* abundances contributed to the vertical clustering with highest values in the lower domain of the chart. However, these trends do not seem to indicate a continuous temporal development as discussed for *T. compressa*. These trends are reflected in the 2012/13 samples because their dissimilarity was mainly due to high cluster contributions of increased abundances of *T. compressa* and *T. libellula* as well as to low abundances of *T. abyssorum*. Interestingly, the 2012/13 winter was characterized by notably high ocean temperatures followed by a subsequent cold summer (Supplementary Figure S1, as mentioned in Gluchowska et al., 2017). We speculate that the abundances of *T. libellula* did not appear to be affected by increased abundances of the intruding *T. compressa*, at least under cold water conditions; however, abundances of *T. abyssorum* appeared to be adversely influenced (see also Stempniewicz et al., 2007). We further speculate that even though *T. abyssorum* is assumed to tolerate a high temperature gradient and show high abundances in Atlantic water masses (Dalpadado, 2002), competition between *T. compressa* and *T. abyssorum* may play a role, given their similar sizes and ecological roles (e.g., carnivorous feeding type – see Kraft et al., 2015).

Variations and possible shifts in amphipod proportions of the three dominant pelagic hyperiids are evident based on our long-term data series. The occurrence of the North Atlantic species *T. compressa* (Kraft et al., 2013) continued until 2014, which may be attributed to higher water temperatures (Supplementary Figure S1; Walczowski et al., 2017). The latter was confirmed by the observation that the abundances observed at the central HAUSGARTEN site were considerably higher than at the northern location. The system is evidently

shifting toward a warm, more North Atlantic-influenced state (Gluchowska et al., 2017), potentially causing Arctic species to decline (Dalpadado et al., 2016). This is corroborated by the low numbers of juveniles of the true Arctic *T. libellula* in the sampling period 2013/14, even though previously, these were commonly detected. The replacement of the larger, lipid-rich *T. libellula* by the sub-Arctic and temperate species *T. abyssorum* and *T. compressa* in the Arctic could change the food chain pattern with possible consequences for fish, whale and bird populations that depend on this species as major prey. For example, little Auks (*Alle alle*) feed predominantly on the largest size class of *T. libellula* (Lønne and Gabrielsen, 1992), and hence, the other *Themisto* species cannot eventually act as substitutes because of their smaller size.

Warming water temperatures are a likely cause of the increasing amphipod abundances between 2000 and 2014 that are potentially affecting trophic interactions and increasing competition between *Themisto* spp. Thus, more temperate species evidently extended their range into the Arctic, as we demonstrated by the seasonal establishment of the North Atlantic species *T. compressa*. Other, previously unsampled species are newly appearing in the Fram Strait sediment traps, with the most abundant being the hyperiid *L. clausii*. These outcomes suggest ongoing environmental shifts taking place in the seasonally ice-covered eastern Fram Strait. For a better understanding of species interactions and for firm predictions regarding future pelagic communities, more regionally and temporally extensive studies on the topic are urgently needed.

DATA AVAILABILITY

The datasets for the 2011–2014 data can be found in the supplementary information. The existing data (2000–2011) can be found in the PANGAEA repository: Oceanographic data sets see Bauerfeind et al. (2015), amphipod numbers see Kraft et al. (2012).

AUTHOR CONTRIBUTIONS

FS wrote the manuscript together with E-MN and CH. AK, AB-M, NK, and EB provided the data of amphipods, hydrography as well as trap, and mooring logistics and analyzed the respective data sets. All authors involved in discussions about the amphipod development in the Fram Strait in the long-term perspective of environmental change in the Arctic Ocean and revised and approved the manuscript.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: <https://www.frontiersin.org/articles/10.3389/fmars.2019.00311/full#supplementary-material>

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Food Web Functions and Interactions During Spring and Summer in the Arctic Water Inflow Region: Investigated Through Inverse Modeling

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We used inverse modeling to reconstruct major planktonic food web carbon flows in the Atlantic Water inflow, east and north of Svalbard during spring (18–25 May) and summer (9–13 August), 2014. The model was based on three intensively sampled stations during both periods, corresponding to early, peak, and decline phases of a *Phaeocystis* and diatom dominated bloom (May), and flagellates dominated post bloom stages (August). The food web carbon flows were driven by primary production (290–2,850 mg C m⁻² d⁻¹), which was channeled through a network of planktonic compartments, and ultimately respired (180–1200 mg C m⁻² d⁻¹), settled out of the euphotic zone as organic particles (145–530 mg C m⁻² d⁻¹), or accumulated in the water column in various organic pools. The accumulation of dissolved organic carbon was intense (1070 mg C m⁻² d⁻¹) during the early bloom stage, slowed down during the bloom peak (400 mg C m⁻² d⁻¹), and remained low during the rest of the season. The heterotrophic bacteria responded swiftly to the massive release of new DOC by high but decreasing carbon assimilation rates (from 534 to 330 mg C m⁻² d⁻¹) in May. The net bacterial production was low during the early and peak bloom (26–31 mg C m⁻² d⁻¹) but increased in the late and post bloom phases (>50 mg C m⁻² d⁻¹). The heterotrophic nanoflagellates did not respond predictably to the different bloom phases, with relatively modest carbon uptake, 30–170 mg C m⁻² d⁻¹. In contrast, microzooplankton increased food intake from 160 to 380 mg C m⁻² d⁻¹ during the buildup and decline phases, and highly variable carbon intake 46–624 mg C m⁻² d⁻¹, during post bloom phases. Mesozooplankton had an initially high but decreasing carbon uptake in May (220–48 mg C m⁻² d⁻¹), followed by highly variable carbon

consumption during the post bloom stages ($40\text{--}190\text{ mg C m}^{-2}\text{ d}^{-1}$). Both, micro- and mesozooplankton shifted from almost pure herbivory (92–97% of total food intake) during the early bloom phase to an herbivorous, detritivorous and carnivorous mixed diet as the season progressed. Our results indicate a temporal decoupling between the microbial and zooplankton dominated heterotrophic carbon flows during the course of the bloom in a highly productive Atlantic gateway to the Arctic Ocean.

Keywords: carbon flow, food web, inverse method, Arctic Ocean, plankton communities

INTRODUCTION

Global ocean annual primary production is declining (Gregg et al., 2003), particularly in the unproductive and expanding oligotrophic gyres (Polovina et al., 2008). The trend is radically different in the Arctic Ocean, where thinning of ice and reduced ice cover (Stroeve and Notz, 2018) drive a spectacular trend toward increased phytoplankton surface concentrations and primary production (Arrigo and van Dijken, 2015; Kahru et al., 2016; Hill et al., 2018).

Climate warming is especially severe in the Arctic, where the average temperature is increasing 0.4°C per decade, several times higher than the global average rate (Stocker, 2014). The Arctic has lost more than half of its summer ice extent since 1980, and predictions suggest that the Arctic Ocean will be ice free in the summer as early as 2050 (González-Eguino et al., 2017). This could further accelerate the Arctic amplification through enhanced sea–ice–albedo feedback, leading to a self-accelerating vicious warming cycle (Graversen et al., 2008; Kashiwase et al., 2017). The net effect is increasing primary production due to longer open water productive seasons and adaptation of algal bloom patterns to earlier melting and later freeze up (Arrigo and van Dijken, 2015).

The European Arctic Ocean (Barents Sea and the Fram Strait) is highly influenced by the warm Atlantic water brought by the North Atlantic Current, causing it to be a relatively ice free area, and introducing also nutrient-rich waters as well as non-indigenous Atlantic species and living biomass (Chan et al., 2018; Neukermans et al., 2018). The effect and fate of this advected biomass is not clear. The nutrients transported may become available for primary production through upwelling events, creating hotspots of increased productivity along the shelf breaks (Tremblay et al., 2011). The region north of Svalbard is projected to become a new productive hot spot in the Arctic Ocean due to the ice retreat.

The inflow of Atlantic water from the North Atlantic Current and the West Spitsbergen Current along the eastern Fram Strait has intensified over recent decades (Beszczynska-Moller et al., 2012). Further, the long-term environmental monitoring revealed a 1°C higher warm water anomaly event in the Atlantic Water inflow from 2005 to 2007, accompanied with shifts in dominant phytoplankton species in summer from large-celled diatoms to smaller flagellates like coccolithophorides and *Phaeocystis*, a change which appeared persistent also after the reversal of the temperature anomaly (Nöthig et al., 2015). These changes at the primary producers level cascaded further into the food web,

where mesozooplankton adapted by shifting from predominantly herbivory to omnivory and detritivory (Vernet et al., 2017).

The pelagic microbial food webs in the Arctic Ocean are commonly described to have distinct community structure and low diversity, with essentially no cyanobacteria, and high levels of endemism (Lovejoy et al., 2006; Pedrós-Alió et al., 2015). The fate and partitioning of the enhanced primary production in the arctic pelagic food web is still largely unknown and only a few field studies exist (Vézina et al., 2000; Forest et al., 2011; Tremblay et al., 2012; Saint-Béat et al., 2018). Food web integrates the transfer of matter and energy between organisms that eat, and are eaten by others, capturing thus essential information about species interactions, material flow, community structure, and ecosystem functioning. The seasonal progression of community maturation is reflected in food web reorganization, which can cause changes in ecosystem performance (Samhuri et al., 2009; Blais et al., 2017).

Here, we use linear inverse modeling (Vézina and Platt, 1988; Vézina et al., 2000; De Laender et al., 2010; van Oevelen et al., 2010) to resolve and quantify food web trophic flows of organic carbon between major planktonic components in the Atlantic Water inflow to the Arctic Ocean during cruises in early and later summer seasons of 2014. Since the pivotal text by Vézina and Platt (1988), the inverse method has become increasingly popular in aquatic food web modeling. It enables estimating elemental budgets and reconstructing otherwise notoriously difficult to measure trophic flows between living compartments, using the relatively easy to measure biomasses of these compartments; a set of measured flows (e.g., primary production and respiration), food web topology, and biologically meaningful constraints on the trophic flows (De Laender et al., 2010). The methodology has been used to quantify planktonic food web flows in natural and experimental systems (Vézina et al., 2000; Olsen et al., 2006; Luong et al., 2014), has been used to track biogenic carbon flow in the Arctic (Vézina et al., 2000; Forest et al., 2011; Vernet et al., 2017), and last but not least, is coded in open source software (*LIM* library of the R software) with good explanatory texts (Soetaert and van Oevelen, 2009; van Oevelen et al., 2010).

The goal of the 2014 summer cruises was to map the physical and biogeochemical properties of the Atlantic Water inflow to the Arctic Ocean. Our synthesis relies on *in situ* data on phytoplankton particulate and dissolved production, bacterial production, community respiration, vertical particle fluxes, and pools of particulate and dissolved organic carbon. The model provides information on the trophic interaction,

assimilation and exudation rates that may regulate the organic carbon export partitioning between the respiration and biological carbon pump.

MATERIALS AND METHODS

Spatial Coverage and Water Column Profiles

Data were collected during two cruises on board the R/V Helmer Hanssen, on and off the shelf northwest and north of Svalbard. Three 24 h process stations were sampled in May, corresponding to early, peak, and decline phase of an algal bloom, and three stations in August, representing post bloom stages (Figure 1 and Table 1). Sampling stations were located to intercept the core of the warm Atlantic water inflow, which enters the Arctic Ocean with the West Spitsbergen Current east and north of Svalbard (Randelhoff et al., 2018).

Vertical profiles of temperature, salinity and fluorescence were mapped with a rosette oceanographic profiler (CTD, Seabird SBE 911 plus). Water for analysis of carbon pools and biological process studies was retrieved with 5 L Niskin bottles from discrete depths (1, 5, 10, 20, 30, 40, 50, 75, 100, and 200 m), and the fluorescence maximum.

Carbon Pools

Total chlorophyll *a* (Chl *a*) samples (100–150 ml) were filtered onto Whatman GF/F glass-fiber filters (nominal pore of 0.7 μm).

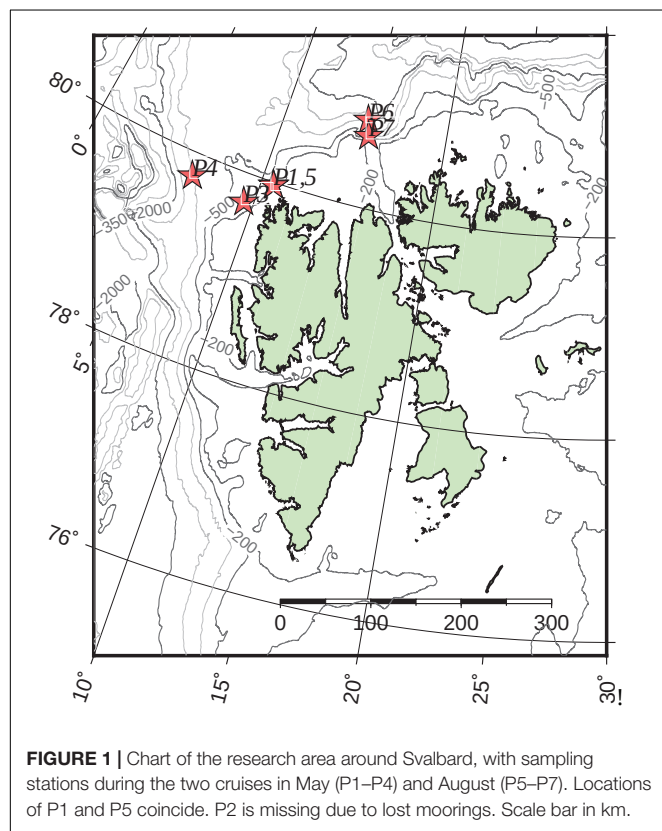


TABLE 1 | Location of 24 h process stations in May and August 2014.

Stn	Date	Lat (°N)	Lon (°E)	d_{ML} (m)	Z_{eu} (m)	Bloom stage
P1	May 18	79.975	10.709	10	23	Early
P3	May 23	79.718	9.457	10	19	Peak
P4	May 25	79.771	6.270	11	22	Late
P5	August 09	79.970	10.725	15	22	Post
P6	August 11	80.860	15.002	10	48	Post
P7	August 13	80.706	15.266	9	45	Post

Depths of the mixed layer (d_{ML}) and photic zone (Z_{eu}) at each station according to Randelhoff et al. (2018). Mixed layer is defined as the depth where MSS-90L microstructure sonde measured potential density (σ_θ) crosses 20% of the density difference between a surface layer density (3–5 m), and deeper (reference depth interval 50–60 m). Photic zone is defined as the depth where downwelling PAR reached 1% surface value. The phytoplankton bloom stage according to Reigstad et al. (in preparation). Stn P2 is missing due to loss of moorings carrying primary production incubations and sediment traps.

In addition, size fractionated Chl *a* (>10 μm , <3 μm) was obtained with membrane filters. Chl *a* was extracted in 5 ml of methanol at room temperature in the dark for 12 h without grinding. Triplicate samples of each size fraction were read with a Turner Fluorometer AU-10 (Holm-Hansen et al., 1965). Size-fractionated Chl *a* biomass was converted into phytoplankton carbon using a conversion factor of 27 (Riemann et al., 1989).

Total organic carbon (TOC) was measured from unfiltered seawater by high temperature combustion using a Shimadzu TOC-VCSH. Samples were acidified with HCl (to a pH of around 2) and bubbled with N_2 gas in order to remove inorganic carbon. Particulate organic carbon (POC) samples were filtered in triplicate (100–500 ml) onto pre-combusted Whatman GF/F (450°C for 5 h), dried at 60°C for 24 h and analyzed on-shore with a Leeman Lab CEC 440 CHN analyzer after removal of carbonate with fumes of concentrated HCl for 24 h (Fischer and Wefer, 2013).

The concentration of dissolved organic carbon (DOC) was calculated from the difference of TOC and POC.

Heterotrophic bacteria (BAC) and heterotrophic nano-flagellates (HNF) were counted on an Attune[®] Focusing Flow Cytometer (Applied Biosystems by Life Technologies) with a syringe-based fluidic system and a 20 mW 488 nm (blue) laser. Samples were fixed with glutaraldehyde (0.5% final conc.) at 4°C for a minimum of 2 h, shock frozen in liquid nitrogen, and stored at –80°C until analysis. For enumeration of bacteria the samples were diluted 10-fold with 0.2 μm filtered TE buffer (Tris 10 mM, EDTA 1 mM, pH 8), stained with a green fluorescent nucleic-acid dye, SYBR Green I (Molecular Probes Inc., Eugene, OR, United States) and kept for 10 min at 80°C. HNF samples were preserved in similar way, following staining with SYBR Green I (Molecular Probes Inc., Eugene, OR, United States) for 2 h in the dark, and minimum 1 ml was measured at a flow rate of 500 $\mu\text{l min}^{-1}$ (Zubkov et al., 2007). HNF were discriminated from nano-sized phytoplankton on basis of green vs. red fluorescence, and from large bacteria on basis of side scatter vs. green fluorescence. Abundances were converted to carbon biomass using a bacterial carbon

content of 15 fg C cell⁻¹, and a HNF mean cell size of 33.5 μm³ and 20% carbon content (Børsheim and Bratbak, 1987; Ducklow, 2000).

Microzooplankton samples were preserved in 2% (final concentration) acid Lugol's iodine, post-fixed with 1% (final concentration) formaldehyde after 24 h and stored at 4°C until counting. Microzooplankton were settled in Utermöhl chambers (50–100 ml) and counted under differential interference contrast (DIC) and fluorescence equipped inverted microscope. The entire chamber was scanned at 200× magnification. At least 40 individual cells within each abundant taxon were sized at 400–600× magnification and converted to carbon biomass according to geometric shapes and volume to carbon conversions (Menden-Deuer and Lessard, 2000). All ciliates, and hetero- and mixotrophic dinoflagellates > 20 μm in maximum dimension were allocated to microzooplankton.

Mesozooplankton composition, biomass, and depth distribution was assessed with net hauls from the bottom (or a maximum depth of 1,000 m at station deeper than 1,000 m) to the surface twice a day (noon and midnight). The vertically stratified samples (0–20, 20–50, 50–100, 100–200, 200–600, and 600–1,000 m) were collected with a MultiNet Midi (180 μm mesh size, 0.25 m² mouth opening, Hydro-Bios, Kiel, Germany) that was deployed vertically with a hauling speed of 0.5 m s⁻¹. Samples were preserved in a solution of 80% seawater and 20% fixation agent (75% formaldehyde buffered with hexamine, 25% anti-bactericide propandiol), resulting in a final formaldehyde concentration of 4% (for details see: Basedow et al., 2018).

From the fixed samples, zooplankton was counted and identified to the level of species (most copepods), genus or family (other groups). Conspicuous, large zooplankton (> 5 mm, chaetognaths > 10 mm) were identified and enumerated from the entire sample. From the rest of the sample, at least 500 individuals from a minimum of three sub samples (2 ml, obtained with an automatic pipette with tip end cut to leave a 5 mm opening) were identified, staged and counted. This procedure allows for the analysis of abundance of common species and taxa with 10% precision and at 95% confidence level (Postel et al., 2000). Copepods of the genus *Calanus* were identified to species level (Kwasniewski, 2003). Specimens other than copepods were measured and sorted into different size categories. For the inverse reconstruction, mesozooplankton was aggregated into two size classes, small (<4 mm), and large (>4 mm). The latter also included the *Calanus* species (*Calanus finmarchicus*, *Calanus glacialis*, and *Calanus hyperboreus*). Mesozooplankton abundance was converted to carbon biomass by using species-specific conversion factors after an extensive compilation (E. Halvorsen, unpublished data) from a range of literature sources (e.g., Richter, 1994; Hanssen, 1997; Hirche and Kosobokova, 2003; Hopcroft et al., 2010), or a generic biovolume to carbon conversion factor of 0.03 mg C mm⁻³ (Zhou et al., 2010).

Community Metabolic Rates

Algal ¹⁴CO₂ fixation was measured by the ¹⁴C method (Nielsen, 1952). Water samples from 1, 5, 10, 20, 30, 40, 50, and 75 m depth were split in 100 ml aliquots into four 150 ml polycarbonate

bottles and spiked with 10 μCi of NaH¹⁴CO₃. One bottle served as a t₀ sample. One dark, and duplicate light bottles were incubated at *in situ* depths for ca 22 h, using a freely drifting or ice-floe attached mooring. Total ¹⁴CO₂ fixation, including organic exudates, was measured from a 2 ml sub-sample, and particulate ¹⁴CO₂ fixation from the remaining 98 ml Whatman GF/F filtered sample, placed in 6 ml scintillation vials. Residues of any inorganic ¹⁴C were removed by acidifying the samples with 0.2 ml of 20% HCl for 24 h. After acidification, 5 ml of Ultima GoldTM XR LSC scintillation cocktail was added, and the samples stored in the dark until measuring on shore in a PerkinElmer Tri-Carb 2900TR scintillation counter. The activity in dark bottle was subtracted from the activities in the light bottles, and to assess dissolved primary production the particulate primary production was subtracted from the total. The detection limit was approximately 1 μg C L⁻¹ d⁻¹. In our study the ¹⁴CO₂ fixation rates were treated as gross primary production (GPP).

Bacterial production (BP) was measured using the radio-labeled leucine incorporation technique (Kirchman, 2001). Aliquots of 1.9 ml were incubated with ³H-leucine (final conc. 20 nmol L⁻¹; specific activity 5.957 TBq mmo L⁻¹) in the dark at 1°C for 2 h. Triplicate samples were taken from each profile depth, as well as one trichloroacetic acid (TCA) killed control (5% final concentration). The reaction was terminated by adding TCA (5% final concentration). Samples were microcentrifuged and aspirated. The remaining pellet was subsequently washed with TCA and ethanol. The samples were dried, and radio assayed with scintillation cocktail (Ultima GoldTM XR LSC) with a PerkinElmer Tri-Carb 2900TR scintillation counter. Bacterial carbon production was calculated with a conversion factor 3.1 kg C mol⁻¹ leucine incorporated (Simon and Azam, 1989).

Community respiration (ComResp) was determined from changes in oxygen over a 24 h period in 100 ml sample aliquots. Oxygen concentrations were analyzed by micro-Winkler titration using a potentiometric electrode and automated endpoint detection (Mettler Toledo, DL28 titrator) following Oudot et al. (1988). Community respiration was calculated by subtracting initial dissolved oxygen concentrations from dissolved oxygen concentrations measured after incubation in the dark. Due to the small aliquot volume, it was unlikely to contain any representative quantity of mesozooplankton. Therefore, the community respiration was not partitioned to mesozooplankton in the inverse reconstruction.

Vertical Particle Flux

To measure the vertical flux of organic particles (SED), we deployed a drifting, semi-Lagrangian array of sediment traps at eight depths (20, 30, 40, 50, 60, 90, 120, and 200 m). The array was free drifting or attached to an ice floe and was deployed for ca. 24 h. The sediment traps were parallel cylinders (7.2 cm in diameter, 45 cm height) mounted in a gimbaled frame equipped with a vane. At moderate current speeds, the cylinders remain vertical and perpendicular to the current direction. No baffles were used in the cylinders opening, and no fixatives were added to the traps prior to deployment. After recovery, the contents of the two replicate sediment trap cylinders were pooled into

plastic bottles and kept cold and dark until processing for POC as described above.

Inverse Model Specification

To estimate the carbon flows between food web compartments with the linear inverse model (LIM), we need food web topology (matrix E), the measured compartment biomasses and rates of change therein ($\Delta \text{biomass}/\Delta t$; vector f), and a set of quantitative constraints. The constraints can be directly measured by flows of the food web (hard constraints), or plausible physiological properties usually based on a literature search, which set the upper or lower bounds of flows (weak constraints). E.g., it is reasonable to consider all food web flows to be non-negative. The web topology (matrix E) describes the mass balances of the compartments, i.e., the flows of mass in and out of pre-defined compartments and is constructed based on our understanding of trophic relationships (who eats what). There are as many columns in matrix E as there are flows in the food web, and as many rows as there are compartments. The E matrix and f vector combined obey the conservation of mass principle, i.e., the compartment mass change equals to the sum of flows in, minus the sum of flows out of the compartment. Each compartment has its own mass balance equation, with unknown food web flow values. To solve the inverse problem, we need to find the unknown food web flows, forming a solution vector x , which simultaneously satisfies all the mass balances equations. In a matrix format the system of linear equations to be solved is:

$$E^*x = f$$

where matrix E is made of the coefficients in the mass balance equation, the solution vector x has a length equal to the number of columns in E , and the compartment mass change vector f has a length equal to the rows of E . Further, the solution vector has to satisfy a set of quantitative constraints. If some of the food web flows, or combination of flows, are measured from the food web under study (hard constraints), we constrain that flow,

or combination of flows, to a particular value, which the solution vector has to satisfy. Each measured flow adds another equation to the system of linear equations. The solution vector also has to satisfy weak constraints (coefficients in matrix G), which set the upper or lower limits (vector h) to certain food web flows:

$$G^*x \geq h$$

E.g., food assimilation cannot be more than food intake by the organisms. Unlike more conventional modeling, which is a predictive tool to forecast changes in standing stocks form a set of deduced properties, inverse modeling does not predict, but inversely back-calculates the properties from observed data and plausible constraints.

In our study we grouped the pelagic food web components into 10 compartments, eight living and two non-living, for which mass balance equations were constructed (**Supplementary Table S1**). The eight living compartments of organism groups comprised the three size classes of autotrophs (PHY0, $<3 \mu\text{m}$; PHY1, $3\text{--}10 \mu\text{m}$; PHY2, $>10 \mu\text{m}$, containing also the colonial *Phaeocystis*), heterotrophic bacteria (BAC), heterotrophic nanoflagellates enumerated with flow-cytometry (HNF), microzooplankton (μZOO), and two size classes of mesozooplankton (ZOO1, ZOO2; **Table 2**). The two non-living compartments were dissolved organic carbon (DOC) and detritus (DET, derived from measured POC minus the carbon biomass of living compartments). All compartments were expressed in units of organic carbon (mg C m^{-3}), and for the inverse reconstruction integrated to the upper 40 m layer (mg C m^{-2}). The upper 40 m layer included the surface mixed layer, and in most cases the euphotic layer (**Table 1**).

The inverse model had three external flows: (i) primary production (GPP), fueling new organic carbon into the food web, and two flows by which carbon left the food web, (ii) respiration, and (iii) sedimentation of organic particles (SED). The model was driven by primary production, measured at each station,

TABLE 2 | Abbreviations of the planktonic food web compartments, the respective stock sizes (mg C m^{-2}) in the upper 40 m water column, and changes of stocks ($\text{mg C m}^{-2}\text{d}^{-1}$) in stations P1–P7.

Comp	P1	P3	P4	P5	P6	P7
PHY0	1350 (+186)	3070 (+24)	593 (–71)	1490 (+108)	364 (–158)	604 (+165)
PHY1	670 (–40)	1100 (–53)	1280 (–60)	327 (+19)	187 (–100)	268 (+103)
PHY2	5020 (+150)	7540 (+6)	4300 (–93)	388 (–1.6)	453 (–137)	598 (+112)
ΣP	7040 (+295)	11700 (–23)	6170 (–225)	2200 (–125)	1000 (–396)	1470 (+380)
BAC	437 (+8.7)	803 (–6.8)	867 (–59)	655 (+7.3)	509 (–168)	856 (+34)
HNF	100 (+38)	357 (–30)	613 (–91)	368 (+4.6)	287 (–139)	224 (+1.7)
μZOO	261 (+37)	418 (–23)	238 (–54)	944 (+4.6)	761 (–139)	910 (–28)
ZOO1	311 (+26)	124 (+9.0)	81 (+0.7)	149 (+13)	214 (+0.4)	382 (+35)
ZOO2	633 (+24)	627 (+4.6)	843 (+1.7)	364 (+7.7)	593 (+1.2)	800 (+27)
ΣZ	1310 (+125)	1530 (–40)	1780 (–143)	1830 (+30)	1860 (–276)	2320 (+36)
DET	220 (+80)	4430 (–11)	6670 (–81)	4220 (+9.3)	3720 (–122)	3260 (+66)
DOC	28500 (+1071)	31300 (+399)	25500 (+79)	29900 (+62)	28400 (–150)	29200 (+20)

PHY0, pico autotrophs $< 3 \mu\text{m}$; PHY1, nano autotrophs $3\text{--}10 \mu\text{m}$; PHY2, micro autotrophs $> 10 \mu\text{m}$, including colonial *Phaeocystis*; BAC, heterotrophic bacteria; HNF, heterotrophic nanoflagellates; μZOO , microzooplankton (ciliates and heterotrophic dinoflagellates); ZOO1, mesozooplankton $< 4 \text{ mm}$; ZOO2, mesozooplankton $> 4 \text{ mm}$ (inc. *Calanus* spp.); DET, detritus; DOC, dissolved organic carbon. ΣP , sum of phototrophs; ΣZ , sum of grazers (HNF + μZOO + ZOO1 + ZOO2).

and integrated vertically to 40 m depth through trapezoidal integration ($\text{mg C m}^{-2} \text{d}^{-1}$).

The measured community respiration (ComResp) was the sum of respiration by all living compartments (three size classes of phytoplankton, bacteria, heterotrophic nanoflagellates, and microzooplankton), with the exception of mesozooplankton. Community respiration measurements were conducted from the upper mixed layer, intermediate layer and chlorophyll maximum, and integrated vertically through trapezoidal integration ($\text{mg C m}^{-2} \text{d}^{-1}$), assuming 1:1 ratio (O:C).

Sedimentation of organic particles was measured as POC ($\text{mg POC m}^{-2} \text{d}^{-1}$) and partitioned by the food web model between three compartments: detritus (DET), large phytoplankton (PHY2), and mesozooplankton fecal pellets.

All three phototrophic compartments acquired CO_2 for photosynthesis, incorporated part of organic carbon as biomass (measured as particulate primary production), and exuded part of the organic carbon to the DOC pool (measured as dissolved primary production), and part of the carbon was respired back to CO_2 . A fraction of the phototrophic biomass was lost to detritus through processes like mortality and lysis. Only the largest phytoplankton fraction (PHY2) contributed directly to sinking particles; smaller phytoplankton fractions contributed to vertical flux indirectly through detritus.

Bacteria took up DOC from the environment (bacterial assimilation), part of it was respired to CO_2 , and part was incorporated into biomass (measured as net bacterial production). Bacterial biomass was lost to detritus through mortality. Viral lysis of bacteria can release significant amount of DOC also in high latitude marine environments (Chénard and Lauro, 2017), which is again taken up by the bacterial community. This viral loop and other causes of inter-bacterial DOC cycling are not dealt with explicitly here and are all incorporated into the bacterial compartment in our model.

Heterotrophic nanoflagellates and microzooplankton fed on smaller living compartments, microzooplankton also on detritus, and lost biomass through respiration to CO_2 , exudation of organic matter to DOC, mortality to detritus, and through grazing by larger organisms. Microzooplankton, composed of heterotrophic dinoflagellates and ciliates in our study, are known grazers on *Phaeocystis* (Grattepanche et al., 2011; Swalethorp et al., 2019), but the grazing pressure depends on whether the prymnesiophyte is in its single-cell or colonial form (Grattepanche et al., 2011). Further, heterotrophic dinoflagellates are known to be voracious predators of large phytoplankton like other dinoflagellates and diatoms (Olseng et al., 2002; Jeong et al., 2004). We therefore allowed microzooplankton to prey on all size classes of phototrophs. We are also aware that several microzooplankton taxa could be mixotrophic, as kleptoplasty is common in both, dinoflagellates and ciliates (Gast et al., 2007; Stoecker et al., 2009), but these pathways are currently not considered in our model.

Mesozooplankton grazed on detritus and all other heterotrophic and phototrophic compartments except bacteria, picophototrophs, and large mesozooplankton also nano phototrophs. Mesozooplankton lost biomass through DOC release (sloppy feeding and other processes), respiration, and

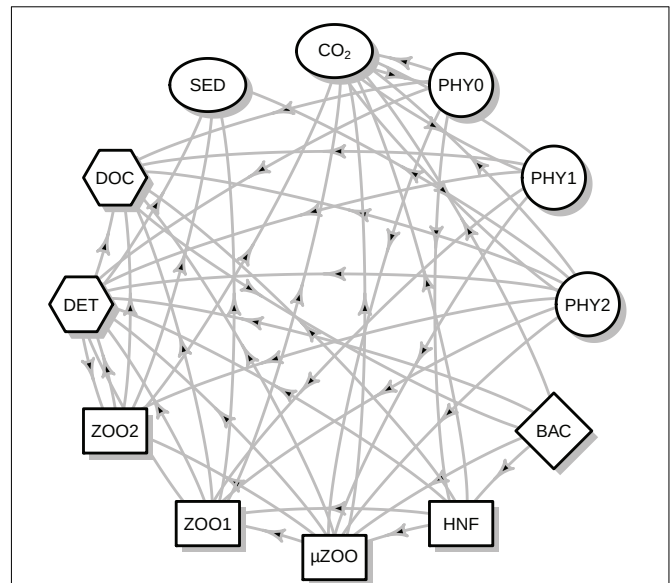


FIGURE 2 | Food web topology of the linear inverse models. The same topology was used for all stations. Arrows represent carbon flows between compartments. Autotrophic compartments are in circle: PHY0, pico autotrophs < 3 μm ; PHY1, nano autotrophs 3–10 μm ; PHY2, micro autotrophs > 10 μm including colonial *Phaeocystis*. Diamond: BAC, heterotrophic bacteria; Heterotrophic grazers are in rectangles: HNF, heterotrophic nanoflagellates; μZOO , microzooplankton; ZOO1, small mesozooplankton < 4 mm; ZOO2, large mesozooplankton > 4 mm; Non-living organic compartments are in hexagons: DOC, dissolved organic carbon; DET, detritus. External compartments, with no mass balance equations, are in ellipses: SED, sedimentary carbon; CO_2 , respired carbon.

defecation. Part of the feces contributed directly to sinking particles, the other part disintegrated in the water column and contributed to the detritus pool (Wexels Riser et al., 2002). The detritus compartment gained biomass through mortality of all living compartments, and lost biomass to DOC through bacterial and chemical degradation, and through sedimentation.

The food web topology, showing all the linkages between compartments, is outlined in **Figure 2**. To narrow the allowable ranges for the reconstructed food web flows, we set an array of biologically relevant constraints (**Supplementary Table S2**). All flows were expected to be non-negative. The particulate and dissolved primary production was partitioned between the three phototrophic size classes according to the respective biomasses, but allowing for allometric negative scaling between cell size and mass-specific photosynthesis rate (Maraóón et al., 2007). We thus constrained the mass-specific primary production for smaller autotrophs to be larger than for the subsequent large autotroph compartment, but not more than two times larger. Autotrophic respiration was constrained to between 1 and 55% of the gross primary production (Falkowski et al., 1985). Phytoplankton mortality was assumed to be at least 1% of the biomass per day.

For mesozooplankton we constrained the assimilation to be 40–80% of the food intake (Parsons et al., 2014). For other heterotrophic grazers (HNF, μZOO) the assimilation was assumed to be 80–90% of the food intake (Straile, 1997). Bacterial

assimilation efficiency was assumed to be 100%. Respiration of the heterotrophic compartments was partitioned into a maintenance respiration, constrained between 1 and 10% of their respective biomass, and respiration associated with growth, which was constrained to be at least 40% of the assimilated food for eukaryotes (Sanders et al., 1992), or at least 10% for bacteria (del Giorgio and Cole, 1998).

Mesozooplankton DOC release (sloppy feeding, other processes) was constrained to be between 1 and 50% of the food intake (Møller et al., 2003; Møller, 2004). Mesozooplankton defecation was constrained between 10 and 60% of the food intake, and was further partitioned into a vertical particle flux of rapidly sinking fecal pellets, and disintegration within the water column into the detritus pool (Wexels Riser et al., 2002). Further, the fraction of sinking fecal pellets was set to be less than the flow to detritus pool, to be consistent with field observations from the Barents Sea (Wexels Riser et al., 2002). Microzooplankton and heterotrophic nanoflagellate exudation to DOC pool was constrained between 1 and 10% of food intake, and mortality between 1 and 10% of biomass per day. Bacterial daily mortality was set to be 1–10% of the bacterial biomass.

If heterotrophic grazers did not discriminate between food sources, the grazing rates would be proportional to the biomass of the respective prey items. We allowed preferential grazing and some discrimination between food sources, but not more than 0.5–2.0 times the respective prey biomass ratios. Further, we assumed that zooplankton grazers (μ ZOO, ZOO1, and ZOO2) feed on both, living compartments and detritus, but that they prefer living prey. Therefore, the grazing rates on detritus divided by the grazing rates on live compartments was set lower than the biomass ratio of detritus to live prey compartments.

In summary, the inverse food web model had 10 compartments with mass balances (eight living, two non-living; **Figure 2** and **Supplementary Table S1**), five measured flows (community respiration, particulate and dissolved primary productions, bacterial net production, vertical flux of organic particles), 48 reconstructed food web flows (**Figure 2** and **Supplementary Table S3**), and 85 biological constraints (**Supplementary Table S2**). The inverse reconstruction was run with the LIM library of the R software (van Oevelen et al., 2010). The food web architecture and biological constraints were kept constant throughout the study and were applied for each individual data set from stations P1–P7. With 15 equations (10 mass balances plus 5 measured flows) and 48 unknown flows (rank parameter equal to 15), the system was under-determined and had infinite number of solutions, which satisfy the equations. A sensible choice is to follow the principle of parsimony, picking a solution with the minimum norm, i.e., the solution with the lowest sum of squared flow values.

However, this minimum norm solution is not based on ecological theory nor supported by empirical evidence. Further, it tends to push some of the flows to the lower bounds of their possible ranges, which should be considered extreme rather than likely values (Kones et al., 2006). We therefore opted here for the alternative likelihood approach, which considers all the possible solutions of the food web by sampling the probability density function (PDF) of LIM solution space by using a Markov Chain

Monte Carlo algorithm (Meersche et al., 2009). This approach has an interesting useful property: although the PDF of the LIM domain is uniform, emphasizing that all valid solutions are equally likely, the marginal probability density function (mPDF) of an individual flow is not uniform. This is because mPDF integrates over the valid areas of all other flows and therefore some selections within the individual flow range render as more likely (van Oevelen et al., 2010). We fed the *xsample()* function with initial minimum norm solution [obtained with function *lse()*] as an initial starting set and sampled the LIM solution space with 10,000 MCMC random draws. The *xsample()* MCMC algorithm uses a symmetrical random jump function that only depends on the previously accepted point to draw a new sample. Each of the realizations corresponds to an equally likely solution vector x of the food web flows, which obeys the mass balances, as well as the data and constraints. Here we summarize the likelihood of each individual flow as the mean ($\pm$ SD) of the sampled mPDF.

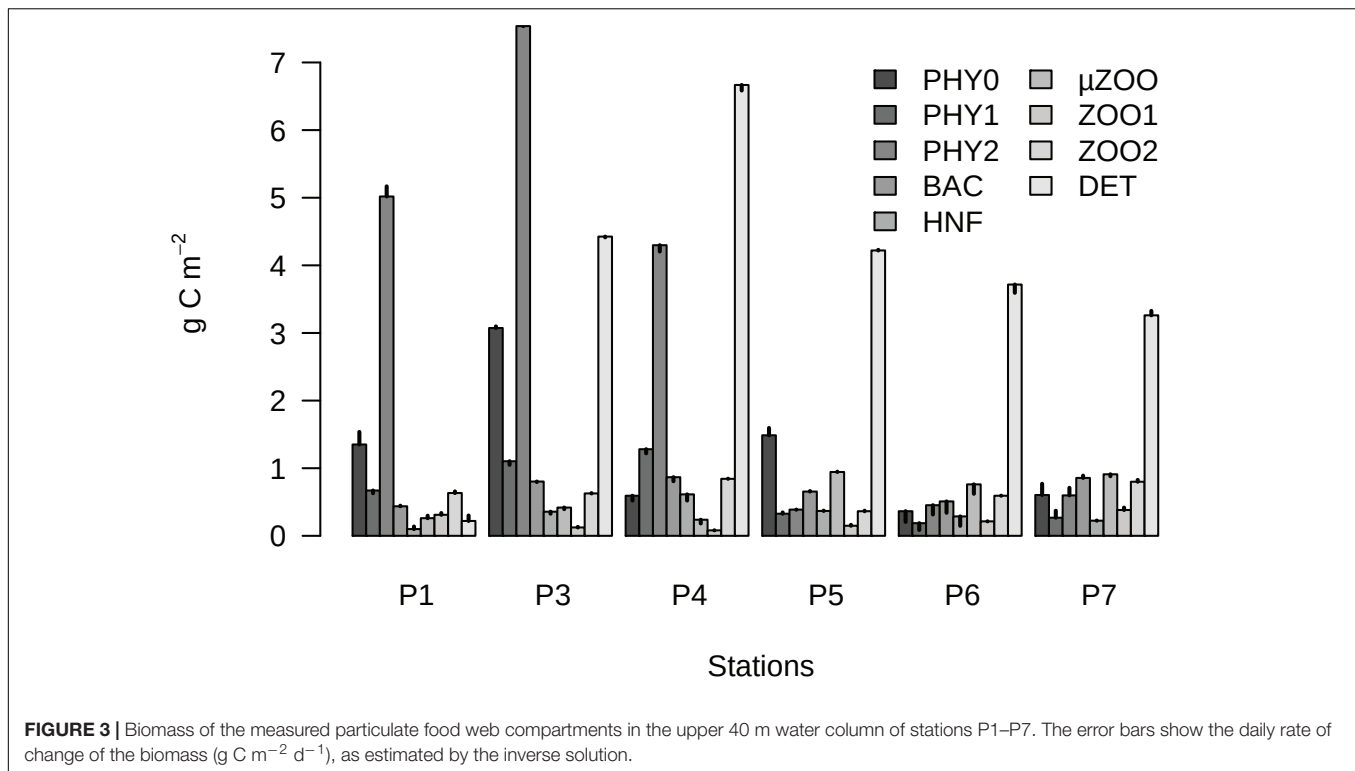
The mass balance equations are usually balanced with rates of change of the compartment biomasses, measured over a period of time (e.g., Forest et al., 2011). In our 24 h process stations no sensible time series was feasible, leaving us with an alternative to assume a steady state food web and consider the rates of biomass change to be zero. However, our measured boundary input flows (primary production) were not balanced by output boundary flows (community respiration plus sedimentation), thus rendering a steady state problem infeasible, unless we introduce new *ad hoc* export or advection functions. To balance the system, we relaxed the steady state assumption, and defined the compartment mass balances as *approximate*, not as *exact* equations in the inverse analysis *lse()* function, which then resolved the biomass changes in the minimum norm sense. This initial minimum norm solution was then inserted as the starting set to the *xsample()* function (see above).

RESULTS

Measured Biomasses

The measured organic carbon masses of the living and non-living compartments, and their reconstructed rates of change, are given in **Table 2**. The raw vertical profiles of biomasses and flows are presented in **Supplementary Figures S1–S5**. The largest organic carbon pool was in the dissolved fraction (25–31 g C m⁻²). DOC exceeded the particulate carbon pool generally by a factor of 3–4, but only by a factor of 1.6–1.7 during the peak and decline phases of the algal bloom (P3 and P4).

The partitioning of the particulate organic carbon revealed a conspicuous and rapid shift from phytoplankton to detritus domination, as the season progressed (**Figure 3**). The early bloom stage had a very low detritus biomass (ca 0.2 g C m⁻²), but a substantial phytoplankton biomass (>7 g C m⁻²), mostly in the larger micro fraction (5 g C m⁻²). By the peak of the bloom the phytoplankton biomass had increased further (up to ca 12 g C m⁻²; mainly in the micro and pico fractions), but there was also a substantial build-up of detritus (up to 4.4 g C m⁻²). By the late bloom stage, the detritus biomass



reached its peak (ca. 6.7 g C m⁻²), while the phytoplankton was on decline (6.2 g C m⁻²). The bloom progression in May followed a shift from *Phaeocystis pouchetii* dominance to a co-dominance with guild of diatoms from the genera *Chaetoceros* (*Chaetoceros socialis*, *Chaetoceros holsaticus*, and *Chaetoceros furcellatus*), *Thalassiosira* (*Thalassiosira hyaline* and *Thalassiosira nordenskiöldii*), *Fragillariopsis* (*Fragillariopsis oceanica* and *Fragillariopsis furcellatus*), and the presence of medium-sized dinoflagellates from the genera *Gymnodinium* and *Protoperidinium*. The post bloom stages in August had only a modest phytoplankton biomass (1–2 g C m⁻²), but the detritus remained high (3.2–4.2 g C m⁻²). Overall the percentage of detritus from POC increased from 2.4 to 24% to 43%, as the bloom progressed in May and varied between 41 and 52% in August. The dominant phytoplankton groups in August were small flagellates, coccolithophorids, cryptophytes, (*Teleaulax*) chrysophytes (*Dinobryon*), chlorophytes (*Pyraminonas*), dinoflagellated (*Gymnodinium* and *Oxyrrhis*), but also some diatoms and *Phaeocystis pouchetii*.

The lower food web components followed the evolution of the successional stages (Table 2). Bacterial biomass doubled from the early to peak and late bloom phases (from 440 to 870 mg C m⁻²) and remained high during the post bloom stages (510–860 mg C m⁻²). Heterotrophic nanoflagellates revealed a rapid biomass increase from early to late bloom (100–610 mg C m⁻²) and retained a modest biomass during post bloom stages (220–370 mg C m⁻²). Microzooplankton retained low biomass during all the bloom stages (240–420 mg C m⁻²) but increased notably during the post bloom stages (760–940 mg C m⁻²). Mesozooplankton biomass

revealed no discernible pattern related to the successional stages, and varied between 80–380 mg C m⁻², and 360–840 mg C m⁻², for the small and large fractions, respectively.

External Flows

The measured external flows were the gross primary production (GPP) into the system, and two competing flows out of the system, respiration and sedimentation. GPP decreased from 2.85 to 1.33 to 0.65 g C m⁻² d⁻¹ and varied between 0.29 and 1 g C m⁻² d⁻¹, during the post bloom phases (Figure 4).

Respiration always exceeded the sedimentation losses (Figure 4), indicating the relative efficiency of the food web in retaining energy resources. The inverse reconstruction partitioned the majority of the community respiration during the pre-bloom phase to bacteria (500 mg C m⁻² d⁻¹, corresponding to 68% of the community respiration), but the rate and proportion decreased rapidly as the bloom progressed (to 50 and 33% at peak and late bloom stages, respectively). Concomitantly, the respiration of the phototrophic compartments increased from 9% during the pre-bloom state to >16% thereafter, and the sum of grazer respiration from 23 to >60% as the community matured during late and post bloom stages (Figure 5).

Sedimentation was relatively higher (251–529 mg C m⁻² d⁻¹) during the bloom stage in May, and 145–223 mg C m⁻² d⁻¹ in August. The vertical flux of organic particles increased from 19 to 20 to 38% of the GPP during the early, peak, and late bloom phases in May, and varied between low values of 17% (P5) to as high as 70% (P7) during post bloom phases. Overall, sedimentation losses were 5.8% of the total particulate carbon standing stock during the early bloom stage,

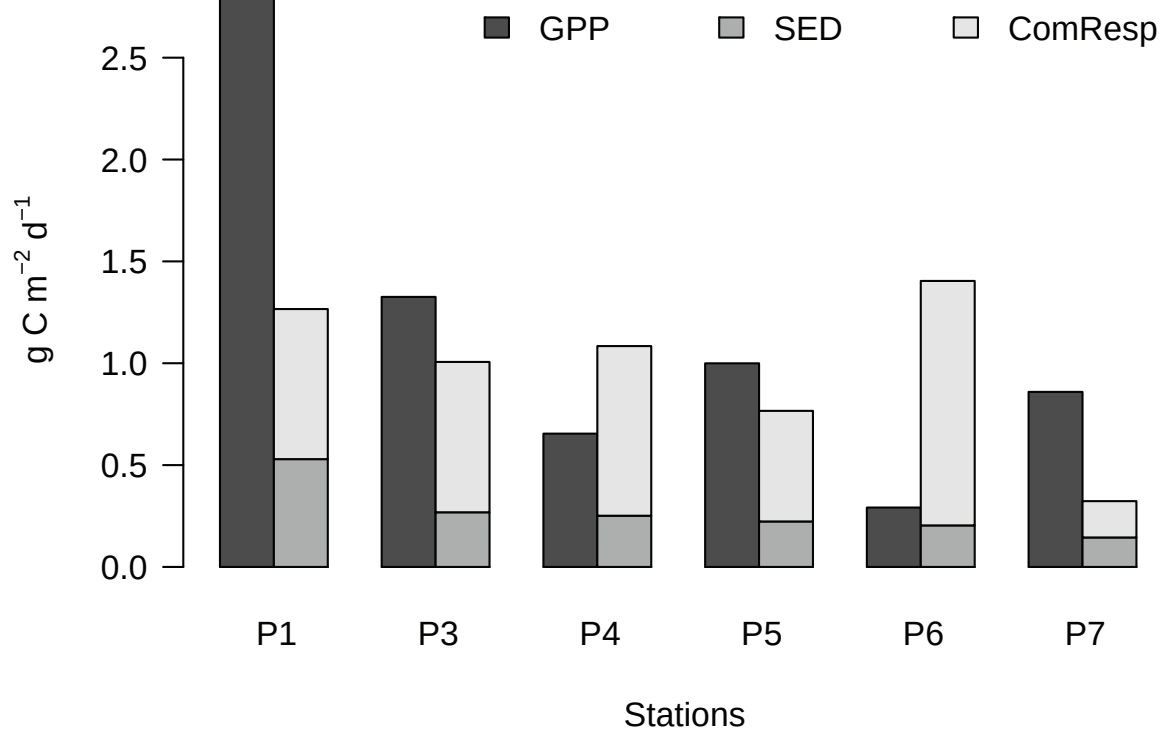


FIGURE 4 | External flows into the food web, gross primary production (GPP), and two loss rates: the vertical flux of particles (SED), and community respiration (ComResp). Whenever GPP exceeds the sum of SED and ComResp, the food web is increasing in mass, and vice versa.

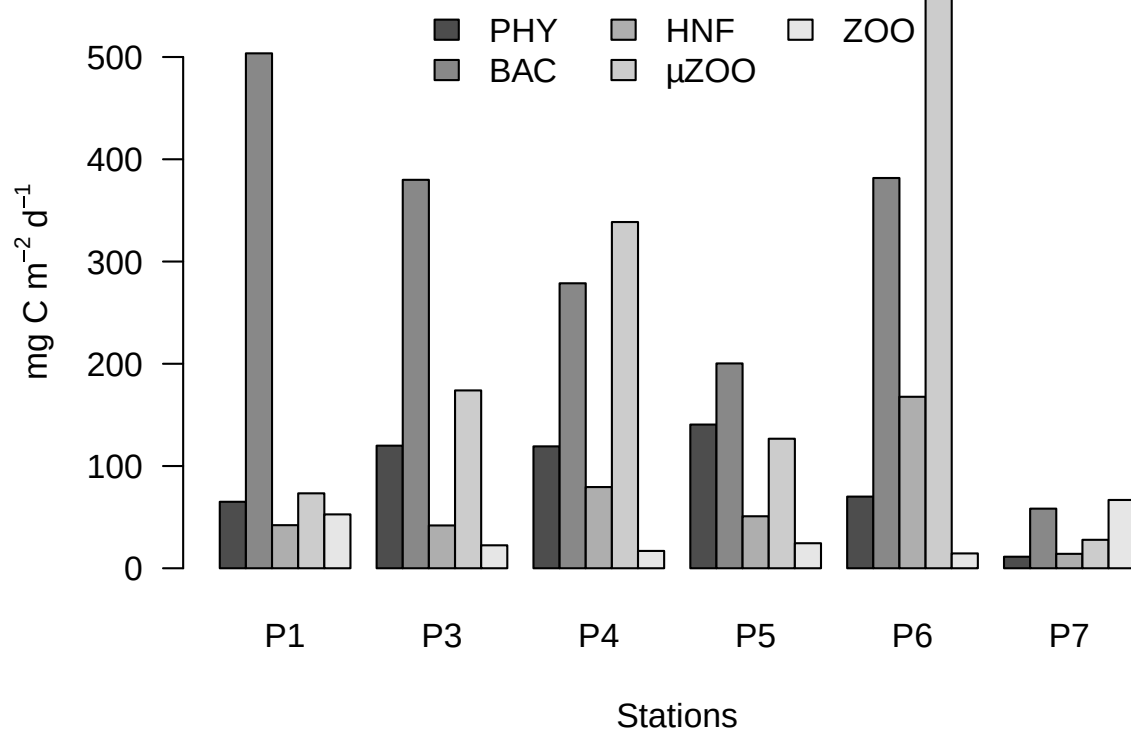


FIGURE 5 | Partitioning of the community respiration flows. Note that all phototrophs are pooled into PHY, and the two mesozooplankton size classes into ZOO.

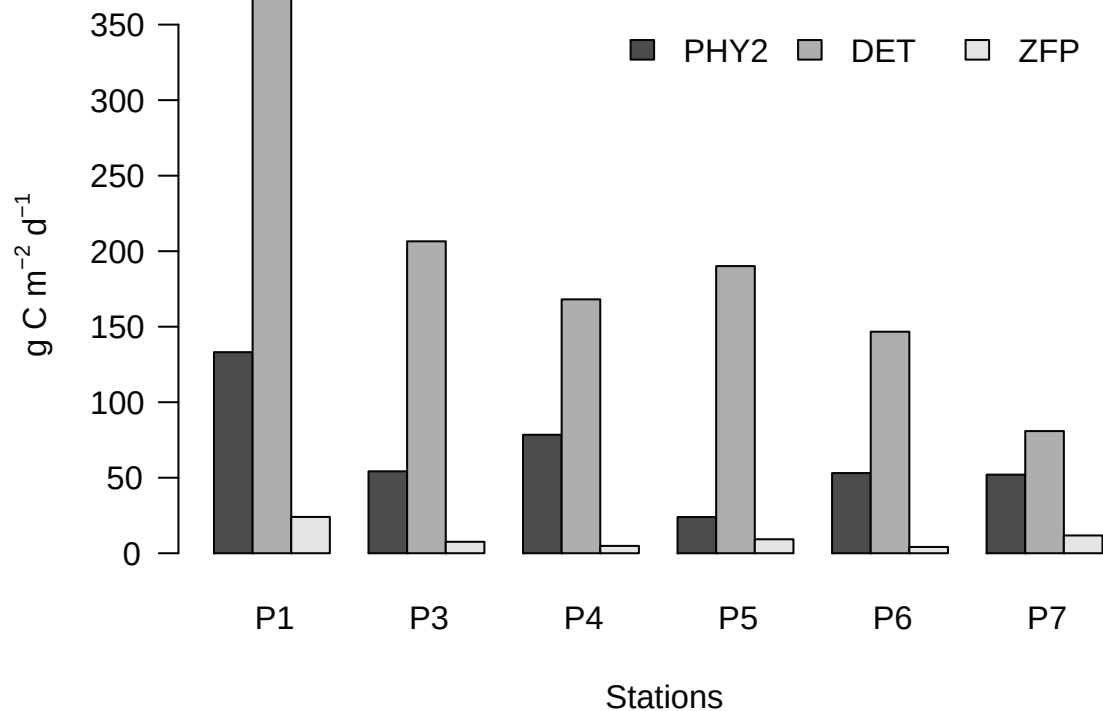


FIGURE 6 | Partitioning of the vertical flux of organic particles. ZFP denoted direct vertical flux of fecal pellet carbon combined from both mesozooplankton size classes.

and only <3% thereafter. The vertical flux of organic particles was predominantly partitioned between detritus (56–85%) and phytoplankton (11–36%), while zooplankton fecal pellets contributed a minor fraction (**Figure 6**).

The difference between the carbon flows in and out of the system shows the growth or shrinkage of the food web. **Figure 4** shows the sum of the external flows, indicating a rapid growth of the system mass during the early bloom phase, where GPP exceeded the sum of respiration and sedimentation losses by $1.6 \text{ g C m}^{-2} \text{ d}^{-1}$. This increase of the food web continued during the peak bloom phase at a slower pace ($0.3 \text{ g C m}^{-2} \text{ d}^{-1}$) and turned into system shrinkage at the late stage of the bloom ($-0.4 \text{ g C m}^{-2} \text{ d}^{-1}$). The post bloom stages showed variation in both directions (**Figure 4**). The food web turned net heterotrophic during the bloom decline phase, and in station P6 during the post bloom stage, where GPP was 78 and 24% of community respiration, respectively.

Reconstructed Internal Food Web Flows

The internal flow pattern was dominated by two flows, exudation by phytoplankton into the DOC pool, and bacterial assimilation of DOC (**Figure 7** and **Supplementary Table S3**). Phytoplankton exudation varied by more than an order of magnitude and was highest during the early bloom stage ($1565 \text{ mg C m}^{-2} \text{ d}^{-1}$), dropped rapidly thereafter to $620 \text{ mg C m}^{-2} \text{ d}^{-1}$ during the peak bloom, and to $205 \text{ mg C m}^{-2} \text{ d}^{-1}$ and below in late and post bloom stages. Phytoplankton exudation formed a decreasing proportion, from 55 to 49 to 31%, of the GPP during the bloom

stages in May. During the post bloom stages in August the dissolved fraction of GPP was generally low, 9–12% (P5 and P7), and 26%, in P6. The other significant source of DOC was dissolution from detritus (up to $170 \text{ mg C m}^{-2} \text{ d}^{-1}$), which formed 1.6 to 4.6% of the detritus biomass, and 20 to 56% of the total food web DOC release (apart from the negligible <1% during the early bloom stage). Heterotrophic grazers contributed little to the DOC pool ($20\text{--}51 \text{ mg C m}^{-2} \text{ d}^{-1}$), which formed 2–18% of the total food web DOC release.

Bacterial assimilation was highest during the early and peak bloom stages, 535 and $406 \text{ mg C m}^{-2} \text{ d}^{-1}$, respectively, and decreased thereafter to $329 \text{ mg C m}^{-2} \text{ d}^{-1}$ and below (except $439 \text{ mg C m}^{-2} \text{ d}^{-1}$ in station P6). Bacterial assimilation was in correspondence with the rate of fresh DOC production, but statistically not significantly (Pearson $r = 0.77$, $p = 0.07$, $n = 6$).

Other internal flows were related to grazing by the zooplankton compartments (collectively $240\text{--}664 \text{ mg C m}^{-2} \text{ d}^{-1}$), as well as zooplankton mortality and defecation (up to $52 \text{ mg C m}^{-2} \text{ d}^{-1}$). Detritus formation was relatively stable ($401\text{--}468 \text{ mg C m}^{-2} \text{ d}^{-1}$) during the bloom phases in May, and somewhat more variable in August ($331\text{--}498 \text{ mg C m}^{-2} \text{ d}^{-1}$). The percentage of GPP channeled to detritus increased from 16 to 31 to 61% during the bloom progression in May and varied from 38% (P7) to 147% (P6) in August. The sources and sinks of detritus were approximately balanced, when averaged over all stations. The ratio between the sum of sources and sinks of detritus varied between 1.25 and 0.78 (mean 1.01 ± 0.19). On average half of the detritus ($194 \pm 98 \text{ mg C m}^{-2} \text{ d}^{-1}$) settled out

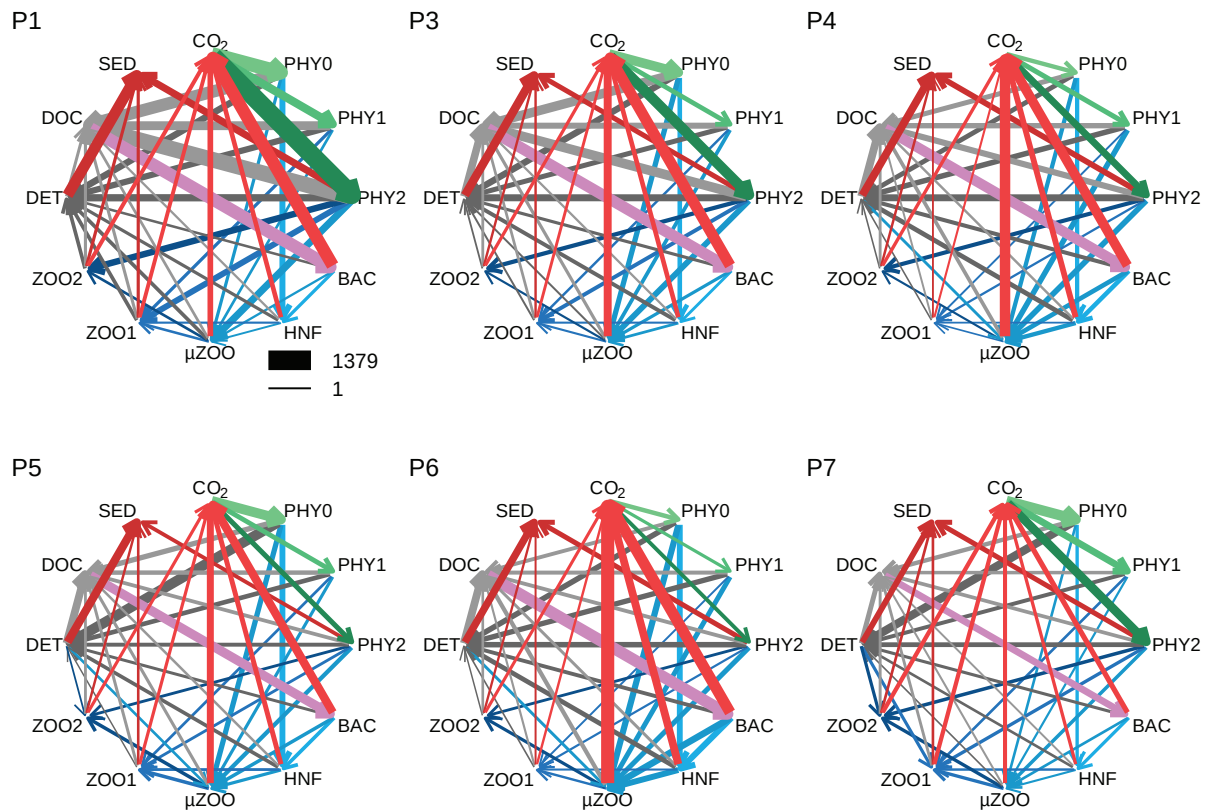


FIGURE 7 | The carbon flows in stations P1–P7, as reconstructed from the field measurements by the inverse method (numerical values in **Supplementary Table S3**). The thickness of arrows is proportional to the square root of the respective flows, and have the same scale in all plots, as indicated by the legend ($\text{mg C m}^{-2} \text{ d}^{-1}$). Note the very low primary production in P6. Phototrophic flows are in green, carbon losses to SED and CO_2 are in red, grazing flows are blue, bacterial assimilation violet, and flows to non-living organic compartments, DOC and DET, are in gray.

of the water column, the other half was almost equally partitioned between dissolution ($119 \pm 70 \text{ mg C m}^{-2} \text{ d}^{-1}$) and grazing ($119 \pm 81 \text{ mg C m}^{-2} \text{ d}^{-1}$). On average, microzooplankton was the main detritivorous group ($86 \text{ mg C m}^{-2} \text{ d}^{-1}$; 62% of detritory), followed by large ($18 \text{ mg C m}^{-2} \text{ d}^{-1}$; 21%) and small ($14 \text{ mg C m}^{-2} \text{ d}^{-1}$; 17%) mesozooplankton.

Sensitivity Analysis

To increase confidence in the model, we analyzed the robustness of the reconstructed fluxes to changes in the 10 measured compartment biomasses and the five measured flows. The sensitivity analysis was done by perturbing each measured input at a time by $\pm 10\%$, while keeping other variables unchanged. The six stations and fifteen input variables, each increased and decreased by 10%, resulted in 180 perturbed food web models and 178 successful solutions. Most flow values changed somewhat after perturbation. For each solution we calculated the absolute sum of these changes. The sum of absolute flow changes, as percentage of the sum of flows in the original unperturbed system was calculated as a variation index for each of the input variable. We used both, the minimum norm, and the likelihood approaches to test the model sensitivity. Both methods gave similar results and for consistency we here present the likelihood approach.

Sensitivity analysis shows that the variation index always remained below 10%, regardless of the input variable perturbed (**Figure 8**). Nevertheless, the overall sensitivity of the reconstructions depended on which input variable was perturbed. Firstly, the inverse solutions tended to be less sensitive to perturbations in the standing stock biomass estimates (PHY0, PHY1, ..., DOC), and more sensitive to boundary condition rate measurements (SED, ComResp, and GPP). The high variability within the individual effects (1–7%; **Figure 8**) indicated that the food web sensitivity during different stages of the bloom development also varied considerably. In summary, our sensitivity analysis indicates that small systematic errors in the input data would not affect the inverse solution in a disproportionate manner.

DISCUSSION

The seasonal stages and community maturation were reflected in the considerable diversity of the food web flows, even though the structural assumptions of the food webs were kept constant. The over-arching commonality was the dissolved fraction as the largest organic carbon pool. Only during the peak and decline phases of the algal bloom did the substantial

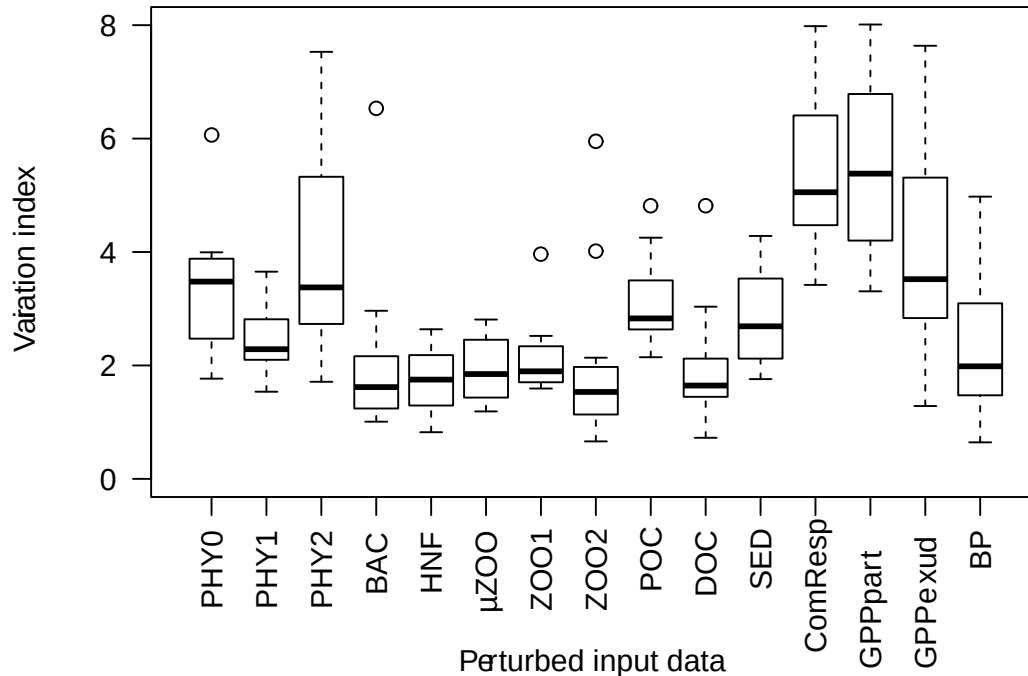


FIGURE 8 | Sensitivity analysis. The boxplots show the spread in the variation index over stations P1–P7. Variation index is calculated as the sum of absolute reconstructed flow changes after perturbing each input variable (x-axis) at a time and divided by the sum of flows in the unperturbed food web. SED, vertical flux of organic particles; ComResp, measured community respiration; GPPpart, particulate GPP; GPPexud, dissolved GPP; BP, net bacterial production; other x-axis abbreviations as in **Table 2**.

build-up of phytoplankton and detritus, respectively, result in relatively lower difference between the dissolved and particulate organic carbon pools.

The input and consumption of DOC revealed considerable seasonal variation. The food web DOC release decreased rapidly during the bloom in May (from 1572 to 275 mg C m⁻² d⁻¹) and remained modest during post-bloom stages (<200 mg C m⁻² d⁻¹). Presumably the large input in spring was due to the predominance of colonial *Phaeocysts* during the bloom phase, which is known to produce conspicuous amounts of extracellular polysaccharides (Billen and Fontigny, 1987; Verity et al., 2007; Thornton, 2014). The released DOC was readily assimilated by bacteria (122–534 mg C m⁻² d⁻¹), but at a high respiration cost (200–504 mg C m⁻² d⁻¹; but in P7 only 58 mg C m⁻² d⁻¹). This led to a substantial seasonal dynamics of bacterial growth efficiency, from low values of 6% during the early and peak bloom phases to 16% at the bloom decline phase. The bacterial growth efficiency was variable, 22, 13, and 53%, during the post bloom stages. These values are within the range of literature reports from various oceanic systems (del Giorgio and Cole, 1998, and references therein). Our evidence thus points that the blooms of colonial *Phaeocysts* are a fresh source of DOC, but the quality of this substrate, low in nitrogen compounds, is low for bacterial consumption (Billen and Fontigny, 1987; Carlson et al., 1999; Williams et al., 2016), and the assimilation by the ambient assemblages has a high energetic cost. Further, bacteria consumed only 33–50% of the freshly released DOC during the early and peak

bloom phases, but as much as 81% during the decline bloom phase. During the post-bloom stages in August the bacterial carbon assimilation matched fairly closely the instantaneous DOC release (80–86% in P5 and P7) or even exceeded it (152% in P6).

The seasonality, driven by the phytoplankton production and DOC release, cascaded through the food web, being more clearly expressed at the lower part of the food web. The seasonality in fresh DOC release was clearly discernible in bacterial biomass accumulation, which almost doubled from 437 mg C m⁻² at pre-bloom stage to 803 and 866 mg C m⁻² at peak and late bloom stages, a hallmark of *Phaeocysts* bloom associated bacterial activity (Billen and Fontigny, 1987). There was thus a time lag between the high DOC release at the early bloom stage, and the bacterial production and biomass response, further supporting only modest degradability of the *Phaeocysts* exudates (Carlson et al., 1999; Williams et al., 2016). Also, heterotrophic nanoflagellates revealed a very rapid biomass build up from 100 to 613 mg C m⁻² during the course of the bloom, suggesting a swift response to the increased resource availability. In contrast, microzooplankton, composed of large protists in our model, revealed only broad seasonal shifts in biomass between May and August, uncoupled from the dynamics of the bloom. The trophic cascade signal become indiscernible in the response of mesozooplankton compartments.

Another conspicuous seasonal feature was a shift from a system, where the POC pool was dominated by phytoplankton during the early bloom stage, to a system dominated by detritus.

This indicates that during the polar winter the water column comes to be low in organic particles, and the new seasonal build-up of POC is initiated by phytoplankton. The rapid build-up of detritus during the early, peak, and decline phases of the bloom, from 220 to 4425 to 6667 mg C m^{-2} were in line with a substantial mortality loss of phytoplankton ($240\text{--}347 \text{ mg C m}^{-2} \text{ d}^{-1}$) already at an early seasonal stage of the community maturation.

The conspicuous shift in organic particle composition from phytoplankton to detritus dominance had a profound effect on zooplankton feeding. Mesozooplankton herbivory decreased from 92 to 78% to 69% of food intake during the bloom progression and was only between 20 and 28% during post bloom stages. During the post bloom stages the drop in herbivory was compensated by detritivory (27–62% of food intake), and carnivory (consumption of HNF and microzooplankton; 17–45% of food intake). The pattern was paralleled by microzooplankton, with rapid drop of herbivory from 97 to 72% to 45% during the bloom progression and staying at that level (32–55%) during the post bloom stages in August. The microzooplankton diet changed predominantly to detritus (27–43% of food intake), with carnivory (4–15%) and bacterivory (7–18%) of lower importance in August. The available evidence thus supports a flexible omnivorous feeding behavior of the dominant zooplankton groups, which is in line with recent studies from the Arctic (Forest et al., 2011; Vernet et al., 2017).

Community respiration was 26, 55, and 126% of GPP in the early, peak, and late bloom stages, indicating switching from net-phototrophy to net-heterotrophy as the spring bloom matured. During the post-bloom stages, the ratio of community respiration

to GPP varied even more, from 21% (P7) to 410% (P6), suggesting high spatial heterogeneity in the physical water mass as well as food webs properties over relatively short distances.

Due to the logistical reasons, compartment biomasses were measured only once per station, and rates of mass change were only approximated by the inverse analysis (Figure 3). Summing up the changes in particulate pools, i.e., the living compartments and detritus, gave the rate of mass change of the particulate organic carbon pool. As expected, there was a strong particulate biomass build-up during the early bloom phase ($509 \text{ mg C m}^{-2} \text{ d}^{-1}$), which turned into a biomass decrease already during the peak ($-80 \text{ mg C m}^{-2} \text{ d}^{-1}$), and even more so during the bloom decline phase ($-509 \text{ mg C m}^{-2} \text{ d}^{-1}$). During the post-bloom stages, the biomass change rates varied even more, from $516 \text{ mg C m}^{-2} \text{ d}^{-1}$ (P7) to $-962 \text{ mg C m}^{-2} \text{ d}^{-1}$ (P6), underlining the high heterogeneity of water masses in close spatial proximity in the Arctic marginal ice zone. The rate of biomass change divided by the GPP indicates the efficiency of the food web to convert primary production to particulate matter. The ratio was relatively low, 0.18, during the early bloom phase, and the positive values during post bloom stages ranged from 0.17 (P5) to 0.6 (P7).

The sum of grazing flows by heterotrophic nanoflagellates, micro- and mesozooplankton ranged from 268 to $834 \text{ mg C m}^{-2} \text{ d}^{-1}$, with no clear seasonal pattern. The total grazing pressure increased from 17 to 27 to 77% of GPP, as the bloom progressed in May. In August the grazing pressure was 31–44%, except in P6, where it was exceptionally high (286%). This suggests that the high gross primary production

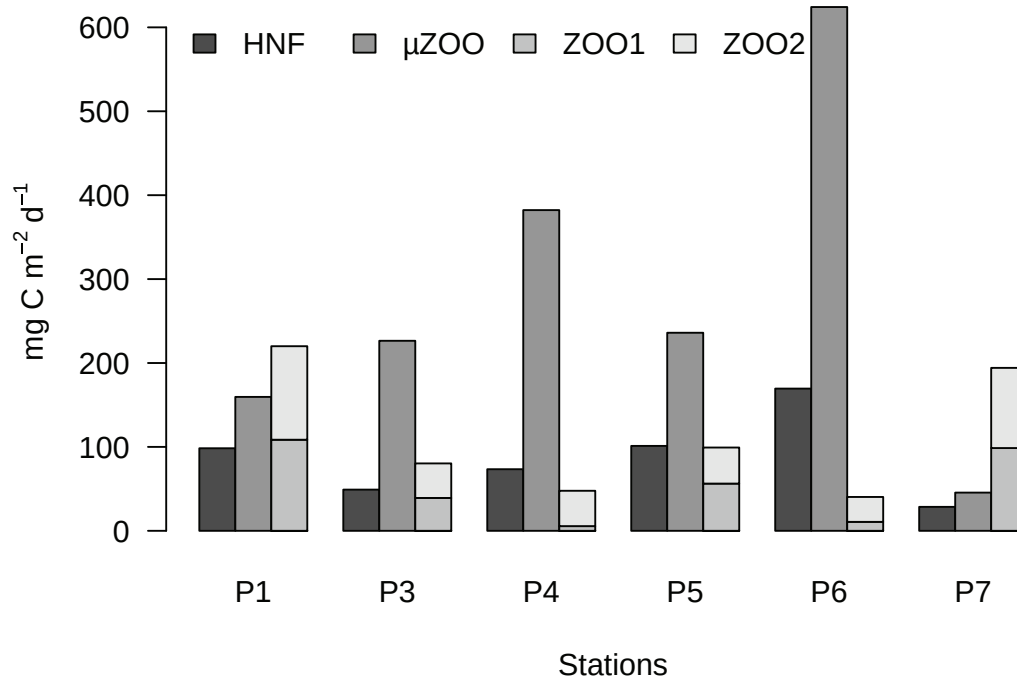


FIGURE 9 | Partitioning of sum of grazing flows into the main heterotrophic grazer compartments. The mesozooplankton compartments are stacked to give the total carbon flow into mesozooplankton.

during a *Phaeocystis* dominated bloom does not support a high carbon turnover in the grazing food web. This is in line with the poor usability of *Phaeocystis* derived dissolved organic carbon by heterotrophic bacteria.

Partitioning the carbon turnover by heterotrophic grazers revealed high variability, an increasing role of microzooplankton during the bloom progression in May, and approximately equal mean apportionment between the two size classes of mesozooplankton (Figure 9). Averaging the carbon intake over all the six stations revealed microzooplankton as the most important grazer group ($279 \pm 202 \text{ mg C m}^{-2} \text{ d}^{-1}$), followed by the sum of the two mesozooplankton compartments ($113 \pm 76 \text{ mg C m}^{-2} \text{ d}^{-1}$), and heterotrophic nanoflagellates ($87 \pm 49 \text{ mg C m}^{-2} \text{ d}^{-1}$). Microzooplankton has been recognized as a main grazer compartment globally, estimated to consume over half of the daily global planktonic primary production (Calbet and Landry, 2004; Schmoker et al., 2013). Further, several specialized microzooplankton taxa, like the heterotrophic *Gymnodinium* and *Gyrodinium* species, and tintinnid ciliates, are known to prey upon *Phaeocystis* cells (Grattepanche et al., 2011; Swalethorp et al., 2019). This takes place particularly in the late bloom stage, when single cells are often released from colonies possibly when nutrients become limited (Jakobsen and Tang, 2002; Nejstgaard et al., 2007).

AUTHOR CONTRIBUTIONS

KO participated in the cruises, designed the study, conducted the model analysis, and was in charge of the writing. EH, MV,

PL, GF, MS-M, MP, and MR provided data for the model, participated in food web construction, data interpretation and writing. EH provided all the mesozooplankton data and searched or measured the values for mesozooplankton carbon content. MV provided data on particulate and dissolved primary production. PL and GF contributed with the microzooplankton data. MS-M provided the data for community respiration. MP provided data for microbial components and TOC. MR organized the cruise, was in charge of the project, and provided the data for chlorophyll, POC, and vertical flux.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: <https://www.frontiersin.org/articles/10.3389/fmars.2019.00244/full#supplementary-material>

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Valuing Blue Carbon Changes in the Arctic Ocean

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The ocean capacity to store carbon is crucial, and currently absorbs about 25% CO₂ supply to the atmosphere. The ability to store carbon has an economic value, but such estimates are not common for ocean environments, and not yet estimated for the Arctic Ocean. With the severe climatic changes in the Arctic Ocean, impacting sea ice and potentially the vertical carbon transport mechanisms, a projection of future changes in Arctic Ocean carbon storage is also of interest. In order to value present and evolving carbon storage in the changing Arctic marine environment we combine an ocean model with an economic analysis. Placing a value on these changes helps articulate the importance of the carbon storage service to society. The standing stock and fluxes of organic and inorganic carbon from the atmosphere, rivers, shelves and through the gateways linking to lower latitudes, and to the deep of the Arctic Ocean are investigated using the physically chemically biologically coupled SINMOD model. To obtain indications of the effect of climate change, trajectories of two IPCC climate scenarios RCP 4.5, and RCP 8.5 from the Max Planck Institute were used for the period 2006–2099. The results show an increase in the net carbon storage in the Arctic Ocean in this time period to be 1.0 and 2.3% in the RCP 4.5 and RCP 8.5 scenarios, respectively. Most of this increase is caused by an increased atmospheric CO₂ uptake until 2070. The continued increase in inorganic carbon storage between 2070 and 2099 results from increased horizontal influx from lower latitude marine regions. First estimates of carbon storage values in the Arctic Ocean are calculated using the social cost of carbon (SCC) and carbon market values as two outer bounds from 2019 to 2099, based on the simulated scenarios. We find the Arctic Ocean will over the time period studied increase its storage of carbon to a value of between €27.6 billion and €1 trillion. This paper clearly neglects a multitude of different negative consequences of climate change in the Arctic, but points to the fact that there are also some positive counterbalancing effects.

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INTRODUCTION

Due to climate change, the Arctic is undergoing rapid transformation (IPCC, 2014; Comiso et al., 2017). The loss of Arctic sea ice is recognized as one of the main indicators of global warming and also affects the ice cover and extent, which shows a decadal decrease of about 13% based on the September minimum extent (Serreze and Stroeve, 2015). Moreover, also the perennial ice cover

shows a similar decadal loss of 11% (Comiso et al., 2017). The loss of summer sea ice has amplified the effect of warming, and currently the Arctic warming is taking place 2–3 times faster than global rates (Comiso and Hall, 2014; Meier et al., 2014; Serreze and Stroeve, 2015). Important ecosystem services exist in the Arctic, including fish and seafood, primary production, nutrient cycling and carbon storage¹. The reduction in ice cover changes and transforms the services provided in the region, resulting in both benefits and costs, as some services are traded off when new ones emerge (Armstrong and Foley, 2018). Where sea ice once served as an impediment, new opportunities are opening for provisioning services of shipping, fishing and natural resource extraction (Meier et al., 2014), as well as the regulating service of carbon storage. The temporary storage of CO₂ in the various components of marine systems provides an important service in regulating atmospheric CO₂ concentration since it prevents the absorbed CO₂ from immediately contributing to the greenhouse effect thus slowing climate change (Melaku Canu et al., 2015).

The oceans serve as the world's largest carbon pool, removing about 25% of atmospheric carbon dioxide emitted by human activities from 2000 to 2007 (Bakker et al., 2016). Of all the biological carbon captured, over half is found in marine living organisms (Nellemann et al., 2009). Marine primary production in the Arctic Ocean is reported to have increased over the last decade mainly due to a decrease in the ice cover, and is expected to continue to increase in the future (Babin et al., 2015). With increased primary production, carbon storage is also expected to increase, though there are large possible regional variations mainly due to stratification which inhibits supply of nutrients from deep waters (Barber et al., 2015; Slagstad et al., 2015). The ability to store carbon has an economic value, but such estimates are not common for ocean environments (blue carbon), and not yet estimated for the Arctic Ocean. Applying a monetary value to the forecasted carbon storage informs policy in the future role of Arctic Ocean blue carbon in climate change mitigation while also highlighting the importance of the service to society. The objective of this paper is to project future changes in Arctic Ocean carbon storage and place a monetary value on present and evolving carbon storage. This is achieved using the physically chemically biologically coupled SINMOD model and later combining the model with an economic analysis of societal and market costs of carbon.

The linkages between nature and the economy are often described using the concept of ecosystem services, or flows of value to human societies as a result of the state and quantity of natural capital (TEEB, 2010). Ocean ecosystems provide a number of services including nurseries and fishing grounds, coastal defenses, climate regulation, and recreation. In recent years a number of studies of ecosystem services and values in marine environments have been carried out, though largely focusing on coastal areas (de Groot et al., 2012; Lique et al., 2013; Beaumont et al., 2014). Valuing ecosystem services captures

the dependence of human well-being on natural capital and the flow of services provided, giving input into how to manage human interaction with these environments and to take into account potential trade-offs between services (Armstrong and Foley, 2018). In the Arctic Ocean important services currently exist and new ones are emerging with retreating ice. Though provisioning services of fish are usually the main ecosystem service valued in the oceans (Liquete et al., 2013; Zarate-Barrera and Maldonado, 2015), the focus of this paper are the regulating services that provide benefits via processes taking place in nature. In the Arctic Ocean these services include water circulation and exchange, and gas and climate regulation. Carbon cycling, the carbon exchange that allows Earth to sustain life, is often categorized as a supporting service, i.e., a service that feeds into most direct services from ecosystems, be they provisioning, regulating, or cultural. However, carbon storage, the natural storage of anthropogenic carbon emissions, is also clearly a regulating service that reduces the costs of climate change via absorption of CO₂ from the atmosphere. With the changing Arctic an increase in uptake of carbon may be expected due to a rise in primary production and reduced ice cover (Slagstad et al., 2015).

While scientific studies of carbon storage have largely concentrated on terrestrial forests, there is now a “blue carbon” initiative pushing for further recognition of the oceans as a climate mitigating environment providing vital regulating services for the wellbeing of humankind. Economic valuation of “blue carbon” sequestration has focused on coastal areas (Pendleton et al., 2012; Luisetti et al., 2013), and studies of ocean ecosystems in this context are limited (Beaumont et al., 2008; Melaku Canu et al., 2015; Barange et al., 2017; Peled et al., 2018), with none to date valuing the expected increase in primary production in the Arctic Ocean. Peled et al. (2018) value carbon sequestration in the Israeli Mediterranean EEZ. Based on different carbon prices using the social cost of carbon (SCC) they estimate the value ranges between 265.1 and 1270.9 €/km² per year. Barange et al. (2017) estimate the potential reduction in carbon sequestration for the North Atlantic. Melaku Canu et al. (2015) estimate the value of carbon sequestration ecosystem services in the Mediterranean Sea. The authors develop a model that combines a biogeochemical model describing plankton productivity and carbon biogeochemical cycle with economic valuation using values of the social cost of carbon. They estimate that the carbon sequestration values of the entire Mediterranean basin range between 127 and 1722 million €/year. Alternatively, values per unit area range from 135 to 1000 €/km². Beaumont et al. (2008) estimate that the value of CO₂ sequestration in United Kingdom territorial waters is between £420 million and £8.47 billion. The estimation is based on the standing stock of phytoplankton locking up 0.07Gt carbon per year valued at £6 to £121 per ton carbon. Using a “back of the envelop” approach, Armstrong et al. (2010) estimate the value of the annual flow of carbon into the deep-sea pool and marine sediments world-wide. Using a figure for a net flow of approximately 1600 Tg C per year and valued using the EU emission trading scheme 2009 value of €15 per tCO₂e, a value of €88 billion per year is estimated. The study presented here focuses on future storage in the Arctic and

¹There are several ways that carbon can be stored/sequestered in the oceans. It can be stored through biological (living organisms), sub-seabed, or human induced (man-made) processes. Differences in temporary vs. permanent storage is clearly an issue. For the purpose of this paper carbon sequestration is defined as the biological capture and storage of carbon.

its value, based on a coupled hydrodynamic-chemical-biological model, SINMOD, taking atmospheric forcing from a climate global, and IPCC's prescription of the future CO₂ content in the atmosphere.

The primary and secondary production for the Arctic Ocean is investigated with the SINMOD model (Slagstad et al., 2015). To obtain indications of the effect of climate change, trajectories of the IPCC RCP 4.5 and RCP 8.5 (representative concentration pathways) climate scenarios were used, where the latter has greater perturbation magnitudes than the former, and the former stabilizes by the end of this century (Moore et al., 2013). The SINMOD model is coupled with an economic analysis using values assigned to carbon through regulatory markets, the European union emissions trading system (EU ETS), as well as estimates for the social cost of carbon, and SCC establishing a value range to allow for uncertainties when considering such a long timeframe.

We find an increase in the carbon storage of the Arctic Ocean, though this increase is declining toward the end of the century. The change in value depends on the assumed discount rates and price growth rates. The value is also highly uncertain, depending on the underlying climate scenarios, the carbon price used and its change over time, and the discount rate applied. Furthermore, it should be noted that this is a partial study of carbon effects in the Arctic, as clearly there are many other potential benefits and costs of climate change within the Arctic Ocean area, and in relation to its effects upon other parts of the planet (Lindstad et al., 2016; O'Garra, 2017; Yumashev et al., 2017). Another side of the ocean CO₂ uptake has resulted in a shift in the ocean's chemistry, so called, ocean acidification (OA), with potentially detrimental effects on marine ecosystems (Orr et al., 2005; Raven et al., 2005; AMAP, 2018). Model results have shown that the Arctic Ocean is the first to be affected by OA (AMAP, 2013, 2018). This is due to its already low pH and carbonate saturation state, and also the cold waters and sea ice processes favoring CO₂ uptake (Chierici and Fransson, 2009; Fransson et al., 2017). However, it is only quite recently that observations support the model results and currently low pH waters spread with increased volume in the Arctic Ocean (Qi et al., 2017).

The remainder of the paper proceeds as follows; the next section presents the Arctic Ocean areas studied, the biophysical SINMOD model and the economic analysis, as well as the data applied in each approach. Results from both analyses are then presented, followed by a discussion and conclusion.

MATERIALS AND METHODS

In the following we present the case study area, the Arctic Ocean, followed by the biophysical SINMOD model, and the underlying economic analysis.

Case Study Area

In this paper we define the Arctic Ocean as the area limited by the Bering Strait, Canadian Archipelago, Fram Strait and the shelf break at the northern Barents Sea, and Kara Sea and Siberia (green polygon in **Figure 1**). This covers a surface area of

7.57×10^6 km² (wet area) and the average depth is 1630 m. From the south, warm Atlantic water enters through the Fram Strait, and the Kara Sea. Pacific water enters through the Bering Strait. Outflow from the Arctic Ocean is mainly through the Canadian Archipelago and Fram Strait. The model domain is shown in **Figure 1**. For more details see Slagstad et al. (2015).

So far, estimates of sea-air CO₂ fluxes during the Arctic summer have shown that the Arctic Ocean (including the Barents and Kara Seas) acts as a net annual atmospheric CO₂ sink, estimated to be about 180 ± 130 TgC.

SINMOD Model Description

The modeling tool (SINMOD) used in this work is a coupled hydrodynamic and ecological model system including a carbon chemistry module. A short description is given here, but more information can be found in references given below. The hydrodynamic model is based on the primitive Navier-Stokes equations and is established on a z-grid (Slagstad and McClimans, 2005; Slagstad et al., 2015).

A comprehensive description of the ecosystem or food web model is found in Wassmann et al. (2006) and a short description, including recent deviations, is given here. The model structure is designed for the Barents Sea ecosystem and state variables and parameter values are set for modeling the carbon flux in this region. The state variables are: nitrate, ammonium, silicate, diatoms, autotrophic flagellates, bacteria, heterotrophic nanoflagellates, microzooplankton, and two mesozooplankters: the Atlantic *Calanus finmarchicus* and the arctic *C. glacialis*. The model contains further compartments for fast and slow sinking detritus, dissolved organic carbon, and the sediment surface. The model uses constant stoichiometry [C:N ratio equal 7.6 is used, as based upon average data from the Barents Sea (Reigstad et al., 2002)].

The model set-up encompasses the Nordic Seas, the central Atlantic Ocean and the Eurasian shelf [see Slagstad et al. (2015)] and uses a horizontal grid point distance of 20 km. The model has 25 vertical levels. The vertical level thickness increases from 5–10 m near the surface to 500 m below 1000 m.

The SINMOD model has open ocean boundaries to the Atlantic Ocean and the Bering Sea. These boundaries have to be specified. We have used the CARINA data base (Tanhua et al., 2010) to calculate the seasonal average temperature (T), salinity (S), nitrate (NO₃), silicate (Si), total inorganic carbon (CT), and alkalinity (AT). For the climatic scenarios monthly, mean values from bergen climate model (BCM) using IPCC's SRES A2 run have been used at the boundaries. Since these data had a significant offset compared with the CARINA data the BCM data has been corrected in the following way: The difference between the average values of T, S, NO₃, Si, CT, and AT in the 1990s near the boundaries for the CARINA and BCM A2 run were calculated. This resulted in an offset of each variable along the boundaries that is added to the BCM A2 data. Since most of the CARINA data originates from the spring-summer season, the depth of winter mixing (Steinhoff et al., 2010) was assumed in order to find winter values. The atmospheric CO₂ concentration was taken from IPCC's projections of annual mean

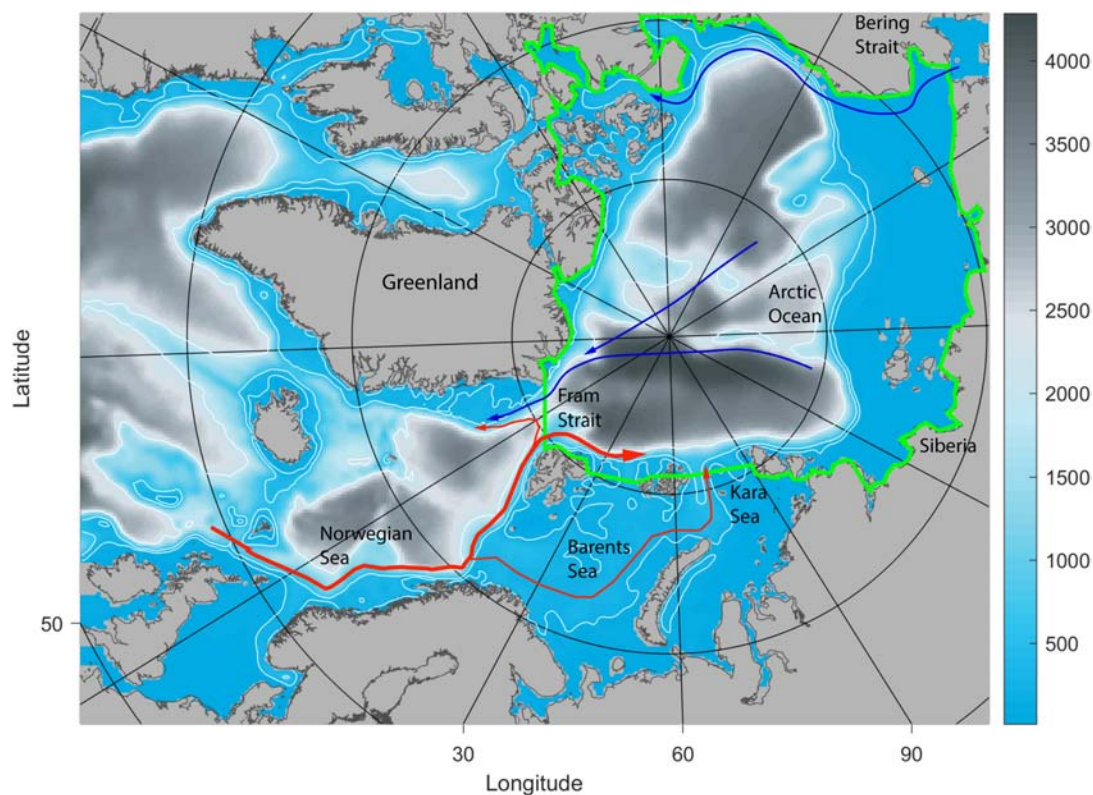


FIGURE 1 | Model domain with depths (m). The relatively warm Atlantic inflow (red) enters the Arctic Ocean through the Fram Strait and the Barents and Kara Seas. Pacific water enters through the Bering Strait. Surface Arctic water (blue) leaves the Arctic through the Canadian Archipelago and Fram Strait. The green polygon shows the area that is analyzed in this paper.

$p\text{CO}_2$ concentration for RCP4.5 and RCP8.5 [see Meinshausen et al. (2011) for description]. Seasonal pattern was adjusted with data from Ocean Weather Station Mike (66°N , 2°E). The CARINA data was also used for initial values of NO_3 , Si, CT and AT. The nutrient concentration (nitrogen and silicate) in the river run-off is taken from Dittmar and Kattner (2003) and Amon and Meon (2004). The CO_2 system follows the DOE (1994) using Mehrbach et al. (1973) and Lueker et al. (2000) calculations of carbonate system dissociation-constants.

We use the following equation for air-sea exchange of CO_2 (F)

$$F = K(1 - A)(f\text{CO}_{2w} - p\text{CO}_{2a})$$

Where $f\text{CO}_{2w}$, $p\text{CO}_{2a}$ are the partial pressures of CO_2 in the water and atmosphere, respectively. A is the fraction of a grid cell covered by ice and K is the gas transfer velocity using the Wanninkhof (1992) relationship between K and wind speed.

Economic Analysis and Data

The ecosystem service of ocean carbon storage provides benefits to society in the form of mitigation of climate change, but has no direct market value (Melaku Canu et al., 2015). Placing monetary value estimates can help underline the importance of the oceans carbon storage service, helping to inform policy and aid decision making. While there is no market for carbon

storage in the oceans, values connected to carbon storage can be taken from carbon markets, national carbon taxes or from estimates inferring the value of stored carbon (or the costs of carbon to society) such as the SCC, or the shadow price of carbon (Pearce, 2003; Tol, 2008; Valatin, 2010; Nordhaus, 2011). Carbon values are much debated with many estimates for long-run damage costs of climate change and abatement costs (Armstrong et al., 2010). For this analysis this valuation of the benefits of carbon storage in the Arctic Ocean is applied using both EU ETS and SCC values of carbon. To allow for the uncertainty regarding future values, growth rates and climate scenarios we apply a high and low bound of values to span the possibilities of the value of carbon uptake in the Arctic.

Emission trading is a market-based tool to limit greenhouse gases. The EU ETS is the largest such trading scheme globally. The EU ETS is a “cap and trade” mechanism where a limit, the “cap,” on all greenhouse gas emissions is set, and reduced over time. Within the total emission limit, companies can receive and/or trade emissions allowances. These allowances therefore receive a market value. There has been an increasing trend in price since 2013 with the market entering the so-called third phase (first phase operated from 2005 to 2007; second phase 2008 to 2012; and third phase 2013 to 2020). There are significant changes in the third phase from the previous two including a

single EU wide cap on allowances, auctioning the allocation of allowances, and more sectors and gases are included. The ETS is designed to steadily reduce the level of carbon emissions over time and therefore the value of an allowance is expected to increase over time. The last five-year mean value of phase 3 is €8 per ton. The minimum price over this stage was €3.54 and increased to a maximum €21.16 in September 2018 (see **Figure 2**). The current price (as of November 2018) has dipped slightly to €19.46.

The question whether a limited market will sufficiently take into account the full cost of carbon emissions has led to substantial work to estimate the SCC (see Tol (2008) for an overview of these studies), the Stern review (Stern, 2006) being the perhaps most well-known. Scientists predict that climate change will lead to negative consequences such as the spread of disease, decreased food production, coastal destruction, and more. The SCC is the estimate of monetary value of the damage done from the emission of one more ton of carbon at some point in time (Pearce, 2003). The SCC signals what society should be willing to pay to avoid the future damage caused by incremental carbon emissions. Models developed to estimate the SCC are known as integrated assessment models (IAMs). They aim to capture the linkages between greenhouse gas emissions, greenhouse gas atmospheric concentrations, temperature change, and monetary costs of climate change damage to society (Melaku Canu et al., 2015). Estimates for the SCC vary, depending on the model used.

In a meta-analysis Tol (2008) reports 211 estimates of the SCC, and explains that estimates of SCC are very dependent on the social rate of discount applied, as well as equity weights chosen. A large amount of climate change damage is expected to occur in the future, thus the present value of those damages depends on the discount rate chosen (ANON, 2016)². The value of the SCC is

not constant over time and is expected to vary between different climate change scenarios (Stern, 2006; Melaku Canu et al., 2015).

To estimate the future value of carbon sequestration in the Arctic Ocean, the values per unit of carbon are multiplied by the carbon estimates from the SINMOD model. The present value V_j , over 80 years from 2019 to 2099, of the change in carbon storage in accordance with the SINMOD model runs, can be calculated as:

$$V_j = \sum_{t=1}^{80} C_{j,t} P_{j,t} \frac{(1+r)^t}{(1+d)^t}$$

where C denotes the increase or decrease in carbon storage estimated by SINMOD at a specific time t . P is the price of carbon measured either as the SCC ($j = \text{SCC}$) or taken from the EU ETS carbon market ($j = \text{ETS}$), at time t .

The future value is discounted with discount rate d . Prices in general usually increase over time, and EU ETS carbon prices are expected to increase substantially due to planned changes in the structure of the market, here included with a rate of increase equal to r .

RESULTS

Biophysical Model Results

The SINMOD model was initialized with data from the CARINA data sets (Tanhua et al., 2010). Using ECMWF (European Centre for Medium-Range Weather Forecasts) atmospheric forcing the model had a spin-up period from 1979 to 2005. We have run 2 climatic scenarios using atmospheric input from the Max-Planck Earth System Models (MPIESM)³ using IPCC scenarios RCP 4.5 and RCP 8.5. The first scenario assumes a continued increase in emissions of greenhouse gases until around 2040 and from then

²Present value is how much a future sum of money is worth today. An important part of the present value calculation is the interest rate used for discounting.

³<https://portal.enes.org/models/earthsystem-models/mpl-m/mpl-esm>

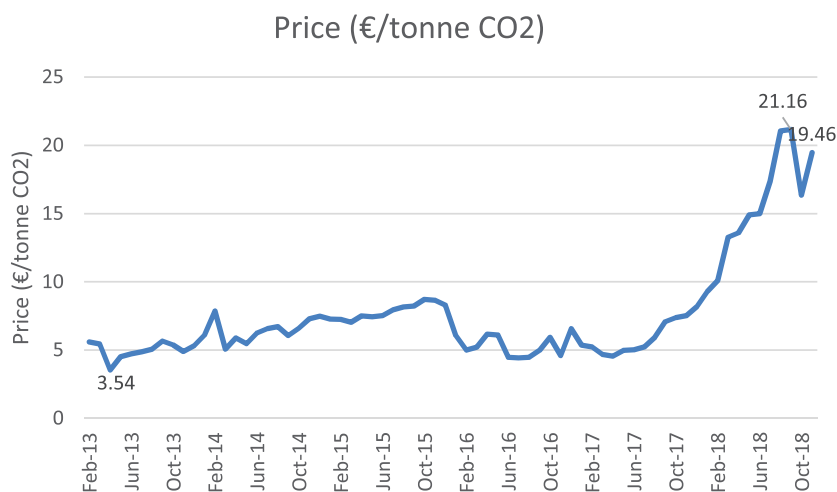


FIGURE 2 | CO₂ emission prices in the European emissions trading system (EU ETS), Phase 3 January 2013 – November 2018. Source: <http://www.investing.com/commodities/carbon-emissions-historical-data>.

on a decline. The RCP8.5 scenario assumes a continuous increase until the end of the century.

Storage

Total inorganic carbon ($C_T = CO_2 + CaCO_3 + CaCO_2H$) content in the Arctic Ocean at simulation start (2006) for the climatic scenarios is about 3.313×10^5 Tg C (1 Tg = 10^{12} g). Increase in the carbon storage depends mainly on the atmospheric concentration of CO_2 .

The net storage of Carbon from 2006 to 2099 (the area under the graphs in **Figure 3**) is 3458 Tg for RCP 4.5 and 7745 Tg for RCP 8.5 scenario, i.e., a 1.04 and 2.33% increase, respectively.

The storage of organic carbon depends strongly on the season. In **Figure 4** we have plotted the time series of organic carbon.

The initial value of biological components (biomass) comes from simulation of the present state (mainly controlled by the ice cover) and the Arctic biological system. The RCP 8.5 Scenario produces more ice than the ERA INTERIM atmospheric forcing

in the first 10 year of the simulation. The biomass in the Arctic experiences a dip before the ice cover is reduced for the remainder of the century. The summer biomass doubles toward the end of the century, but is still only 0.024% of the total inorganic carbon content of the Arctic Ocean.

Fluxes

The fluxes in and out of the Arctic Ocean have several transport roads. Horizontal fluxes are dominating. Here we only divide between Fram Strait and all other shelves (Barents and Kara Seas, Bering Strait, and Canadian Archipelago). Ice flux of carbon is mainly through the Fram Strait, but we handle carbon transported within the ice as the sum of all openings to the Arctic Ocean.

Since we are using climatological river run-off and constant inorganic content the river input of carbon is the same for all the scenarios and for each year (around 15 Tg).

Air-sea fluxes are calculated using standard methods depending on the difference between the partial pressure of CO_2

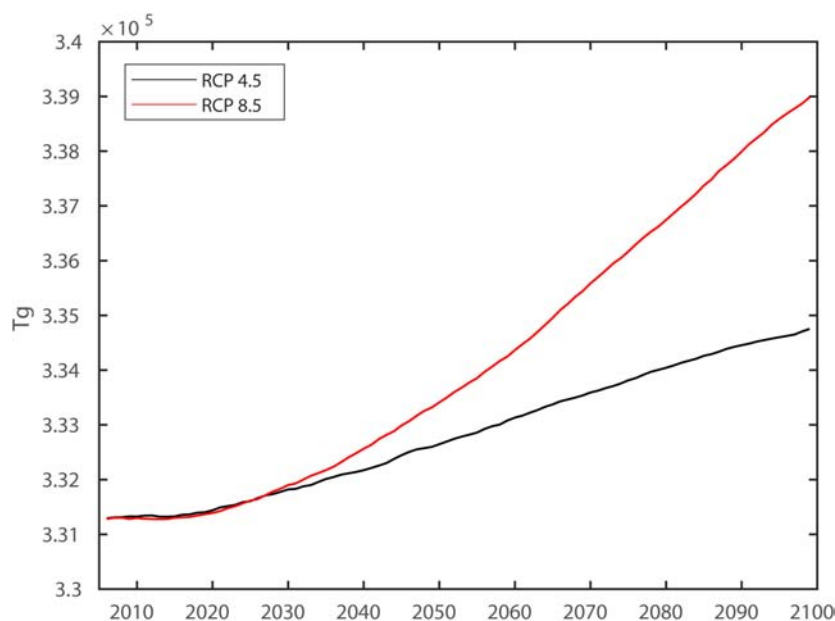


FIGURE 3 | Development of total inorganic carbon in the Arctic Ocean the 21st century for two climatic scenarios.

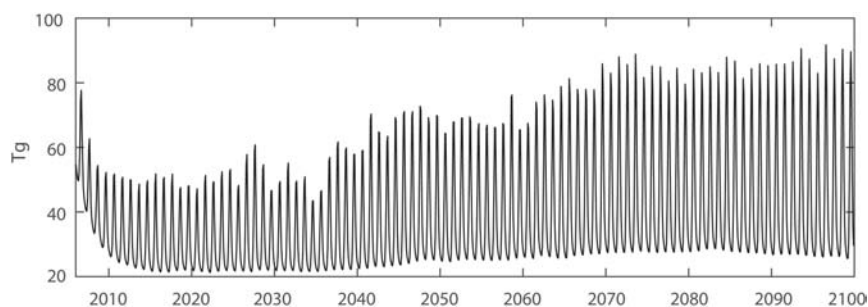


FIGURE 4 | Scenario RCP 8.5. Total amount of simulated organic carbon in the Arctic Ocean.

in the atmosphere and the sea surface. In the Arctic the ice cover will reduce the annual average of air sea exchange.

The biological fluxes are calculated from all the transport of all the carbon-containing state variables in the biological model (diatoms, flagellates, detritus, bacteria, H₂N₂, DON, DOC, Ciliates, C_{fin}, and C_{gla}). **Table 1** gives an overview of all fluxes in and out of the Arctic Ocean.

The accumulation of carbon in the Arctic Ocean seems to be controlled by the horizontal fluxes. The water entering the Arctic Ocean absorbs CO₂ from the atmosphere on its journey from the North Atlantic, Norwegian Sea, and Barents Sea. Cooling of these water masses allows more CO₂ to be absorbed. Time series of annual flux through Fram Strait and through the shelves are shown in **Figure 5**. As we could expect, the trajectories mirror each other.

Air-sea flux is shown in **Figure 6**. As the ice cover gradually diminishes and the atmospheric concentration of CO₂ increases, the air to sea flux of carbon increases.

TABLE 1 | Integrated fluxes (2006–2099) in Teragram carbon (TgC).

	RCP 4.5	RCP8.5
Net flux Fram Strait (out of the Arctic Ocean)	$-1.15 \cdot 10^5$	$-1.17 \cdot 10^5$
Net flux shelves	$1.14 \cdot 10^5$	$1.16 \cdot 10^5$
Net C-flux with ice (out of the Arctic Ocean)	-334	-284
Air-Sea flux (in to the ocean)	2425	5966
River flux of	1410	1410
Net bio flux Fram Strait (into the Arctic)	335	330
Net bio flux shelves (into the Arctic)	917	847
Net accumulation of carbon in the Arctic Ocean	3458	7745
Net accumulation of carbon in the Arctic Ocean per year	36.8	82

As we see in **Figure 6** the net accumulation appears to stabilize after 2065 (for RCP 4.5 much earlier), even when the atmospheric CO₂ continues to increase. Based on measurements, Yasunaka et al. (2018) found that the present annual air-sea flux is about 180 ± 130 Tg C when including the Barents and Kara Seas in addition to the area studied in this paper (**Figure 1**). Applying a similar area as used in Yasunaka et al. (2018) to the SINMOD simulations, we find that the air-sea flux increases from 60 Tg C in the 80 s (not shown), when the ice cover was extensive, to 115 Tg C in the period of 2010–2017. This is well within the range of air-sea flux found in Yasunaka et al. (2018). The climatic simulations have more ice in the start of this century than simulations using ERA INTERIM forcing, but when the summer ice is gone the uptake of CO₂ from the atmosphere levels out at around 150 Tg C for RCP 8.5.

For the economic analysis, accumulated total and annual carbon storage is used to assess the total value and value over time. **Figure 7** shows the net annual accumulation of carbon for the two IPCC scenarios, and worth noting is the increasing trends up to 2070, followed by a decreasing trend.

Values

Applying the current EU ETS carbon price €19.46 (November 2018) to the net accumulation of carbon in the Arctic for RCP8.5 and RCP4.5, and assuming growth is equal to the discount rate (we ease this assumption later), we obtain the picture in **Figure 8**, for the years 2019–2099. We observe that the annual value for the two scenarios follow relatively similar paths the first ten years, whereupon the RCP8.5 storage value has an increasing trend for another 60 years while the RCP4.5 value shows no such increasing trend. Both show a decreasing trend the last 10 years studied.

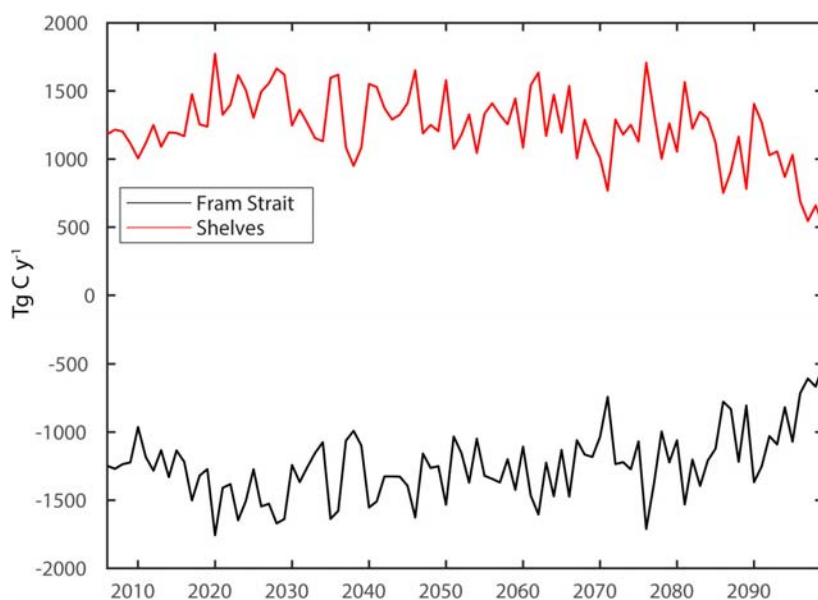


FIGURE 5 | Net annual inorganic C-flux through Fram Strait and the shelves areas for the RCP8.5 scenario.

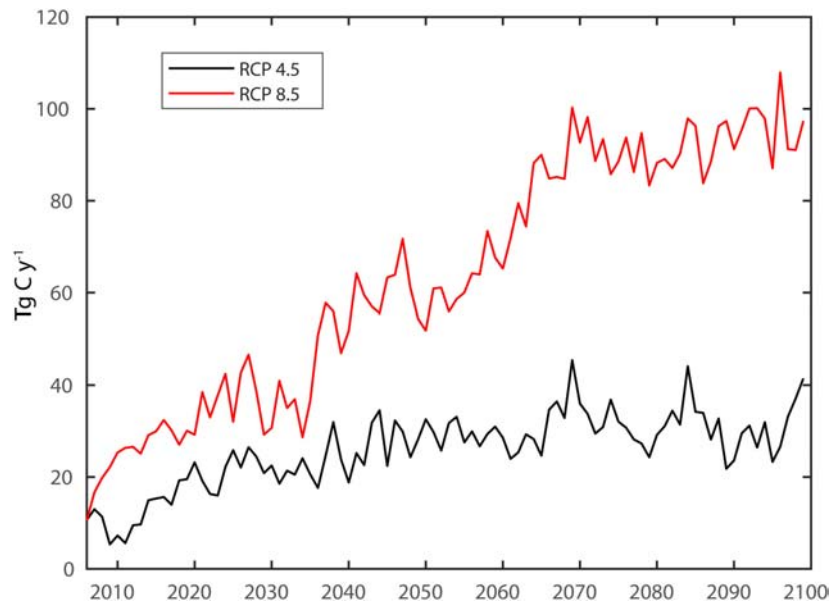


FIGURE 6 | Annual air-sea flux of CO₂ (RCP 8.5 and RCP 4.5).

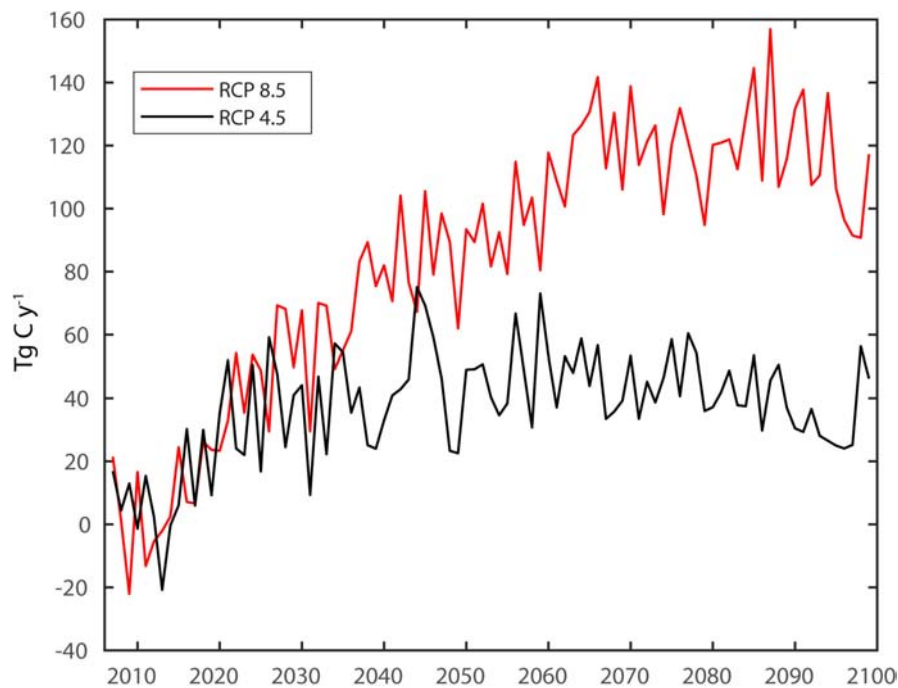


FIGURE 7 | Net annual accumulation rate of carbon in the Arctic Ocean for RCP 8.5 and RCP 4.5.

We see from **Table 2** that the Arctic Ocean is expected to store carbon worth €6.1 and €10.5 billion for RCP4.5 and RCP8.5, respectively, from 2019 to 2099, using the current EU ETS market value as the starting price (€19.46 per ton CO₂). Here the discount rate and the price growth rate is set equal to 0.

However, that the growth in carbon prices should equal the discount rate is not to be expected, and that they should be set

equal to 0 is usually not seen as acceptable. In the following, we present an upper and a lower bound for the change in carbon storage values in the Arctic, as shown in **Figure 9**. This range is to allow for the uncertainty in future carbon values. We have chosen a high and low discount rate of 5 and 3% [following Nordhaus (2007) and Riahi et al. (2017)]. United Kingdom department of energy and climate change

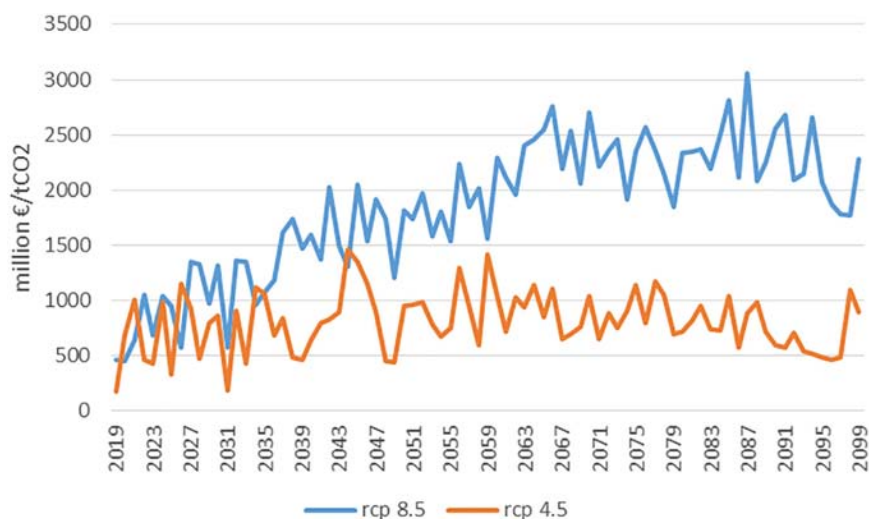


FIGURE 8 | Value of annual carbon storage 2019 – 2099 using current market price (€19.42 per tonne) and assuming growth in price is equal to the discount rate.

TABLE 2 | Total and average increased carbon storage and value in the Arctic Ocean, 2019–2099, with current EU ETS market price (€19.46 per tonne), with zero price growth and discount rates.

IPCC RCP-scenario	4.5	8.5	4.5	8.5	4.5	8.5	4.5	8.5
	TgC	TgC	bill €	bill €	ton/km ³	ton/km ³	€/ km ³	€/km ³
Net accumulation of carbon	3358	7643	6.1	10.5	2	619	5296	12054
Average net carbon accumulation per year	41.4	94.3	75	130	3.3	7.6	65	149

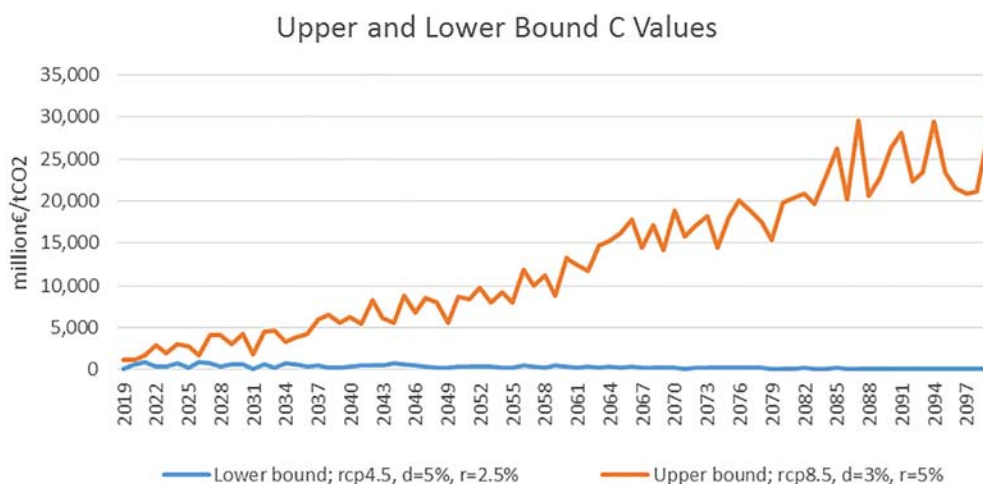


FIGURE 9 | Upper and lower bound of value of carbon in the Arctic Ocean, as present value in each year, discounted back to 2019, in million euros. The upper bound consists of RCP 8.5, a discount rate of 3% and a starting SCC price of €50 with a growth of 5%. The lower bound includes the RCP 4.5 scenario, a discount rate of 5% and starting ETS of €19.46 (November 2018), and growth rate in the price of 2.5%.

(DECC) models estimate that carbon values increase on average 5.5% per year over the 2030 – 2050 period (DECC, 2011). In our analysis we use a high price growth rate of 5% and a low price growth of 2.5%. The low price growth rate can be understood to include a minimal inflation rate and an incremental damage from increasing temperatures, where the former is 0.5%, and

the latter is 2% [the latter as in Barange et al. (2017)]. For the lower bound we apply the current EU ETS price (€19.46 per ton⁴), while for the upper bound we apply a high SCC price (€50 per ton) (ANON, 2016; Barange et al., 2017). Forecasts of

⁴November 2018.

carbon prices have been carried out by a number of countries to 2050 (for example United Kingdom, Ireland, and France) (DECC, 2011; Kevany and Cleary, 2018). The UK DECC extends their forecast to 2100. The prices in this paper are in line with those estimated by others to 2050. Our upper bound is within the range estimated by the DECC while the lower bound prices used here is more conservative. After 2050, the UK DECC prices are impacted by their assumptions regarding technological change, which we do not include in our analysis. Our price data are therefore higher than the DECC values after 2050.

By combining the RCP 8.5 and the low discount rate (3%) with the high SCC price and high price rise (5%) we obtain an overall upper bound. Likewise, the RCP4.5 and the high discount rate (5%) with the relatively low EU ETS price and low price rise give an overall lower bound.

We see from **Figure 9** that the lower bound value is declining over time, as the discount rate is greater than the rate of price increase, and when summing up the values leads to an accumulated value over the time period studied equal to €27.6 billion. The upper bound is increasing, but at a decreasing rate toward the end of the century, and when aggregated is valued at more than €1 trillion in total. While the lower bound variability declines over time, the upper bound variability increases. This picture clearly shows a large variation between the upper and lower bound, and indicates the uncertainties involved, both biophysically and economically, and especially when the two are combined.

DISCUSSION AND CONCLUSION

An important result from this study is the minor effect reduced ice cover has on the total carbon accumulation and storage. The importance of horizontal advection resulting in carbon accumulation in the Arctic Ocean, illustrates the connectivity of the Arctic Ocean to lower latitudes. Not only is the ocean buffering the increased atmospheric carbon globally, but ocean currents cause an additional accumulation in the Arctic Ocean resulting from the global ocean current transport. In a carbon storage perspective, this is regarded as positive, and represents major economic values. At the same time, the increased inorganic carbon will have a direct negative consequence in the form of ocean acidification. Accumulation of contaminants in the high Arctic resulting from long-range transport by atmospheric circulation or ocean currents is well known (AMAP, 2016), and the present study demonstrates similar patterns for carbon.

The biological contribution to increased carbon storage is negligible compared to the inorganic carbon pool. Only 0.024% of the carbon pool at the end of the century comes from summer biomass, despite a doubling over this time-period. However, the Arctic basin is deep, up to around 5000 m, storing huge volumes of water. Furthermore, the circulation is relatively slow, and the carbon that is stored will be isolated from the atmosphere in a millennial perspective.

Another output from the simulations is the lower influx of biomass to the Arctic Ocean both over the shelves and through

the Fram Strait in the RCP8.5 compared to the RCP 4.5 scenario (**Table 1**). At present, the advection of biomass from lower latitudes represents a considerable energy supply to the Arctic Ocean inflow regions, providing a basis for increased production also on higher trophic levels in the slope areas north of Svalbard (Basedow et al., 2018; Vernet et al. unpublished). A projected reduced inflow of organic carbon and biology in terms of phytoplankton and zooplankton reflecting reduced production or changing communities at lower latitudes in the future, may have stronger regional impact than local increases in primary production. The potentially negative economic impacts of this are also an unknown.

Barange et al. (2017) estimated the value of the loss in carbon storage service in the North Atlantic (not including the Arctic) as a result of climate change, to lie between € 150–2640 billion in abatement costs and €20–353 billion in social costs, over the period 2010 – 2099 (conversion: 1 USD = 0.88 EUR, 25/11/19). We observe that the value of carbon storage increase in the Arctic, estimated to lie somewhere between 27.6 billion and €1 trillion, though calculated using a somewhat different approach, has potential to reduce the costs described by Barange et al. (2017) related to carbon storage loss in the North Atlantic, and can be seen in connection with the borealisation of the Arctic (Fossheim et al., 2015). However, large uncertainties regarding the extent of these carbon storage values remain, and these results must therefore be taken with caution.

To sum up the uncertainties, we note (1) Simulations were based on two chosen climate change scenarios, with their inherent uncertainties, (2) The value of carbon storage is based on EU ETS and SCC estimates which are subject to discussion and change, and (3) The discount rate, where there are extensive debates amongst economists. A number of countries recommend using declining discount rates over time [see for the United Kingdom and for Norway (ANON, 2012, 2018)]. This will raise further the upper bound as portrayed in **Figure 9**, and given similar percentage point declines in the upper and lower bound discount rates, only increase the difference between the two. Regardless, the results show the potential for increases of carbon storage in the Arctic Ocean, and its value.

It is worth noting that the estimates of increased Arctic blue carbon storage and its value, is only one ecosystem service change related to carbon. Clearly, increased carbon in the oceans has potential cost not identified here, not the least represented by OA (Mathis et al., 2015). Furthermore, a multitude of other climate effects, not necessarily related directly to carbon storage, are not assessed here. However, putting together the many pieces of the climate change puzzle requires assessments not only of costs, but also of the potential benefits.

AUTHOR CONTRIBUTIONS

All authors took part in planning, developing, and writing the manuscript. DS did the natural science modeling analysis. CA and NF did the economic analysis.

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The handling Editor is currently organizing a Research Topic with one of the authors MR, and confirms the absence of any other collaboration.

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