UiT The Arctic University of Norway

Faculty of Biosciences, Fisheries and Economics

Spatial and temporal patterns of mesozooplankton secondary production in the northern Barents Sea

Are small copepods important?

Christine Gawinski

A dissertation for the degree of Philosophiae Doctor — July 2024

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the Nansen LEGACY

Preface

Depicted on the front page is a photograph of the copepod *Paraeuchaeta glacialis* (bottom left) that I took during one of the research cruises that were part of my PhD project. This choice might be surprising, as the sub-title of my thesis is: ‘Are small copepods important?’ and *P. glacialis* is anything but a small copepod. However, I decided to use this photograph, as it is one of my favourites and I hope it can convey the beauty of copepods and my fascination with them to the reader. The colourful, grapelike structures that look like little jewels, are actually the egg sacs of *P. glacialis* and *P. norvegica.* It was really exciting to follow their development, because you can see the state of the cell division inside the eggs. The light blue eggs of *P. norvegica* for example, are in an earlier developmental state and will become more ‘bubbly’ and turn a darker blue colour, before the nauplii hatch. It was also possible to see the movement of the nauplii inside the eggs before they hatched.

In the Arctic Ocean basin, there are four *Paraeuchaeta* species and each is generally restricted to a certain depth range, with *P. glacialis* and *P. norvegica* occurring from the surface to 500 m depth, *P. barbata* from 900–1300 m depth and *P. polaris* at depths below 1500 m (Auel and Hagen, 2005). On one of the last pages of this thesis, there are photographs of each of these species. What fascinated me the most was that you could clearly see the differences in their body build depending on the depth where they live. The deep-sea species had a bright orange colour, which camouflages them in deep waters where red light is almost entirely absent. They also had larger eggs, which supply their offspring with more resources in an environment with harsh food conditions.

When I started this PhD, I did not know what I was getting myself into, as I had never worked with Arctic copepods before. I knew what a copepod was, but that was about it. My working contract started just a week before the first of one of many research cruises that would be part of this PhD project. In retrospect, even though I was ‘thrown into cold water’ because I had only a day or two to learn how to identify my target copepod, *Oithona similis* (a photograph can be found on the cover page of Paper III), I am really happy with how everything turned out in the end. It was a very special first cruise, as it was my first time seeing sea ice in the Arctic and the time on the ship formed the basis for friendships and collaborations with many of the scientists that were part of the national research project ‘The Nansen Legacy’, within which my PhD project is situated. Through the two research cruises in 2019 and the Nansen Legacy annual meeting, I really bonded with a lot of people and the connections that I formed helped me feel less lonely and well supported in the times of Covid that were to come. To this day, I think one of the most exciting things is when a zooplankton net comes up from the depths of the ocean and we get to explore the fascinating species that live there. I hope this PhD thesis can give a glimpse into the intriguing marine ecosystems of the Arctic and the many-faceted interplays between the organisms that live there.

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Acknowledgements

In light of what a journey this PhD and the last five years have been, it is hard to know where to start. It was a truly challenging time, but also incredibly inspiring and enriching, both in terms of academic and personal growth. This achievement was only possible with the great help and support of many colleagues, friends, and family along the way.

First and foremost, I would like to thank my supervisors for their guidance, support, encouragement and constructive feedback all these years. It has been an immense pleasure working with all of you and learning from you. Thank you to Camilla Svensen, for leaving me the freedom to develop my own ideas, but for also guiding me in the right direction when my path seemed lost. I really appreciate that you always had an open door or e-mail inbox, even when you were on the other side of the world. Thank you for saying yes when I wanted to go on yet another research cruise or conference. It was a lot of fun to see your enthusiasm for zooplankton live in action on the Arctic Basin cruise. Thank you to Malin Daase, for your insights and for finding the time to read and comment on yet another draft, even when you were busy with field work. Thank you to Sławomir Kwaśniewski, I am truly grateful for all your warm encouragement and thorough feedback these past years. Even though Covid made it much harder to travel, I am happy we managed to realize a research stay with you at the Institute of Oceanology, Polish Academy of Sciences. Many thanks to you and the institute for hosting me. I enjoyed our scientific and non-scientific discussions and am truly impressed by your knowledge of copepod taxonomy and zooplankton in general.

I am immensely grateful to have met Yasemin and Martí, my office mates, who have become so much more than that over the past years. It is hard to put into words how much we have learnt from each other and with one another. I truly loved sharing an office and a brain cell with you. Yasemin, thank you for being my quarantine buddy, for sharing a cabin at sea and for getting Hugo and all the adventures that came with it. Thanks to Martí, for all the discussions of scientific and non-scientific nature and for teaching me everything fermentation, plant-care and crafting related. To our duckling mom, Miriam, thank you for your warmth, generosity, problem solving skills and support all these years. You always made sure that we were doing well. To Griselda, thank you for exploring Tromsø city life with me and for going on our little culinary adventures. To my remote office mate Fee, thank you for being there for me, even after having finished our master's long ago. You have significantly contributed to this thesis by having countless working sessions together and by supplying me with 480 bags of Yorkshire tea, which have fuelled my creative writing for one and a half years.

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A big thanks to all my co-authors for helping me find the stories in my data. Your insights have greatly improved the papers. Thanks to my colleagues and friends at AMSE, ARCTOS, TODOS and outside of UiT. Especially to Paul Dubourg, Ulrike Dietrich, Fride Tonning and Elisabeth Halvorsen for their help with my lab work. To Bodil, thank you for always looking out for me and ensuring that my PhD progress was on track. To Tiziana, Eva and Alejandro, thanks for the many laughs we shared during our lunch breaks. To Ronan, thank you for our adventures together and the stimulating discussions we had (maybe white copepods are the future?). To Roweena, thanks for our Newfoundland adventure, who would have thought that getting stranded at Gatwick airport would lead to such a giggly friendship? Thanks to Cheshtaa and Victor for our great American road trip after the conference. To Anna, Zoe and Salomé, thanks for recharging with me in the mountains and at sea. To Adam, thank you for making the last, most stressful weeks more relaxed and enjoyable. Thank you to Jules for understanding the PhD journey, especially since you are navigating your own in a different country, and for offering your unwavering support. To Marie, thank you for being my biggest supporter for as long as I can remember, always cheering me on, and believing in me. You mean the world to me. And finally, I am incredibly grateful for the love and support of my family. Thank you for giving me the opportunity to pursue my dreams and for always standing by my side, no matter what or where.

I acknowledge that I live on the ancestral homelands of the Sámi, the Indigenous people of the Fennoscandian region. On the land of Sápmi, the Sámi have lived since time immemorial. I pay respect to their elders, past and present, and recognize their deep and enduring connection to this land.

Summary

Secondary production, the generation of heterotrophic biomass over time, is crucial for understanding energy transfer in food webs and population performance in habitats. Despite its significance, it remains understudied in the Arctic, particularly in offshore regions. Zooplankton, especially copepods, are primary contributors to secondary production in Arctic marine ecosystems. *Calanus* spp., large lipid-rich copepods, dominate the mesozooplankton biomass in the Arctic and sub-Arctic, while small copepods (adult body size <2 mm) like *Oithona* spp. are most abundant, but historically understudied due to the use of traditional mesozooplankton nets with coarse mesh sizes (>180 µm) and seasonal study biases towards the productive season. Recent studies have highlighted the important role of small copepods in ecosystem processes such as trophic interactions and energy transfer, especially during winter when *Calanus* spp. hibernate. However, detailed knowledge on seasonal changes in their energy transfer rates and life-history traits is limited, particularly in winter.

The Barents Sea, divided into southern and northern climatic domains by the polar front, provides a glimpse into future scenarios for Arctic ecosystems. The southern domain, characterized by warm Atlantic Water, has a mesozooplankton community resembling North Atlantic ecosystems. Conversely, the northern domain, influenced by cold Arctic Water, is seasonally ice covered with a community dominated by true Arctic species. With ongoing, anthropogenic climate change, Arctic ecosystems, like the Barents Sea, are rapidly evolving, with sea ice decline and increased Atlantic Water inflow altering local conditions. This shift is expected to favour smaller and more boreal copepod species, impacting secondary production.

The main goals of this PhD thesis were to elucidate spatial and temporal patterns in secondary production and its drivers in the Barents Sea, enhance our understanding of the role of small copepods in Arctic marine ecosystems, and improve methodologies for the estimation of secondary production. Mesozooplankton was sampled during nine cruises (2011, 2018–2022) along a transect from 75–83 °N, covering all seasons, using traditional net sampling with different mesh sizes and an optical sensor (Laser Optical Plankton Counter). This approach enabled a high-resolution assessment of mesozooplankton community composition and secondary production.

Results indicated distinct spatial patterns in mesozooplankton secondary production across the study region. High total mesozooplankton secondary production was found in the Atlantic region, where Rotifera, Appendicularia, Chaetognatha and gelatinous zooplankton were common, while being almost absent in other parts of the study area. Copepod secondary production in the Atlantic region was low, with high contributions of small copepods. In the northern Barents Sea, the opposite trend was observed. Mesozooplankton secondary production was low and copepod secondary production

high, being clearly dominated by the large *Calanus* spp. This suggests more direct energy flow through the food web in the northern Barents Sea compared to the Atlantic region, where small copepods increase the steps between primary producers and higher trophic levels, impacting trophic dynamics.

Copepod secondary production showed clear seasonal patterns and peaked in summer, driven by *Calanus* spp. Even though the secondary production of small copepods was highest in summer, their overall contribution to total copepod secondary production in this period was minimal. The most common small copepod *Oithona similis* reproduced year-round, with highest reproductive output in summer, linked to high weight-specific egg production rates, resulting from a high percentage of ovigerous females with large clutches and high hatching success. Once the majority of *Calanus* spp. descended to hibernate at depth in autumn, the contribution of small copepods to total copepod secondary production increased and remained high during the winter. This seasonal shift underscores the importance of small copepods in Arctic ecosystems in winter, highlighting their role in maintaining trophic dynamics when larger species are less active. Interannual variations in environmental factors did not significantly impact total copepod secondary production, although community composition differed. Warmer, ice free conditions favoured smaller *Calanus finmarchicus*, whereas extensive sea ice and colder temperatures favoured larger *C. glacialis*. Small copepods thrived in warmer, ice free areas, correlating with higher water temperatures and ciliate abundance. These findings suggest that Arctic warming and reduced sea ice will enhance the prominence of smaller copepod species.

This PhD study emphasizes the need for selecting appropriate empirical growth rate models for the study system, such as including chlorophyll *a* concentration during potential food limitations. It also reveals that estimated secondary production rates can be significantly higher than field measurements, especially in winter, indicating copepods may be limited by low microzooplankton standing stock as their food source—a factor often overlooked. With minimal seasonal variations in water temperature, growth rates did not vary much seasonally and the observed changes in copepod secondary production were rather linked to biomass variations. Thus, this thesis stresses the importance of gathering seasonal carbon weight data for key Arctic copepod species. Developing growth rate models that account for small copepods' growth at low temperatures and various food limitations is crucial. Future Arctic studies should combine optical sensors with traditional net sampling to ensure high spatial and taxonomic resolution and minimize sampling biases.

This PhD thesis advances our understanding of Arctic marine ecosystems and provides essential insights for predicting and managing the impacts of anthropogenic climate change on secondary production and food web dynamics.

Sammendrag

Sekundærproduksjon, genereringen av heterotrof biomasse over tid, er avgjørende for å forstå energioverføring i næringsnett og bestandsytelse i habitater. Til tross for sin betydning, er den fortsatt lite studert i Arktis, spesielt i offshore-regioner. Dyreplankton, spesielt hoppekreps, er de viktigste bidragsyterne til sekundærproduksjon i arktiske marine økosystemer. Store, lipidrike hoppekreps av slekten *Calanus* dominerer mesozooplanktonbiomassen i Arktis og sub-Arktis, mens små hoppekreps (voksen kroppsstørrelse <2 mm) som *Oithona* spp. er de mest tallrike, men historisk lite undersøkt på grunn av bruk av tradisjonelle mesozooplanktonnett med grov maskevidde (>180 µm) og sesongbaserte studieforvrengninger. Nyere studier har fremhevet den viktige rollen små hoppekreps spiller i økosystemprosesser som trofiskeinteraksjoner og energioverføring, spesielt om vinteren når *Calanus* spp. er i dvale. Detaljert kunnskap om sesongmessige endringer i deres energioverføringsrater og livshistorietrekk er imidlertid begrenset, spesielt om vinteren.

Barentshavet, delt inn i sørlige og nordlige klimatiske domener av polarfronten, gir et glimt inn i fremtidige scenarier for arktiske økosystemer. Det sørlige domenet, preget av varmt, atlantisk vann, har et mesozooplankton samfunn som ligner nordatlantiske økosystemer. Det nordlige domenet, påvirket av kaldt, arktisk vann, er sesongmessig isdekket med et samfunn dominert av ekte arktiske arter. Med pågående, menneskeskapt klimaendring, endrer arktiske økosystemer, som Barentshavet, seg raskt, med sjøisnedgang og økt innstrømning av atlantisk vann som endrer lokale forhold. Denne endringen forventes å favorisere mindre og mer boreale hoppekrepsarter, noe som vil påvirke sekundærproduksjonen.

Hovedmålene med denne doktoravhandlingen var å belyse romlige og tidsmessige mønstre i sekundærproduksjon og dens drivere i Barentshavet, forbedre vår forståelse av rollen til små hoppekreps i arktiske marine økosystemer, og forbedre metodene for beregning av sekundærproduksjon. Mesozooplankton ble samlet inn på ni tokt (2011, 2018–2022) langs en transekt fra 75–83 °N, som dekket alle årstider, ved bruk av tradisjonell nettoppsamling med forskjellige maskevidder og en optisk sensor (Laser Optical Plankton Counter). Denne tilnærmingen muliggjorde en høyoppløselig vurdering av mesozooplanktonsamfunnets sammensetning og sekundærproduksjon.

Resultatene viste tydelige romlige mønstre i mesozooplankton sekundærproduksjon over studieområdet. Høy total mesozooplankton sekundærproduksjon ble funnet i den atlantiske regionen, hvor Rotifera, Appendicularia, Chaetognatha og gelatinøst dyreplankton var vanlige, mens de nesten var fraværende i andre deler av studieområdet. Hoppekreps sekundærproduksjon i den atlantiske regionen var lav,

med høy andel små hoppekreps. På Barentshavet nord for polarfronten ble det motsatte trenden observert. Mesozooplankton sekundærproduksjon var lav og hoppekreps sekundærproduksjon høy, tydelig dominert av de store *Calanus* spp. Dette antyder mer direkte energiflyt gjennom næringsnettet i den arktiske regionen sammenlignet med den atlantiske regionen, hvor mindre hoppekreps øker antallet trinn mellom primærprodusenter og høyere trofiskenivåer, noe som påvirker de trofiskedynamikkene.

Hoppekreps sekundærproduksjon viste klare sesongmønstre og nådde toppen om sommeren, drevet av *Calanus* spp. Selv om sekundærproduksjonen av små hoppekreps var høyest om sommeren, var deres samlede bidrag til total hoppekreps sekundærproduksjon i denne perioden minimal. *Oithona similis* reproduserte året rundt, med høyeste reproduktive utbytte om sommeren, knyttet til høye vektrelaterte eggproduksjonsrater, som følge av en høy andel egg bærende hunner med store egg sekker og høy klekkesuksess. Når majoriteten av *Calanus* spp. gikk i dvale på dypt vann om høsten, økte bidraget av små hoppekreps til total hoppekreps sekundærproduksjon og forble høyt gjennom vinteren. Denne sesongmessige endringen understreker viktigheten av små hoppekreps i arktiske økosystemer om vinteren, og fremhever deres rolle i å opprettholde trofiskedynamikker når større arter er mindre aktive. Årvisse variasjoner i miljøfaktorer påvirket ikke total hoppekreps sekundærproduksjon betydelig, men samfunnssammensetningen varierte. Varmere, isfrie forhold favoriserte mindre *C. finmarchicus*, mens omfattende havis og kaldere temperaturer favoriserte større *C. glacialis*. Små hoppekreps trivdes i varmere områder uten havis, korrelert med høyere vanntemperaturer og høy tetthet av ciliater. Disse funnene antyder at arktisk oppvarming og redusert havis vil øke fremtredenen av mindre hoppekrepsarter.

Denne doktoravhandlingen fremhever behovet for å velge passende empiriske vekstrate modeller for studiesystemet, for eksempel inkludere klorofyll a-konsentrasjon ved mulige begrensninger av mat. Den avslører også at estimerte sekundærproduksjonsrater kan være betydelig høyere enn feltmålinger, spesielt om vinteren, noe som indikerer at hoppekreps kan være begrenset av lav mikrozooplanktonbestand—en faktor som ofte overses. Med minimale sesongvariasjoner i vanntemperatur, var vekstratene lite varierende sesongmessig, og de observerte endringene i hoppekreps sekundærproduksjon var heller knyttet til biomassevariasjoner. Dermed understreker denne avhandlingen viktigheten av å samle sesongmessige karbonvekstdata for nøkkelarter av arktiske hoppekreps. Å utvikle vekstratemodeller som tar hensyn til vekst av små hoppekreps ved lave temperaturer og ulike matbegrensninger er avgjørende. Fremtidige arktiske studier bør kombinere optiske sensorer med tradisjonell nettoppsamling for å sikre høy romlig og taksonomisk oppløsning og minimere prøvetakingsskjevheter.

Denne doktoravhandlingen fremmer vår forståelse av arktiske marine økosystemer og gir viktige innsikter for å forutsi og håndtere klimaendringenes innvirkning på sekundærproduksjon og næringsnettdynamikk.

Supervisors

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Publication list

The synthesis is based on the following publications, referred to as **Paper I, II, III** throughout the thesis:

Paper I: Secondary production at the Barents Sea polar front in summer: contribution of different size classes of mesozooplankton

Gawinski, C., Basedow, S.L., Sundfjord, A., Svensen, C. (2024)

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Paper II: Response of the copepod community to interannual differences in sea-ice cover and water masses in the northern Barents Sea

Gawinski, C., Daase, M., Primicerio, R., Amargant-Arumí, M., Müller, O., Wold, A., Ormańczyk, M.R., Kwasniewski, S., Svensen, C. (2024)

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Paper III: Seasonality of *Oithona similis* population dynamics, reproductive characteristics, and contribution to copepod secondary production in the northern Barents Sea

Gawinski, C., Kwasniewski, S., Halvorsen, E., Daase, M., Svensen, C. (manuscript draft 2024)

Author contributions

	Paper I	**Paper II**	**Paper III**
Concept and idea	CG, SLB, CS	CG, MD, MAA, CS	CG, CS, MD, SK
Study design and methods	CG, SLB, CS	CG, MD, RP, MAA, CS	CG, CS, MD, SK
Data gathering and interpretation	CG, SLB, AS, CS	CG, MD, RP, MAA, OM, AW, MRO, SK, CS	CG, EH, CS, MD, SK
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1 Introduction

1.1 What is secondary production and why is it important?

Secondary production is the generation of heterotrophic biomass over time and is among the key processes in all ecosystems on Earth, be it terrestrial or aquatic (Benke and Huryn, 2007). Secondary production is performed by heterotrophic organisms that are consumers of primary production, bacterial production, or of other heterotrophic organisms (Stites, 1999). Primary production is the generation of organic compounds by autotrophic organisms through photosynthesis over time and is performed by primary producers, such as terrestrial plants and freshwater and marine phytoplankton or macroalgae (Fahey and Knapp, 2007). Alongside primary production, bacterial production at the base of the microbial food web, serves as a carbon source to higher trophic levels (Azam et al., 1983). When considering secondary production on the level of individual organisms, it results from the ingestion of food, of which parts are assimilated (absorbed) and parts are egested (Figure 1a; Benke, 2010). Parts of the assimilated energy are used for respiration and parts of it result in the growth or reproduction of the individual (Figure 1a). When considering secondary production on a population level, it results from the somatic growth and reproductive output of the individuals combined, and is eventually lost to mortality, predation, and emigration (Figure 1b; Benke, 2010). Secondary production of a population is defined as the product of biomass and growth rate (Figure 1b), which are influenced by the population characteristics (e.g. individual biomass, reproductive rates, growth rates), biotic interactions (e.g. predation, competition) and by the environmental conditions of the habitat that the population resides in (e.g. temperature, food availability) (Figure 1b,; Downing, 1984; Benke, 2010). Therefore, measurements of secondary production give overarching information about the performance of populations, as they describe the balance between matter input and output.

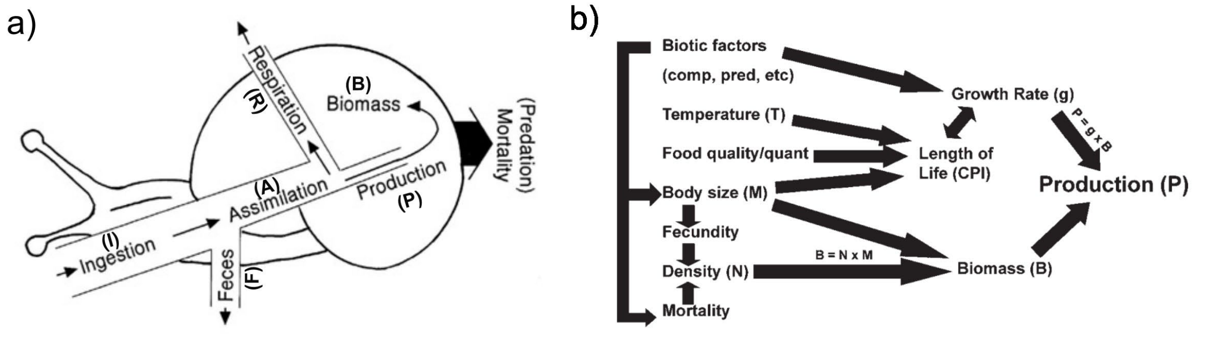

Figure 1: a) ‘Energy flow diagram of a stream snail. The ingested energy (I) results in respiration (R), excretion of faeces (F) and production (P). Therefore, production can be defined as: P = I – F – R’. Modified from Benke (2010). b) ‘ecological variables (abiotic and biotic) that influence or contribute to secondary production. Production (P) is the product of growth rate (g) and biomass (B) (i.e. P = g x B), biomass is the product of mean body size (M) and population density aka abundance (N) (i.e. B = M x N), and length of life (cohort production interval, CPI) is influenced by temperature, body size and food quality/quantity’. Modified from Benke (2010).

Many ecological studies have used static parameters, such as abundance and biomass, i.e. the density and standing stock of populations at a given moment, to describe the performance of populations in a habitat. However, secondary production is a much better suited tool to describe the response of animal populations to biotic and abiotic factors in a habitat (Dolbeth et al., 2012). Populations in a habitat can have low biomass, but high secondary production, for example when biomass is decimated through high predation pressure, and vice versa (Dolbeth et al., 2012). Secondary production can also be used to improve our understanding of the flux of energy and organic matter in ecosystems (Odum, 1968; Benke, 1993; Heymans and Baird, 1995), to study the effects of environmental stressors and pollutants on populations and to quantify the harvesting potential of natural resources (Downing, 1984; Dolbeth et al., 2012).

Table 1: Secondary production papers in the time periods 1999–2008 (n = 332, January 1998 through August 2008, from Benke, 2010) and 2008–2024 (n = 395, September 2008 through May 2024, this thesis) among habitats (terrestrial, marine, freshwater) and animal groups (zooplankton, benthic invertebrate, vertebrate) from Web of Science. Some papers are included in more than one category (e.g. reviews dealing with multiple animal groups and habitats). Indicated are the number (# of papers) and the percentage of relevant papers that each category represents (%). Due to the focus of this PhD thesis, the relevant papers were additionally screened for their sampling locations, to determine the percentage of high-latitude studies. In this search, no studies from Antarctica were found. The number and percentage of Arctic studies is indicated.

	1998–2008		**2008–2024**	
	# of papers	%	# of papers	%
Terrestrial invertebrates	3	0.9	7	1.6
Terrestrial vertebrates	1	0.3	5	1.2
Marine zooplankton	47	14.2	59	13.8
Marine benthic invertebrates	118	35.5	123	28.7
Marine vertebrates	9	2.7	13	3.0
Freshwater zooplankton	12	3.6	39	9.1
Stream/river benthic invertebrates	111	33.4	118	27.5
Lake/wetland benthic invertebrates	30	9.0	51	11.9
Freshwater vertebrates	10	3.0	14	3.3
Total terrestrial studies	4	1.2	12	2.8
Total marine studies	172	51.8	195	45.5
Total freshwater studies	154	46.4	222	51.7
Total Arctic studies	2	0.6	24	6.1

Studies on secondary production date back to as early as the 1910s (Boysen-Jensen, 1919). One of the earlier, most influential works on secondary production was conducted by Lindeman (1942), who formulated the concept of the ecological efficiency of energy transfer between trophic levels. After the establishment of the 'International Biological Program' in the 1960s with the goal to study 'the biological basis of productivity and human welfare' (Biesheuvel, 1968), the interest in secondary production grew significantly. In the 1970s, the first handbooks on the methodology of estimating secondary production of freshwater invertebrates (Edmondson, 1971), freshwater fishes (Bagenal and others, 1978), marine benthos (Holme and McIntyre, 1971) and terrestrial animals (Petrusewicz and Macfadyen, 1970) were published, followed by a section on secondary production of marine zooplankton in the ICES Zooplankton Methodology Manual in the 2000s (Harris et al., 2000). However, in contrast to the widely established method of measuring net primary production and bacterial production through the uptake of radioactive isotopes (Nielsen, 1952; Hama et al., 1983; Smith and Azam, 1992), there is no routine method to measure secondary production. Because of the difficulty of estimating secondary production, there is much less work done on this topic compared to primary production. A Web of Science search for papers with ‘primary production’ in the title or keywords resulted in 5952 hits, while ‘secondary production’ resulted in only 719 hits for the last 25 years (methodology described in the Appendix). This search also showed that most secondary production studies have focused on aquatic environments, with a strong emphasis on benthic invertebrates (Table 1, from Benke, 2010 for time period 1998–2008; this thesis for the time period 2008–2024). There was an imbalance in terms of where studies on secondary production were conducted, with high latitude ecosystems generally being underrepresented. Although the contribution of papers focusing on Arctic regions has generally been low, it increased in the 2010s and 2020s, from 0.6 % to 6.1 % of all listed papers (Table 1).

1.2 Mesozooplankton secondary production and its role in the carbon cycle

Most studies on secondary production in the Arctic have focused on the production of zooplankton (54 % of the studies from the Arctic listed above, Table 1), with a strong emphasis on copepods. Zooplankton (derived from the Greek words *zoion*, meaning ‘animal’ and *planktos*, meaning ‘wanderer’ or ‘drifter’) encompasses diverse groups of animals that can range from micrometres to meters in size, including for example copepods, euphausiids, amphipods, pteropods, polychaetes and gelatinous taxa (cnidarians and ctenophores) (Levinton, 2001). Zooplankton are heterotrophic organisms that can, by definition, not actively swim against ocean currents and can be divided into size classes according to their body size (Sieburth et al., 1978). This PhD thesis focuses on mesozooplankton, which is 0.2–20 mm in size. More than 50 % of all Arctic zooplankton species are copepods (Kosobokova and Hopcroft, 2010; Kosobokova et al., 2011) and they can comprise more than 90 % of mesozooplankton abundance (Kosobokova and Hirche, 2000) and 80 % of mesozooplankton biomass (Thibault et al., 1999). Copepods are among the key players in Arctic marine ecosystems, as they link primary producers to higher trophic level consumers and channel energy and organic matter through the food web (Sigman and Hain, 2012). Copepods also play an important role in linking the microbial loop to the classical food chain (Møller et al., 2006). The microbial loop describes the incorporation of dissolved organic carbon (DOC) into bacterial biomass (Figure 2), which is then grazed on by flagellates and ciliates and can be coupled to the classical food chain by predation of copepods on these organisms (Figure 2, Azam et al., 1983). Copepods can play a part in producing DOC themselves, by sloppy feeding, excretion and leaching from faecal pellets. Dead tissue and particulate organic carbon can aggregate into fast sinking particles, called marine snow (Figure 2, Saba et al., 2011). Through diel vertical migration to deeper water layers and hibernation at depth (Figure 2), copepods further play an important role in fertilizing the deep ocean (Jónasdóttir et al., 2015). The sinking particles can be remineralized through respiration by bacteria and small copepods (Figure 2; Svensen and Vernet, 2016; Shoemaker et al., 2019), turning the organic carbon back into inorganic carbon and making it available for reuse in primary production (Guidi et al., 2015). A small amount of the sinking particles reaches the seafloor, where it can either be buried (Figure 2) or serve as food for benthic communities. These remineralize the organic matter and release inorganic nutrients back into the water column, which can be resupplied to the surface ocean and be used by primary producers.

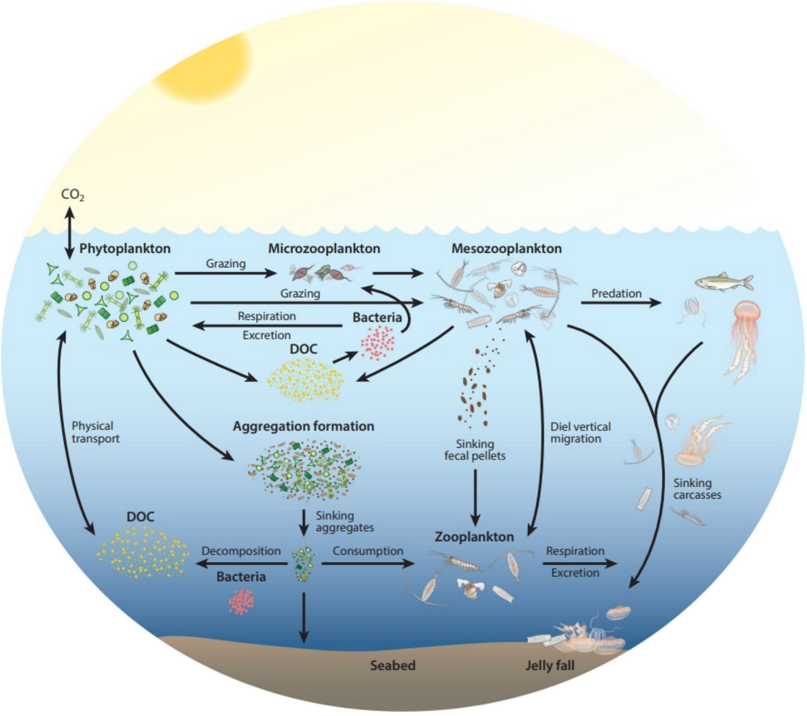

Figure 2: Carbon dioxide (CO_2) is taken up by phytoplankton through photosynthesis and the produced particulate organic carbon is grazed upon by micro- and mesozooplankton. Microzooplankton are consumed by mesozooplankton, which are consumed by higher trophic levels. Zooplankton respire CO_2 and produce dissolved organic carbon (DOC) through excretion, sloppy feeding, and leakage from faecal pellets. DOC is incorporated into bacterial biomass through the microbial loop. Zooplankton contribute to carbon export through diel vertical migration, seasonal migration and through sinking carcasses. Zooplankton and bacteria can contribute to the reduction of particulate organic carbon fluxes through grazing on aggregates (Steinberg and Landry, 2017).

Because of the poor accessibility and challenging logistics in winter, studies on secondary production in the Arctic have mainly been conducted in the summer months (e.g. Sastri et al., 2012; Kimmel et al., 2018; Dvoretsky and Dvoretsky, 2024). However, the mesozooplankton community shows seasonal differences in abundance and composition due to the strong seasonality of food availability and copepods have developed special adaptations to the Arctic environment (Box 1). To date, there are only three studies that have investigated copepod secondary production in a seasonal context in the Arctic (Rysgaard et al., 1999; Madsen et al., 2001; Madsen et al., 2008), in addition to one study describing the seasonal secondary production of a specific copepod species (*Oithona similis*, Zamora-Terol et al., 2013).

Copepod secondary production in the Arctic is highly seasonal and follows primary production dynamics with a temporal shift of some weeks, reaching its highest quantities in the summer months (Madsen et al., 2001). Due to the strong seasonality of light availability and sea-ice cover, Arctic ecosystems have a characteristic primary production regime. With the return of the sun after the polar night, highly shade-adapted sea-ice algae start to bloom. This initial bloom is followed by a bloom of open-water phytoplankton later in spring, when the melt of sea ice due to solar radiation creates a stable vertical stratification, which traps phytoplankton in the euphotic zone. Here, nutrients and light availability are sufficient to initiate a bloom, which results in brief but intense primary production in the seasonal ice zone (Wassmann and Reigstad, 2011). The phytoplankton spring bloom is mainly composed of large-celled diatoms that are dependent on nitrate for growth (Parrish et al., 2005). Associated with the phytoplankton spring bloom is the secondary production of large copepods of the genus *Calanus* (Madsen et al., 2001). Once nitrate is depleted, the microbial community will shift towards smaller organisms (Parrish et al., 2005), e.g. flagellates and ciliates (Seuthe et al., 2011), which can use alternative nitrogen sources for growth, such as ammonium and urea (Kristiansen et al., 1994). Associated with the dominance of the microbial food web is the secondary production of small copepods (Figure 3, Madsen et al., 2008; Zamora-Terol et al., 2013). In some Arctic regions other mesozooplankton groups, e.g. Appendicularia, Chaetognatha and gelatinous zooplankton, are commonly found and can reach considerable biomass (e.g. van Engeland et al., 2023; Wold et al., 2023). Because the growth rates of many of these groups are difficult to determine, even less information is available about their secondary production in Arctic marine ecosystems. One study that has investigated the production of other mesozooplankton groups has shown that their contribution to total mesozooplankton secondary production can be high (Basedow et al., 2014). The above named studies investigating the seasonality of copepod secondary production have been conducted in coastal Arctic ecosystems and so far, no work on this topic has been performed in high-latitude offshore regions, where seasonal dynamics can be more pronounced.

Box 1: Adaptations of copepods to the Arctic environment

Copepods in high latitude ecosystems usually store their energy in the form of lipids, as these are compact, long-term forms of metabolic energy storage, with twice the calorific density as proteins and carbohydrates (Kattner and Graeve, 1991; Hagen and Auel, 2001; Falk-Petersen et al., 2009). Another adaptation to the strong seasonality is diapause, where copepods descend into deeper water layers to hibernate during the food scarcity of winter (Hagen, 1999). This dormant state with a minimal metabolism allows them to survive on their accumulated lipid reserves for longer (Hirche, 1996) and the dark water layers shield them from visual predation (Kvile et al., 2019). Arctic copepods have adapted their reproductive strategies and life cycles to match the highly seasonal food availability in Arctic marine ecosystems (Hagen, 1999; Lee et al., 2006; Daase et al., 2021). There are two main reproductive strategies, one where reproduction relies entirely on internal lipid reserves, called capital breeding, and one where reproduction is governed by food uptake, called income breeding. Capital breeders can reproduce at a time that maximizes their offsprings' fitness, while income breeders exhibit extended periods of reproduction if food availability is sufficient (Sainmont et al., 2014). There are two common life cycle strategies among Arctic copepods. *Calanus* spp. have aligned their reproduction with the ice-algae and phytoplankton bloom phenology, which provides their offspring with a nutritious food source (Figure 3). The timing of reproduction is however crucial, as premature spawning can result in the starvation of the developing nauplii, while delayed spawning can result in copepodids not being able to accumulate enough energy storage for overwintering (Varpe et al., 2007). *Oithona similis*, on the other hand, exhibit a strategy of year-round reproduction, that is not directly tied to the spring bloom. This is because they are predominantly omnivores, allowing them more flexibility in their food acquisition (Figure 3, Ashjian et al., 2003; Dvoretsky and Dvoretsky, 2009; Zamora-Terol et al., 2013).

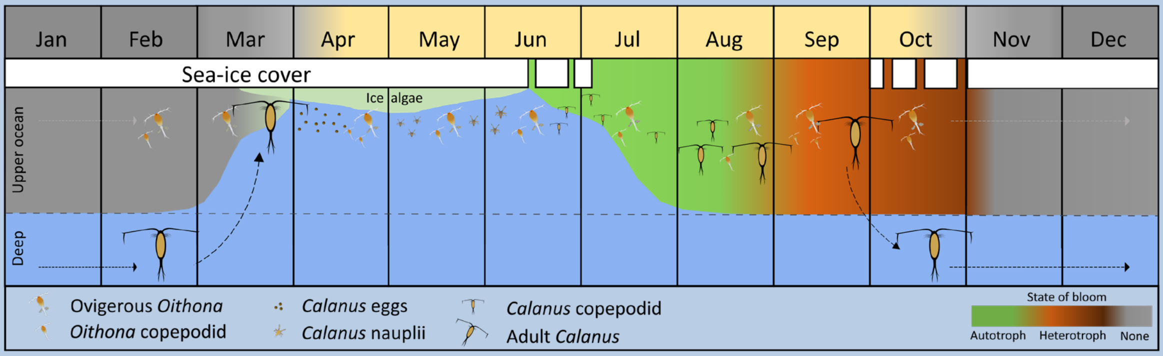

Figure 3: Conceptual figure of the life cycles of *O. similis* and *Calanus* spp. in the Arctic. *Calanus* spp. lays eggs in winter or spring and depending on the species, nauplii and copepodids feed on the spring bloom and/or the ice-algae bloom. Once copepodids have reached the overwintering stage in autumn, they descend into deeper water layers to hibernate. Ovigerous *O. similis* females are observed throughout the year, with a peak in reproduction occurring during spring and late summer (Falk-Petersen et al., 2009; Zamora-Terol et al., 2013; Balazy et al., 2021).

Box 2: Life cycles of *Calanus* spp. and *Oithona similis*.

Three copepod species of the genus *Calanus* co-exist in the Barents Sea. They differ in life history traits such as length of life cycle and reproductive strategies. C. *finmarchicus* has the shortest life cycle with one year at the northern end of its distributional range. It is mainly an income breeder (Richardson et al., 1999) and reproduces during the open water spring bloom (Hirche, 1996). Because of the seasonal bloom phenology and low water temperatures, *C. finmarchicus* is likely not able to successfully reproduce in the Arctic (Hirche and Kosobokova, 2007; Melle et al., 2014) and its occurrence depends on advection with the Norwegian Atlantic Current (Wassmann et al., 2015). However, with increasing water temperatures, conditions for *C. finmarchicus* in the future Arctic will likely become more favorable (Freer et al., 2022). *C. glacialis* has a life cycle of 1–3 years and shows a highly flexible reproductive strategy, being able to switch between income and capital breeding (Falk-Petersen et al., 2009; Daase et al., 2013). It can spawn prior to the phytoplankton spring bloom but can also utilize the ice algae bloom to fuel reproduction (Kosobokova, 1999; Søreide et al., 2010). *C. hyperboreus* has a 2–5-year life cycle, depending on food availability and sea-ice cover (Hirche, 1997; Falk-Petersen et al., 1999). It is almost exclusively a capital breeder (Conover and Siferd, 1993; Hirche and Niehoff, 1996) and reproduces at depth before the ice-algae bloom (Hirche and Niehoff, 1996; Daase et al., 2021). Depending on the species, nauplii and young copepodids feed on the spring bloom and/or the ice-algae bloom (Søreide et al., 2010), while the development and growth of older copepodids can additionally be fueled by grazing on microzooplankton during the summer months (Svensen et al., 2019). After reaching the first diapausing stage, copepodids descend to hibernate at depth in July-August. If necessary, *Calanus* may undergo one or more additional periods of hibernation, before molting into adults and reproducing (Daase et al., 2021). The overwintering depth is highly dependent on bathymetry, with oceanic populations descending to depths >1000 m in the deep basins, while the descent of shelf populations is limited by bathymetry (Hirche and Niehoff, 1996).

O. similis has a bi-modal life cycle in coastal Arctic regions, meaning it produces two generations within one year. The two reproduction peaks occur during the phytoplankton bloom and in late summer, when the microbial food web is the most dominant. One generation has a longer life cycle of about 10 months, developing from egg to adult in September-May and reproducing in June. The next generation has a shorter life cycle of about 3 months, developing from egg to adult in June-August and reproducing in August-September. Ovigerous females have however been observed throughout the whole year, although in lower abundance (Dvoretsky and Dvoretsky, 2009; Balazy et al., 2021).

1.3 Why should we study the secondary production of small copepods in the Arctic?

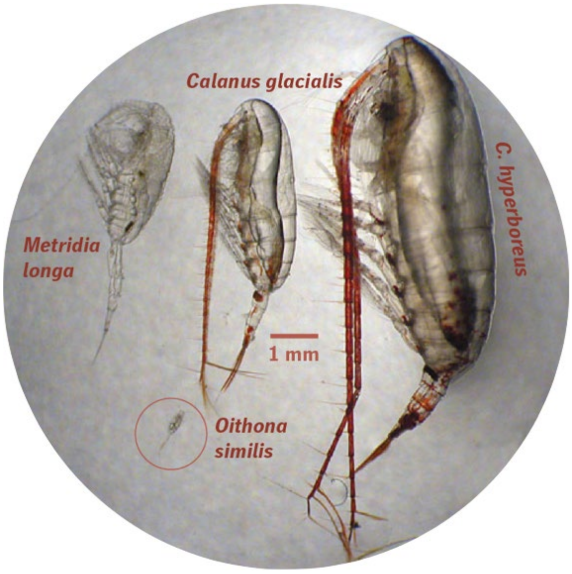

Figure 4: Size comparison of the small copepod *Oithona similis* and the large copepods *Calanus glacialis*, *C. hyperboreus* and *Metridia longa* commonly found in the Arctic. A 1 mm scale bar is indicated. Photo credit: Carin Ashjian, https://neilbanas.com/projects/coltrane/

Most mesozooplankton studies in the Arctic have focused on the larger, more conspicuous *Calanus* spp. (Figure 4). This focus is due to the traditional use of zooplankton nets with relatively coarse mesh sizes of 180 µm or larger (e.g. Kosobokova and Hirche, 2009; Hop et al., 2019b), which effectively capture *Calanus* spp. but result in the extrusion of copepod nauplii, small copepods (e.g. *Oithona similis*, Figure 4) and young developmental stages of larger copepod species (e.g. Gallienne and Robins, 2001). Using inappropriate sampling gear can lead to an underestimation of mesozooplankton abundance of up to 90 %, biomass of up to 33 % and secondary production of up to 66 % (Gallienne and Robins, 2001). Furthermore, studies were mainly conducted during the summer months, when *Calanus* spp. are active (Berge et al., 2015b). Additionally, due to their high lipid content, *Calanus* spp. are considered to be the main link between primary producers and higher trophic levels (Falk-Petersen et al., 2007), meaning that many studies focused solely on *Calanus* spp.

In the last two decades, it has been shown that small copepods generally dominate Arctic mesozooplankton communities in terms of abundance and can at times also play an important role for total mesozooplankton biomass (Nielsen and Sabatini, 1996; Gallienne and Robins, 2001; Turner, 2004). Similar to large copepods, small copepods play an important role in linking primary producers and the microbial food web to higher trophic levels (Roura et al., 2018). Small copepods can play an important role in reducing vertical carbon flux, by grazing on aggregates (Mayor et al., 2020). They are thought to be especially important for food web processes during the months when *Calanus* spp. are hibernating. Based on observations of high abundance of copepod nauplii during the winter months, recent studies suggest that this time of the year could be an important period for the reproduction of some small copepod species in the Arctic (Berge et al., 2015b). However, the reproductive rates of small copepods in winter are poorly known, yet they are essential for predicting population dynamics over the annual cycle (Barth-Jensen et al., 2022). In addition, the ecological role of small copepods in Arctic marine ecosystems, such as their actual contribution to the carbon transfer through the food web, is not well understood at present (Svensen et al., 2011). One contributing factor to this knowledge gap is that small copepods can be difficult to rear in the laboratory, making the investigation of their metabolic rates, such as respiration, excretion, ingestion, and growth rates, a challenging task (Barth-Jensen, 2023). As small and large copepods exhibit different life-history and feeding strategies (Box 1, 2), and they occupy different trophic niches (Boissonnot et al., 2016; Lischka and Hagen, 2016), it is important to estimate their secondary production and the driving factors of production in a seasonal context, in order to improve our understanding of food web interactions and carbon flux. Therefore, in this PhD thesis, special focus was given to the secondary production of the small copepod *Oithona similis* and how its production compares to that of the three *Calanus* species in the Arctic.

O. similis is the most abundant small copepod in the Arctic (Ashjian et al., 2003; Dvoretsky and Dvoretsky, 2009; Balazy et al., 2021) and generally highly abundant in the world's oceans (Gallienne and Robins, 2001; Turner, 2004). Its wide distribution range and high abundance can be attributed to its high tolerance to variations in salinity and temperature, to its high reproductive success that exceeds predation losses (Turner, 2004) and to its omnivorous feeding strategy (Balazy et al., 2021). *O. similis* is an ambush predator (Svensen and Kiørboe, 2000) and its diet preferably consists of mobile prey, such as ciliates. It also feeds on phytoplankton if available (Zamora-Terol et al., 2013), on faecal pellets of *Calanus* (Gonzalez and Smetacek, 1994) and of euphausiids (Castellani et al., 2005), and on detritus during periods of low food availability (Kattner et al., 2003). It is a sac-spawning copepod, also referred to as egg-carrying copepod, meaning that it carries its eggs until hatching. This reduces the mortality rate of eggs through predation by at least one order of magnitude compared to eggs that are freely released into the water column (Kiørboe and Sabatini, 1995). *O. similis* is found in the upper 100 m water column throughout the year and preferably resides in the surface layer during spring-autumn and in deeper waters in winter, but does not diapause (Lischka and Hagen, 2005; Zamora-Terol et al., 2014). The lipids of small copepods are not as energy rich as those of *Calanus* spp. (Lischka and Hagen, 2007; Kattner et al., 2003) and their lipid storage capacity is also lower (Lischka and Hagen, 2007; Narcy et al., 2009).

Arctic marine ecosystems are rapidly changing due to the ongoing, anthropogenic climate change. The Arctic is warming at a rate of up to four times the global average (Rantanen et al., 2022) and the increasing air and sea temperatures have led to a continuous decrease in the extent and thickness of sea ice and of the occurrence of multi-year ice and snow cover (Pörtner et al., 2019). Furthermore, the Arctic is undergoing a borealisation, i.e. 'Atlantification' in the Atlantic-influenced and 'Pacification' in the Pacific-influenced parts of the Arctic, as a result of increasing inflow volumes of Atlantic and Pacific Waters, which transport heat, saline water, and boreal organism northwards (Polyakov et al., 2017; Meredith et al., 2019; Polyakov et al., 2020). With warming water temperatures, the distribution range of both Arctic and boreal copepod species will shift northwards, as copepods occupy distinct thermal niches, based on their species-specific temperature tolerance levels (Villarino et al., 2015). Ocean warming also impacts the size of copepods, resulting in a reduction of the body size of individuals at higher water temperatures (Daufresne et al., 2009; Renaud et al., 2018; Evans et al., 2020). Therefore, the future Arctic ecosystem will likely constitute of smaller copepods and more boreal species, which will lead to changes in the lipid availability on an individual and population level and therefore impact the food quality and transfer efficiency to higher trophic levels (Renaud et al., 2018; Kaiser et al., 2022). In a future Arctic, large copepods will likely become less important and small copepods more important for copepod secondary production (Stabeno et al., 2012; Kimmel et al., 2018; Kimmel et al., 2023). However, to what extent this influences the quantity of secondary production in a future Arctic remains largely unknown. Therefore, it is even more urgent to improve our understanding of the role of small copepods in Arctic marine ecosystems, in order to enhance the accuracy of future predictions.

1.4 Methods of determining mesozooplankton secondary production

There are several ways of estimating secondary production and the quantity and accuracy of the production values depend heavily on the choice of method (Figure 5; Runge and Roff, 2000; Kobari et al., 2019). Mesozooplankton secondary production can be determined directly, by measuring zooplankton growth and reproductive rates, or indirectly by deriving growth rates from relationships with different environmental and biological variables. Among the direct methods are different incubation techniques, including the egg incubation method, that determines female reproductive output (Marshall and Orr, 1955); the moult rate method, that determines somatic growth through moulting rates of individual developmental stages (Burkill and Kendall, 1982); and the artificial cohort method, that follows the size, weight and stage development of artificial cohorts of specific sizes, which were created through size-selective sieving of the zooplankton community (Figure 5, Kimmerer and McKinnon, 1987; Yebra et al., 2017). Another direct method is the natural cohort method (Heinle, 1966), which follows the size, weight, and stage development of natural cohorts through frequent, repeated sampling. Indirect methods include the use of empirical models, which can include different factors, such as temperature, chlorophyll *a* concentration, body weight, spawning type, and developmental stage; the use of annual production to biomass (P/B) ratios (Runge and Roff, 2000; Kobari et al., 2019); or the physiological method that derives growth rates from other metabolic rates, such as respiration or excretion (Winberg, 1956; Ikeda and Motoda, 1978). More recent, alternative techniques to estimate secondary production have been developed, such as biochemical methods, including nucleic acid indices that use specific dyes to follow the enzymatic degradation of RNA or DNA or use RNA:DNA ratios as approximations of somatic growth or reproductive output (Runge and Roff, 2000; Yebra et al., 2017). Another biochemical method is the measurement of enzyme activities, such as Chitobiase activity as a proxy for molting rates of crustaceans, or aminoacyl-tRNA synthetases (AARS) activity as a proxy for somatic growth (Runge and Roff, 2000; Yebra et al., 2017). So far, none of the above mentioned methods has been properly tested for Arctic conditions and at low temperatures and only a few studies have compared the secondary production values from direct and indirect methods (Liu and Hopcroft, 2006a, 2006b; Madsen et al., 2008). Therefore, in this PhD thesis, I used a combination of methods to estimate copepod secondary production, including several empirical growth rate models and the egg incubation method. The modelled growth rates were validated through field-based experiments for the small copepod *Oithona similis*.

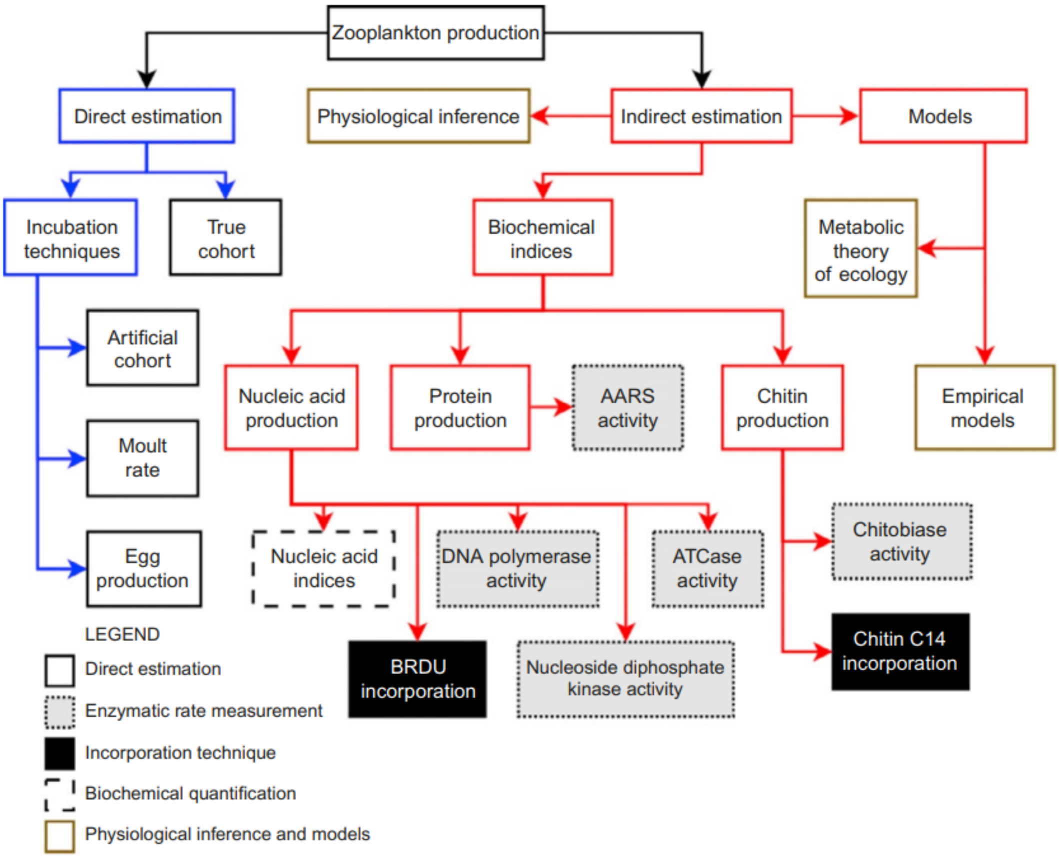

Figure 5: Different methods to estimate zooplankton growth rates and production, by Yebra et al. (2017). Marked with blue arrows are direct estimations of zooplankton production and marked in red are indirect estimations. In this thesis, the egg production method and empirical models were used.

1.5 Objectives and research questions

This PhD thesis has three main objectives and several research questions:

1) Provide new understanding of the spatial and temporal patterns in secondary production and its key drivers in an Arctic offshore region, namely the northern Barents Sea.
    a) Does mesozooplankton secondary production show spatial differences? (**Paper I, II, III**)
    b) Are there temporal differences in copepod secondary production, such as seasonal (**Paper III**) and interannual variability? (**Paper II**)
    c) What is the annual budget of copepod secondary production in the Barents Sea? (**thesis**)
    d) Which environmental and biological factors are decisive for the observed temporal and spatial variability in secondary production? (**Paper I, II, III**)
    e) How could copepod secondary production in a future Barents Sea look like? (**Paper II**)

2) Improve our understanding of the role of small copepods in the Barents Sea ecosystem.
    a) How do vital rates of *Oithona similis* change in a seasonal context? (**Paper III**)
    b) How does secondary production of small and large copepods compare (**Paper I, II, III**) and what is the importance of small copepods for the energy transfer in the Barents Sea food web in a seasonal context? (**thesis**)

3) Assess different methods to determine secondary production and formulate methodological recommendations for future studies in Arctic marine ecosystems.
    a) Which empirical growth rate models is best suited to estimate copepod secondary production in the Arctic? (**Paper I**)
    b) How do secondary production estimates of *O. similis* from a direct and an indirect method, namely the egg incubation method and an empirical growth rate model, compare? (**Paper III**)
    c) What are recommendations for future secondary production studies in the Arctic? (**thesis**)

2 Methods

2.1 Study area — the Barents Sea

The Barents Sea stretches from the shelf break in the west, which constitutes the border with the Norwegian Sea, to Novaya Zemlya in the east and from the Norwegian and Russian coast in the south to the Arctic Ocean shelf break in the north (Sakshaug et al., 2009). It is a relatively shallow shelf sea, with an average bottom depth of 230 m and a maximum depth of about 500 m (Sakshaug et al., 2009). The Barents Sea is strongly influenced by the advection of Atlantic Water, which transports heat, nutrients, saline water, and boreal organisms into the region (Box 3, Midttun and Loeng, 1987; McBride et al., 2016). The Barents Sea can be divided into two distinct domains: a southern domain, which is permanently ice free, well mixed and characterised by warm Atlantic Water; and a northern domain, which is seasonally ice covered, stratified, and characterised by cold, Arctic Water (Loeng, 1991). The Barents Sea experiences the fastest decline of winter sea-ice cover of all Arctic regions (Comiso et al., 2017; Onarheim and Årthun, 2017) and large interannual variability of sea-ice cover. This has been linked to variability of the Atlantic Water inflow into the region (Årthun et al., 2012; Efstathiou et al., 2022), variations of sea ice being transported from the central Arctic Ocean into the Barents Sea (Koenigk et al., 2009; Efstathiou et al., 2022), changes in the atmospheric circulation (Sorteberg and Kvingedal, 2006; Herbaut et al., 2015; Boisvert et al., 2016) and the number of cyclones (Sorteberg and Kvingedal, 2006; Boisvert et al., 2016). The loss of sea ice, the warming of the water masses and the advection of boreal species results in an Atlantification of the Barents Sea, meaning it increasingly resembles a boreal ecosystem (Årthun et al., 2012; Wassmann et al., 2019; Gerland et al., 2023; Wold et al., 2023). Resulting from the variability of water masses and sea-ice cover in the Barents Sea, phytoplankton bloom dynamics, as well as the zooplankton and fish biomass can show significant year to year differences (Skjoldal et al., 1992; Dalpadado et al., 2003; Orlova et al., 2010; Dalpadado et al., 2012). Primary production in the Barents Sea follows a characteristic pattern: in the northern Barents Sea, the sea-ice melt creates a stable stratification, which results in a short but intense phytoplankton bloom that follows the retreating sea ice northwards. In the Atlantic region, the phytoplankton bloom is initiated by stratification through seasonal near-surface heating from solar radiation and is comparably slower and less intense (Wassmann et al., 1999). The Atlantic Water inflow in the Atlantic region can resupply nutrients, which increases the bloom duration in this region (Reigstad et al., 2011). There are indications for autumn blooms in the region, which are initiated by the resupply of nutrients through storm mixing (Ardyna et al., 2014).

Box 3: Circulation patterns in the Barents Sea

The Norwegian Atlantic Current splits into two branches at the Barents Sea Opening in the south (Figure 6). One branch, the northern North Cap Current, enters the Barents Sea through the Bear Island Trough in the south-west (Midttun and Loeng, 1987; McBride et al., 2016). The other branch, the West Spitsbergen Current, flows along the western Svalbard shelf break towards the Arctic Ocean, where it forms the Atlantic Water Boundary Current (Figure 6). Atlantic Water from the Atlantic Water Boundary Current can enter the Barents Sea in the north-west through the Kvitøya and Franz Victoria Troughs (Figure 6, Lind and Ingvaldsen, 2012; Lundesgaard et al., 2022). Cold Arctic Water from the central Arctic Ocean enters the Barents Sea between Nordaustlandet and Franz Josef Land (East Spitsbergen Current) and between Franz Josef Land and Novaya Zemlya (Persey Current, Figure 6). The East Spitsbergen Current follows the eastern coast of Svalbard southwards and the Persey Current flows westwards across the Barents Sea shelf, before they meet and form the Bear Island Current (Figure 6, Sakshaug et al., 2009). When the warm Atlantic Water and the cold Arctic Water meet on the Barents Sea shelf, a density-compensated thermohaline front is formed, the Barents Sea polar front (Figure 6, dashed grey line; Sakshaug et al., 2009; Fer and Drinkwater, 2014). In the western part of the Barents Sea, the polar front is relatively stationary, as it is governed by bottom topography, while it is more variable in the eastern part of the Barents Sea (Oziel et al., 2016).

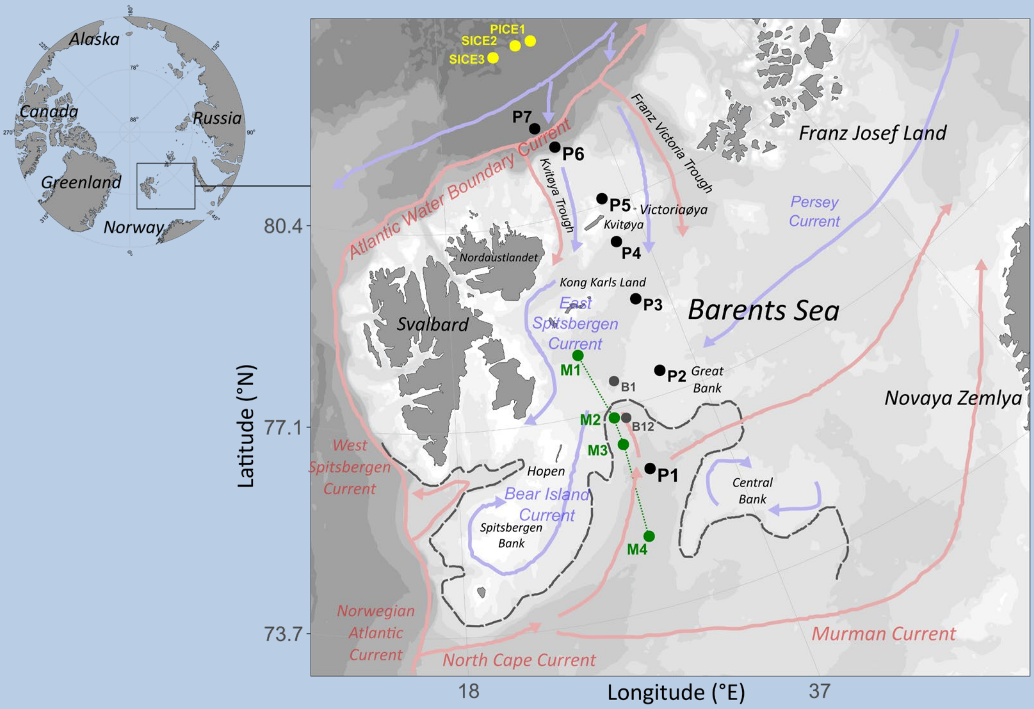

Figure 6: Map of the study area with names of islands and trenches, major currents (after Midttun and Loeng, 1987; McBride et al., 2016) and the locations of the sampling stations for **Paper I, II, III**. The warm, Atlantic Water currents are marked in red and the cold, Arctic Water currents are marked in blue. The approximate location of the polar front in the western part of the Barents Sea is depicted as a dashed grey line and based on the 200 m isobath. Marked in green are stations included in **Paper I**, marked in black are stations included in **Paper II, III**, marked in yellow are stations only included in **Paper II** and marked in grey are stations only sampled in October 2020 and included in **Paper III**.

Calanus copepods are the main drivers of the mesozooplankton biomass variations in the Barents Sea (Aarflot et al., 2018; Dalpadado et al., 2020). In the period from 1990–2010, estimates of the annual mean mesozooplankton biomass in the northern Barents Sea have varied from 1.4 g m^{-2} to > 10 g m^{-2} dry mass (Dalpadado et al., 2012), but have remained rather stable at 5.8–8.4 g m^{-2} dry mass since the mid-2000s (Dalpadado et al., 2020). Typical boreal species, such as *Oithona atlantica, Calanus finmarchicus,* euphausiids (*Thysanoessa inermis*, *T. longicaudata*) and the amphipod *Themisto abyssorum,* are more common in the Atlantic region south of the polar front (Dalpadado et al., 2008). The taxonomic composition of the mesozooplankton community is rather similar across the northern Barents Sea. Here, *C. glacialis*, the amphipod *T. libellula*, pteropods (*Limacina helicina*, *Clione limacina*) and ctenophores (*Mertensia ovum*, *Beroe cucumis*) can contribute significantly to mesozooplankton biomass (Blachowiak-Samolyk et al., 2008; van Engeland et al., 2023; Wold et al., 2023). In the adjacent Arctic Ocean basin, species of Arctic origin and bathypelagic species, such as *Paraeuchaeta* spp. and *Heterorhabdus norvegicus* are more common (Figure 7, Daase et al., 2021; Wold et al., 2023).

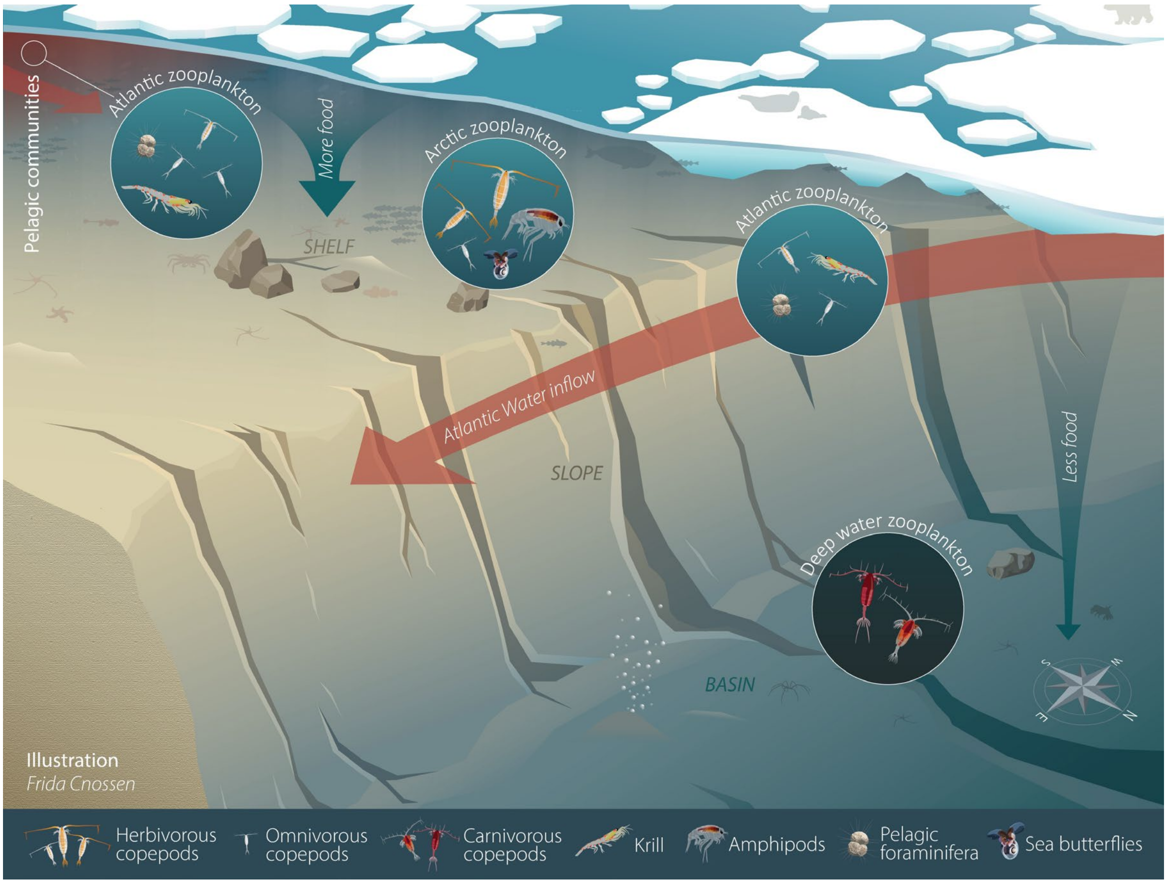

Figure 7: Schematic of zooplankton communities found in the Barents Sea. Illustration: Frida Cnossen, modified from The Nansen Legacy (2024) Fact Sheet: Biodiversity. Zenodo. DOI: 10.5281/zenodo.10842727

2.2 Field work

Samples and measurements for this PhD thesis were collected as part of 'The Nansen Legacy' project and the 'Conflux' project in the Barents Sea. The 'Conflux transect' covered different areas of the Barents Sea polar front (75–78 °N). The 'main transect' covered an environmental gradient from Atlantic to Arctic waters (76–83 °N) in the Atlantic region, the northern Barents Sea, on the continental shelf break and in the Arctic Ocean basin. In total, samples and measurements from 9 cruises were compiled for this PhD thesis. For **Paper I**, data on mesozooplankton abundance, biomass, secondary production, and hydrography were collected in June 2011 along the Conflux transect in the area of the Hopen Deep and Great Bank (Figure 6). For **Paper II**, data on copepod abundance, biomass, and secondary production were collected along the main transect in the Barents Sea in August 2018 and August 2019. For **Paper III**, data on copepod secondary production were collected during 8 cruises along the main transect in February 2022, March 2021, May 2021, August 2018, August 2019, August 2021, October 2020, December 2019.

Throughout this PhD thesis I am using the term 'Atlantic region', when referring to the Atlantic Water influenced, southern region on the Barents Sea shelf, south of the polar front, which includes stations M1 (**Paper I**) and P1 (**Paper II, III**). The term 'polar front' is used when referring to the region within the polar front, which includes stations M2, M3 (**Paper I**) and B1, B12 (**Paper III**, at stations B1, B12 only data on the vital rates of *Oithona similis* were collected and these stations are not included in the discussion section when describing spatial and temporal trends in secondary production). I am using the term 'northern Barents Sea', when referring to the region north of the polar front on the Barents Sea shelf, up to the continental shelf break in the north, which includes stations M1 (**Paper I**) and P2, P3, P4, P5 (**Paper II, III**). In some of the papers included in this thesis, the term 'Arctic domain', 'Arctic region' or 'Barents Sea shelf' is used interchangeably to refer to the northern Barents Sea. The term 'continental shelf break' is used to refer to station P6 (**Paper III**), which was located on the continental shelf break at the northern edge of the Barents Sea shelf. The term 'Arctic Ocean basin' is used to describe stations P7 (**Paper II, III**) and PICE1, SICE2, SICE3 (**Paper II**) located in the Nansen Basin in the Central Arctic Ocean (Box 3, Figure 6).

2.3 Zooplankton sampling for community composition and secondary production

In order to study the mesozooplankton community composition (abundance, biomass) and secondary production with high spatial and taxonomic resolution, the sampling design in this PhD thesis consisted of a combination of different zooplankton nets (**Paper I, II, III**) and an optical sensor (**Paper I**). By using zooplankton nets with different mesh sizes, both the small and large copepods could be collected adequately.

2.3.1 Zooplankton net sampling

For the study presented in **Paper I**, mesozooplankton was sampled for abundance, biomass, and secondary production analyses along the ‘Conflux transect’ with stratified vertical net hauls using a 180 µm WP-2 net and GoFlo bottles (General Oceanics) at different depths. For **Paper II and III**, mesozooplankton was sampled with stratified vertical net hauls along the main transect, using both a 64 µm and a 180 µm MultiNet® Type Midi. The samples from the 180 µm WP-2 net and GoFlo bottles (**Paper I**) and from the 64 µm and 180 µm gauze MultiNet (**Paper II, III**) were analysed separately, and the analytical results were then combined (Wold et al., 2023; Gawinski et al., 2024a). All zooplankton individuals were identified to the lowest possible taxonomic level, also specifying developmental stage (copepodid stage for copepods). Abundance data of mesozooplankton <2 mm, copepod nauplii, all stages of ‘small copepods’, and early developmental stages (CI-CIII) of ‘large copepods’, were obtained from the GoFlo bottles or the 64 µm MultiNet results. Abundance data of all mesozooplankton >2 mm, older developmental stages (CIV-adult) of ‘large copepods’ were based on 180 µm WP-2 or 180 µm MultiNet results. For **Paper I, II, III** we obtained copepod stage-specific carbon mass from literature, which can be found in the Appendix of **Paper II**. For copepod species and life stages for which no published carbon mass was available, a conversion factor of 0.4 (individual dry weight to carbon weight) was used (Peters and Downing, 1984).

To determine the egg production rates of *Oithona similis*, the egg incubation method was used in **Paper III**. Live copepods were collected with a non-filtering 64 µm meshed Bongo net in surface waters (0–100 m) at selected stations along the main transect. Additional mesozooplankton samples were taken with a 64 µm meshed Bongo net from surface to bottom at selected stations, in order to determine the percentage of ovigerous females of *O. similis*.

2.3.2 Laser Optical Plankton Counter (LOPC)

High-resolution abundance data of mesozooplankton in three size classes (small, 0.25–0.6 mm equivalent spherical diameter (ESD), medium, 0.6–1.5 mm ESD and large, 1.5–4 mm ESD) were obtained using a Laser Optical Plankton Counter in the study presented in **Paper I**. The LOPC is a plankton remote observation instrument that uses laser light (other remote technics use e.g. acoustics) and records the number, size, transparency and silhouette of zooplankton and other particles while being towed through the water. When particles pass through the sampling channel of the LOPC, they occlude a laser light that is received on a matrix of photo elements. Based on the number of occluded photo elements, inferences about the size and shape of the particle can be made (Herman et al., 2004). The LOPC was attached to a moving vessel profiler that took close-to-vertical profiles from surface to 10 m above bottom along the Conflux transect (dotted green line in Figure 6). LOPC biovolumes were converted into carbon weight using a biovolume-carbon content regression (Forest et al., 2012).

2.4 Estimates of mesozooplankton and copepod secondary production

Mesozooplankton secondary production is defined as the increase of mesozooplankton biomass in a certain area over a certain period of time (expressed in e.g. mg C m^{-2} d^{-1}). The flux of energy can be measured in carbon, dry weight, wet weight, or energy content (Benke and Huryn, 2017). In **Paper I, II, III** we used the increase in carbon weight to describe secondary production, as it is a standardized ecological unit that helps to compare secondary production to other fluxes of energy in the ecosystem, such as primary production and vertical flux. Secondary production was estimated as the product of the biomass (B_i) and the weight-specific growth or egg production rate (g_i) of each individual stage within the mesozooplankton population (Kimmerer and McKinnon, 1987; Runge and Roff, 2000; Kobari et al., 2019):

$$p = \sum B_i \times g_i$$

Ideally, the growth rates of all developmental stages of individual mesozooplankton species would be determined directly at *in situ* temperatures and food conditions. However, this task is extremely labour-intensive and unrealistic. As a result, growth rates are typically only determined experimentally for selected key species and consequently only few direct measurements exist. One of the most commonly used direct methods to determine copepod growth rates is the egg incubation method. This straightforward approach measures the egg production rate of females, which is then assumed to equal the growth rates of all other developmental stages, making it a relatively labour efficient method. Alternatively, growth rates can be estimated using 'short-cut methods' that derive growth rates through empirical growth rate models from easily measured variables, such as temperature, chlorophyll *a* concentration, copepod body weight, and spawning type (Runge and Roff, 2000). Different growth rate models provide distinct estimates of secondary production, and each model has a specific set of assumptions and approximations, which need to be taken into consideration when selecting the appropriate model for the study system.

In **Paper I**, secondary production of only the copepod community was estimated from WP-2 net and GoFlo bottle sampling, as the applied growth rate models were only suited to estimate growth rates of copepods (Runge & Roff 2000). A different approach was applied for data acquired with the LOPC. With this data, mesozooplankton secondary production (including the copepod community and non-copepod mesozooplankton groups) was estimated for three different size classes, by applying a zooplankton growth rate model developed for the usage with optical plankton counters. In **Paper II**, the production of the copepod community was estimated with a combination of different copepod growth rate models. In **Paper III**, the secondary production of *Oithona similis* was calculated with the egg incubation method and estimated with a copepod growth rate model and the production of the entire copepod community was estimated using a combination of different copepod growth rate models.

The study in **Paper I** focused on the upper 50 m water layer, as the LOPC identified this depth range as the active mesozooplankton layer. The studies in **Paper II, III** focused on the upper 100 m water column, as copepods found in this depth range were assumed to be active and hence to contribute to secondary production (Gawinski et al., 2024b). The estimates presented in this PhD thesis are therefore conservative, as some copepods residing in water layers below a depth of 100 m are also active and can contribute to the secondary production taking place in the local ecosystem. Including hibernating individuals would however significantly overestimate production, which is why the conservative approach was applied (Gawinski et al., 2024b).

Throughout this thesis, the term ‘mesozooplankton secondary production’ will be used when referring to the production of the mesozooplankton community, including copepods and non-copepod mesozooplankton groups and the term ‘copepod secondary production’ will be used when referring to the production of the copepod community only, including copepod nauplii and all copepodid and adult stages.

2.4.1 Empirical models

In **Paper I**, the applicability of three copepod growth rate models (A-C) and one zooplankton growth rate model (D) was evaluated to estimate secondary production of copepods and the entire mesozooplankton community in the Barents Sea. The models were chosen because they are among the most commonly used empirical growth rate models in Arctic regions, but their applicability to estimate copepod secondary production in a seasonal context has not been evaluated yet. The models are based on global literature reviews of growth and reproductive rates of a variety of copepod species, which were then related to different forcing variables:

(A) Hirst and Bunker, 2003: water temperature, copepod body weight, chlorophyll *a* concentration

(B) Hirst and Lampitt, 1998: water temperature, copepod body weight

(C) Huntley and Lopez, 1992: water temperature

(D) Zhou et al., 2010: water temperature, body weight, chlorophyll *a* concentration; accounts for assimilated food input of zooplankton.

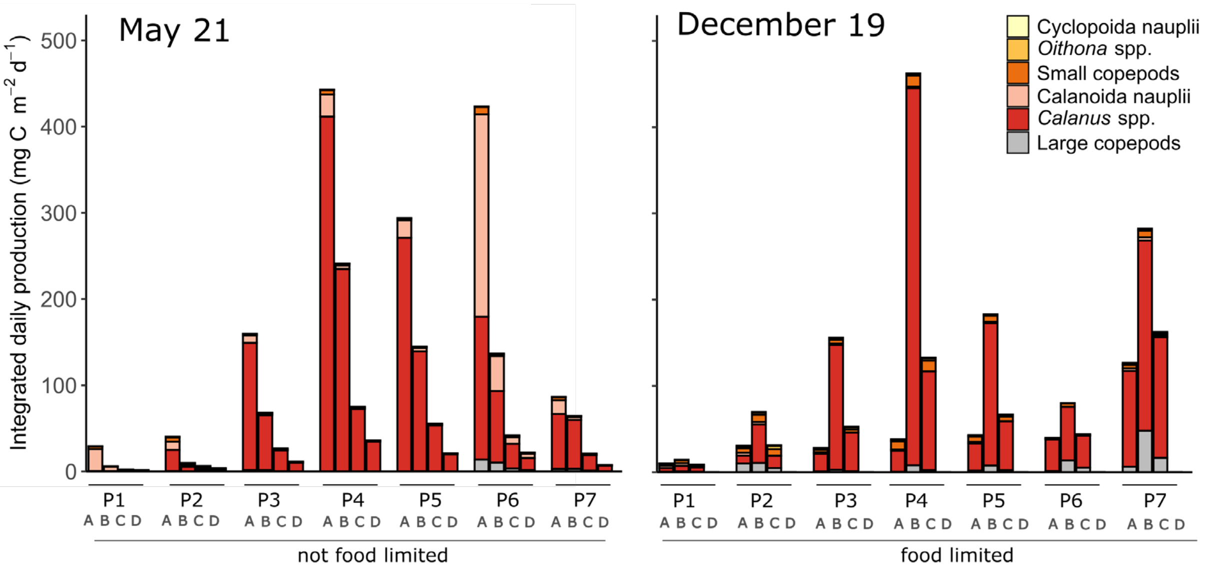

Figure 8: Comparison of integrated copepod secondary production (mg C m^{-2} d^{-1}) in the upper 100 m at stations P1-P7 in the Barents Sea, when calculated using growth rate models A-D. Model A: Hirst and Bunker (2003), B: Hirst and Lampitt (1998), C: Huntley and Lopez (1992), D: Zhou et al. (2010). Daily secondary production is depicted during a period when conditions for primarily herbivorous copepods were considered not food limited (May 2021) and a period when conditions were considered food limited (December 2019). The different colours indicate contribution of different copepod groups.

The range of copepod secondary production values varied considerably with the choice of growth rate model (Figure 8, Table 2). Overall, the Hirst and Bunker (2003) model resulted in the highest range of copepod secondary production under non-food limiting conditions, followed by the Hirst and Lampitt (1998) model and the Huntley and Lopez (1992) model (**Paper I,** Figure 8). Under food limiting conditions, copepod secondary production values were higher when calculated with the Hirst and Lampitt (1998) model than with the Hirst and Bunker (2003) model (Figure 8). The copepod growth rate models (A-C) generally resulted in higher copepod secondary production than the zooplankton growth rate model (D) (**Paper I**).

Based on the evaluation of the different growth rate models (Table 2), we decided to use the Hirst and Lampitt (1998) model to describe secondary production of predominantly herbivorous copepods, e.g. *Calanus* spp., during times of non-food limiting conditions (May, June, July, August, October, **Paper I, II, III**), as it approximates the maximum possible growth under food saturation at certain temperatures. We used the Hirst and Bunker (2003) model to estimate secondary production of these copepods during periods of food limitation (December, February, March **Paper III**). The Hirst and Lampitt (1998) model was used to estimate secondary production of small copepods year-round, as their reproduction is not limited by phytoplankton availability (February, March, May, June, July, August, October, December, **Paper I, II, III**). The Zhou et al. (2010) model was used to estimate secondary production of the whole mesozooplankton community based on LOPC sampling (June, **Paper I**).

Table 2: Comparison of three copepod growth rate models (A-C) and a zooplankton growth rate model (D), including an assessment of the production to biomass (P/B) ratios derived from the different models with those documented in literature and recommendations for the use of each model (**Paper I**). BS indicates broadcast-spawning copepods and SS indicates sac-spawning copepods. This table was taken from **Paper I**.

	Growth rate model			
	(A) Hirst & Bunker (2003)	(B) Hirst & Lampitt (1998)	(C) Huntley & Lopez (1992)	(D) Zhou et al. (2010)
Included parameters	Temperature, copepod body weight, chl *a* concentration	Temperature, copepod body weight	Temperature	Temperature, copepod body weight, chl *a* concentration
Copepod groupings	All copepods Separate equations for SS adults & juveniles, BS adults & juveniles	All copepods Separate equations for SS adults & juveniles, BS adults & juveniles	All copepods	Mesozooplankton
Data set size	4831 measurements across 88 copepod species within 29 genera	952 measurements across 41 copepod species	181 measurements across 33 species	na[a]
Percentage of variance explained	35.7% for BS adults; 39% for BS juveniles; 11.3% for SS adults; 28.9% for SS juveniles	43.5% for BS adults, 49.0% for BS juveniles, 31.1% for SS adults, 39.9% for SS juveniles	91%	na[a]
Applicable temperature range	−2.3 to 30.6°C	−2.3 to 29.0°C	−1.7 to 30.7°C	na[a]
Applicable copepod body weight	Adults: 0.199–3260 µg C ind.$^{-1}$ Juveniles: 0.017–72.1 µg C ind.$^{-1}$	0.075–3620 µg C ind.$^{-1}$	nd	na[a]
Applicable chl *a* range	0.016–321.6 mg chl *a* l^{-1}	nd	nd	na[a]
Estimated P/B ratios	P/B ratio for total copepod community higher than literature values. Best fit for medium and large size classes, overestimation of small size class of mesozooplankton	P/B ratio for total copepod community similar to literature values. Best fit for medium and large size classes, overestimation of small size class of mesozooplankton	P/B ratio for total copepod community similar to literature values. Best fit for medium and large size classes, overestimation of small size class of mesozooplankton	P/B ratio for total copepod community lower than literature values. Best fit for small size class, underestimation of medium and large size class of mesozooplankton
Recommended use	Estimation of secondary production of large, predominantly herbivorous copepods during food-limiting conditions, e.g. fall and winter	Estimation of secondary production of large, predominantly herbivorous copepods during non-limiting food conditions, e.g. spring and summer. Year-round estimation of secondary production of small, omnivorous copepods	Not recommended in high-atitude ecosystems, due to temperature being the only factor considered and production consequently following temperature trends in the study area	Estimation of mesozooplankton production in combination with biomass data in size bins from optical plankton instruments

[a] The model of Zhou et al. (2010) originates from the model of Hirst & Bunker (2003) and incorporates the theoretical definition of zooplankton growth by Huntley & Boyd (1984)

To calculate the annual copepod secondary production in the different regions of the Barents Sea, the daily values were integrated over a period of 365 days. To avoid a possible overestimation of production, as only one value per month was available in the present study, the highest secondary production values were integrated over a time period of two weeks, based on a study from Disko Bay, western Greenland, where the highest secondary production of large copepods occurred over a relative short time period of about two weeks (based on biweekly sampling, Madsen et al., 2001). All other values were evenly integrated across the year.

2.4.2 Egg incubation method

In order to validate the modelled secondary production of *Oithona similis*, growth rates of females were determined experimentally through the egg incubation method. Weight specific egg production rates (SEPR) were investigated through incubations of egg-carrying *O. similis* females at *in situ* temperatures at certain stations during cruises in August 2019, December 2019, October 2020, March 2021, May 2021, August 2021, and February 2022 (**Paper III**; following the approach by Nielsen and Sabatini, 1996):

$$SEPR = HR\, x \frac{E}{F} x \frac{Wegg}{Wfemale}$$

where *HR* is the temperature-dependent egg hatching rate (d^{-1}), *E* and *F* are the total abundance of eggs (eggs m^{-3}) and females (ind. m^{-3}) at the stations, and *Wegg* and *Wfemale* are the individual egg and female carbon content (µg C), respectively.

The detailed experimental protocol can be found in **Paper III**.

2.5 Supplementary physical and biological data

Multiple biological and environmental factors can influence the copepod community composition and its production, such as water temperature and salinity (e.g. Daase and Eiane, 2007; Trudnowska et al., 2016; Balazy et al., 2018), sea-ice cover (e.g. Kimmel et al., 2018; Kimmel et al., 2023), the protist community composition (e.g. Levinsen et al., 2000; Leu et al., 2011) and primary production (e.g. Svensen et al., 2019). To analyse which factors are decisive for the temporal and spatial variability in mesozooplankton and copepod secondary production, data on water column temperature (**Paper I, II, III**) and salinity (**Paper I, II**), chlorophyll *a* concentration (**Paper I, II, III**), protist abundance, primary production, and bacterial production rates (**Paper II**) were included in the analyses in the different papers.

Detailed sampling procedures for the environmental and biological properties measured can be found in The Nansen Legacy sampling protocol (The Nansen Legacy, 2020) and in **Paper I, II**.

3 Key findings, discussion, and synthesis

In this PhD thesis, I aimed to enhance our understanding of the spatial and temporal patterns of mesozooplankton and specifically copepod secondary production in the Barents Sea, with a focus on small copepods, and to improve the methodologies used to study mesozooplankton secondary production in Arctic marine ecosystems. The aims of this thesis were achieved through field and laboratory work conducted during research cruises and a research stay at the Institute of Oceanology of the Polish Academy of Sciences, along with an extensive literature review and the presentation and discussion of results at international conferences. The main findings were: 1) the Atlantic region exhibited very different mesozooplankton secondary production dynamics compared to the northern Barents Sea; 2) seasonal trends in copepod secondary production were more pronounced than interannual variability; 3) a seasonal shift in trophic dynamics was related to a higher contribution of small copepods to copepod secondary production in winter; 4) under current climate conditions, small copepods played a minor role in the energy transfer through the food web in the northern Barents Sea in summer; 5) their importance is likely to increase in a future Barents Sea; 6) using direct and indirect methods and different empirical models to determine copepod secondary production resulted in a considerable spread of production values; 7) biomass rather than growth rate was decisive for copepod secondary production in the Barents Sea; 8) a combination of optical sensors and traditional net sampling with different mesh sizes ensured high spatial and taxonomic resolution of mesozooplankton secondary production and minimized sampling biases. The results of my PhD thesis suggest that future research on mesozooplankton secondary production in Arctic marine ecosystems should address seasonal biomass estimates of key species, develop a copepod growth rate model incorporating food limitation by microzooplankton standing stock and data on the growth rates of small copepods at low water temperatures, and to create methods to determine the production of mesozooplankton groups other than copepods.

The following synthesis consists of six parts. The first part outlines the spatial patterns of mesozooplankton and copepod secondary production and its main drivers in different regions of the Barents Sea (**Papers I, II, III**). The second part summarizes the temporal patterns of copepod secondary production, including seasonal (**Paper III**) and interannual variability (**Paper II**), as well as an annual budget of copepod secondary production (**thesis**), and its main drivers (**Papers II, III**). The third part discusses the role of small copepods in the Barents Sea ecosystem (**Papers I, II, III**). The fourth part outlines potential implications of anthropogenic climate change for copepod secondary production (**Paper II**), the fifth part compares the different methods used in this thesis (**Papers I, III**) and provides methodological recommendations for future studies and the final part identifies research gaps and future perspectives.

3.1 Spatial patterns of mesozooplankton and copepod secondary production in the Barents Sea in summer

There were clear differences in mesozooplankton secondary production between the different regions of the Barents Sea (Figure 9, considering summer production in June and August). Both the quantity and the contribution of different species to mesozooplankton secondary production changed throughout the study area (**Paper I, II, III**). Mesozooplankton secondary production concentrated mainly in the upper 50 m of the sea (**Paper I**) and its local levels were influenced by a combination of different factors. Some factors, such as water temperature and food availability in relation to the pattern of retreating sea ice, directly influenced secondary production by impacting growth rates, while other factors, such as advection of mesozooplankton with the Norwegian Atlantic Current, predation pressure and seasonal migration patterns, influenced secondary production indirectly by impacting biomass. These factors had varying importance in the different regions of the Barents Sea.

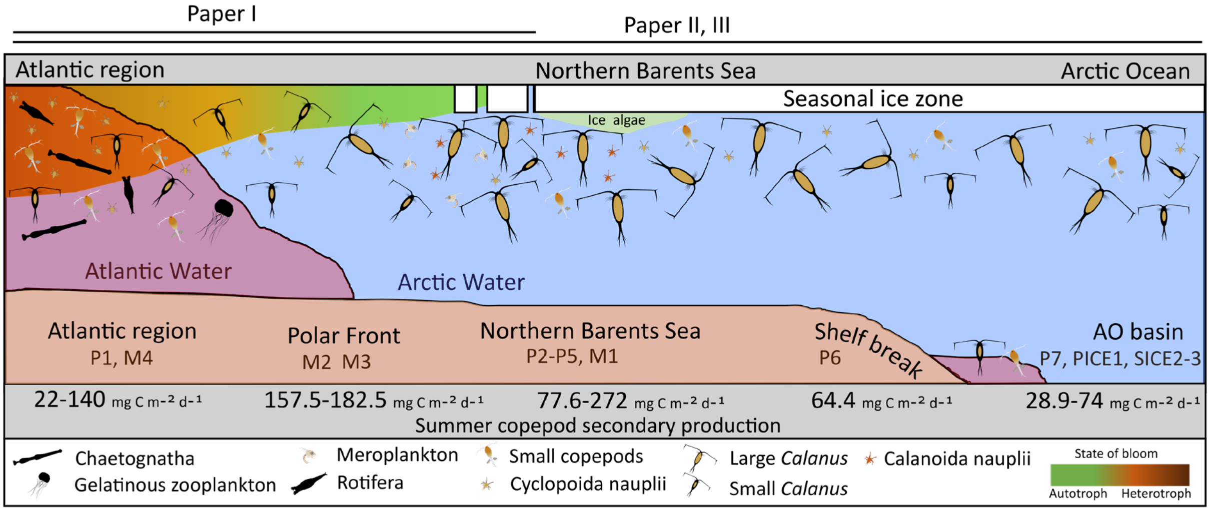

Figure 9: Highest mesozooplankton secondary production was observed in the Atlantic region in summer. Here, Rotifera, Appendicularia, Chaetognatha, and gelatinous zooplankton were common, while they were almost absent in other parts of the study area. Copepod secondary production in the Atlantic region was low, likely due to high predation pressure on large *Calanus* spp. Copepod production was characterized by a high contribution of small copepods, mainly represented by *Oithona similis*, which showed high reproductive rates due to higher water temperatures. In the northern Barents Sea, copepod secondary production was generally the highest and dominated by *Calanus* spp., while production on the continental shelf break and in the Arctic Ocean basin was lower than in the northern Barents Sea. These spatial patterns suggest a more direct energy flow through the food web in the northern Barents Sea compared to the Atlantic region, where smaller copepods increased the steps between primary producers and higher trophic levels, impacting trophic dynamics.

Atlantic region

In the Atlantic region (station M4, **Paper I**), mesozooplankton secondary production was overall the highest and decreased towards the northern Barents Sea (station M1, **Paper I**, Figure 9; Basedow et al., 2014). When considering only copepod secondary production, a different trend emerged. Copepod secondary production was lowest in the Atlantic region (station M4, **Paper I**; station P1, **Paper II, III**) and increased towards the northern Barents Sea (station M1, **Papers I**; stations P2-P5, **Paper II, III**, Figure 9). This indicates that in the Atlantic region, a significant portion of the mesozooplankton production came from organisms other than copepods, whereas copepods constituted the majority of mesozooplankton secondary production in the northern Barents Sea (Figure 9). The abundance and biomass of other mesozooplankton groups in the northern Barents Sea (stations P2-P5) and the Arctic Ocean basin (station P7) were low (Wold et al., 2023), indicating that their contribution to mesozooplankton secondary production was likely low in the rest of the study region. The main factors influencing secondary production in the Atlantic region in summer were the advection of boreal mesozooplankton, increased predation pressure and faster growth rates due to higher water temperatures and the seasonal migration behaviour of *Calanus* spp. (**Paper I, II, III**). In the following section, their effects on secondary production are discussed in more detail.

Mesozooplankton abundance and biomass in the Barents Sea are strongly influenced by the advection of boreal organisms with the Norwegian Atlantic Current (e.g., (Edvardsen et al., 2003a; Edvardsen et al., 2003b; Aarflot et al., 2018; Wold et al., 2023). Pronounced seasonal pulses in the occurrence of boreal species can be observed in the Atlantic region (station P1) in summer and along the slope north of Svalbard (stations P6, P7) in autumn, following periods of increased Atlantic Water inflow (Wold et al., 2023). Boreal organisms locally contribute to mesozooplankton secondary production in these regions (Basedow et al., 2014, for the Atlantic region). In our study, high abundance of Rotifera and high biomass of Appendicularia, Chaetognatha and gelatinous zooplankton were observed in the Atlantic region, suggesting a high contribution to mesozooplankton secondary production (**Paper I**). Chaetognatha are carnivorous predators, feeding on a variety of zooplankton and fish larvae, with copepods being their main prey (Feigenbaum and Maris, 1984). They can significantly affect copepod populations in Arctic marine ecosystems through top-down control (Sameoto, 1973; Grigor et al., 2014; Patuła et al., 2023), resulting in a decrease in copepod biomass and, consequently, copepod secondary production. In Bedford Basin, Nova Scotia, the chaetognath *Sagitta elegans* consumed as much as 36 % of the annual copepod secondary production (Sameoto, 1973). Additionally, planktivorous fish, such as capelin (*Mallotus villosus*), Norwegian spring spawning herring (*Clupea harengus*) (Aune et al. 2021) and planktivorous juvenile stages of piscivorous fish, e.g. Atlantic cod (*Gadus morhua*), haddock (*Melanogrammus aeglefinus*), saithe (*Pollachius virens*), and beaked redfish (*Sebastes mentella*) (Bogstad et al., 2000) can contribute to top-down control of copepods in the Barents Sea. The occurrence of large copepods in the different regions of the Barents Sea is related to predation pressure (Basedow et al., 2014; Langbehn et al., 2023). On the shallow banks in the Atlantic region south of the polar front, high mortality rates from predation (Basedow et al., 2014) lead to decreased abundance of *Calanus* spp. and they are mostly found in deeper troughs (Langbehn et al., 2023). In the northern Barents Sea, *Calanus* spp. are located in shallower waters in the seasonal ice zone, where sea-ice cover shields them from visual predation (Langbehn et al., 2023). An additional factor impacting the production of *Calanus* spp. is their seasonal migratory pattern. In the Atlantic region, the majority of *Calanus* spp. had already descended to hibernate at depth in August, leading to decreased biomass and secondary production in the upper ocean (**Paper III**). In the Atlantic region, small copepods had a much higher contribution to total copepod secondary production than in the rest of the study area (**Paper I, II, III**). Here, they contributed up to 62 % to total copepod secondary production (**Paper I, II, III**), while their contribution was only 0.2–9.2 % in the northern Barents Sea (**Paper I, II, III**) and 1.8–4.6 % in the Arctic Ocean basin (**Paper II, III**). The production of *Oithona similis* formed the main part of the secondary production of small copepods (**Paper I, II, III**). Compared to large copepods, the predation pressure on *O. similis* is lower due to its smaller size, more transparent body build and feeding strategy (Turner, 2004; Zamora-Terol et al., 2013). As an ambush-predator (Paffenhöfer, 1998), *O. similis* creates very little disturbance in the water, because it remains stationary for most of the time, only jumping to capture prey once it has been mechanically detected (Kiørboe et al., 2009). *Calanus* spp., on the other hand, are much more conspicuous in the water due to their filter-current feeding behaviour, resulting in higher mortality rates (Eiane and Ohman, 2004). The high relative contribution of small copepods to copepod secondary production in the Atlantic region (**Paper I, II, III**) can further be explained by higher water temperatures than in the northern Barents Sea and on the continental shelf break and in the Arctic Ocean basin, which resulted in higher reproductive rates of *O. similis* in summer (**Paper III**). Fecundity of *O. similis* is positively correlated with water temperature (Ward and Hirst, 2007; Dvoretsky and Dvoretsky, 2009), as higher temperatures lead to faster egg hatching times because the embryonic development is faster. The potential hatching rates of *O. similis* in the Atlantic region were at least 7 times higher than in the northern Barents Sea (**Paper I**). Egg hatching time influences the egg production rate, as a new egg clutch cannot be extruded until the current egg clutch has hatched. Consequently, the egg production rate (i.e. female growth rate) increases linearly with temperature (Nielsen et al., 2002; Barth-Jensen et al., 2020), explaining why highest secondary production of *O. similis* in summer was observed in the Atlantic region (**Paper III**).

Barents Sea polar front

The Barents Sea polar front (stations M2, M3, **Paper I**) affected the mesozooplankton community composition and its production, as it acts as a habitat boundary for different boreal and Arctic species (Hassel, 1986; Owrid et al., 2000; Fossheim et al., 2006). The position of the polar front in the western part of the Barents Sea is rather stationary, as it is bound by bottom topography, while its position in the eastern part can show interannual variability due to differences in Atlantic Water inflow (Oziel et al., 2016). Therefore, the contribution of boreal and Arctic copepods to copepod secondary production in the northern Barents Sea can vary between years (**Paper II**). The polar front is often found coupled with a meltwater front as a result of sea-ice melt in spring and summer (Fer and Drinkwater, 2014), which was also the case in our study in June (**Paper I**). The meltwater layer led to the development of a horizontal density gradient that influenced the pattern of small mesozooplankton secondary production across the polar front, as it acted as a barrier to their northward dispersal (**Paper I**). The meltwater layer also facilitated the phytoplankton bloom and the highest concentrations of chlorophyll *a* were observed right below it (**Paper I**). Secondary production of medium and large-sized mesozooplankton, with the main contributors being *Calanus* spp., was rather patchily distributed across the polar front and was associated with areas of high chlorophyll *a* concentration (**Paper I**), indicating its dependency on food availability (Trudnowska et al., 2016). Total mesozooplankton secondary production across the polar front was lower than in the Atlantic region (**Paper I**). On the other hand, copepod secondary production across the polar front was higher than previously reported for the eastern Barents Sea polar front (Dvoretsky and Dvoretsky, 2024**; Paper I**) but it did not exceed the highest copepod secondary production observed in the northern Barents Sea (**Paper II, III**).

Northern Barents Sea

The overall highest copepod secondary production was observed in the northern Barents Sea (station M1, **Paper I**; stations P2, P3, P4, P5, **Paper II, III**) and exceeded that reported from some other Arctic regions (**Paper I**). *Calanus* spp. formed the main part of copepod secondary production in the northern Barents Sea (**Paper I, II, III**), contributing 25.9–92.8 % to total copepod secondary production. This high production can be explained by high biomass of *Calanus* spp. (**Paper II**), likely due to a combination of decreased predation pressure and favourable feeding conditions. Sea-ice cover and the resulting phytoplankton bloom dynamics stood out as the most important factor influencing copepod secondary production in the northern Barents Sea (**Paper II**). Spatial trends in the changes of taxonomic composition and secondary production of the copepod community clearly reflected the retreat pattern of the sea ice (**Paper I, II, III**). Calanoid nauplii were highly abundant in areas where sea ice had just broken up and their contribution to total copepod secondary production in these regions was substantial, accounting for up to 74 % (**Paper I**). The developmental state of the *Calanus* community and its contribution to copepod secondary production followed a south-north gradient, where communities in the south were in a more advanced developmental state (including predominantly young copepodid stages, as reproduction had happened some weeks prior) and communities in the north were in an earlier developmental state (including predominantly adults and nauplii, indicating recent reproduction) (**Paper I, II, III**). The low water temperatures in the northern Barents Sea restricted the reproduction of small copepods, as water temperatures below 5 °C (Ward and Hirst, 2007) can limit the overall fecundity of *O. similis* (Metz, 1995; Ward and Hirst, 2007; Dvoretsky and Dvoretsky, 2009). Consequently, the contribution of small copepods to total copepod secondary production in the northern Barents Sea was rather minor, except at the southernmost station P2 (**Paper I, II, III**).

Continental shelf break and Arctic Ocean basin

Copepod secondary production on the continental shelf break (station P6, **Paper III**) and in the Arctic Ocean basin (station P7, **Paper II, III**; stations PICE1, SICE2, SICE3 **Paper II**) was mostly lower than in the northern Barents Sea (**Paper I, II, III**) and in the Atlantic region (**Paper I**). 79.4–95.4 % of the copepod secondary production in these regions was contributed by large copepods. Unsurprisingly, due to the high latitude, the Arctic *C. hyperboreus* showed its highest contribution to copepod secondary production in the Arctic Ocean basin. There was also a high contribution of *C. finmarchicus* to total copepod secondary production on the continental shelf break and in the Arctic Ocean basin, which can be explained by the previously discussed advection of boreal organisms into the central Arctic with the Atlantic Water Boundary Current that flows along the northern Svalbard coast (Wold et al., 2023).

3.2 Temporal patterns of copepod secondary production in the northern Barents Sea

Copepod secondary production exhibited clear seasonal patterns in the northern Barents Sea, both in terms of quantity and contribution of different copepod species to copepod secondary production, following primary production dynamics with a temporal shift of some weeks (**Paper III**). Interannual variations in environmental factors between two summers did not significantly alter the quantity of copepod secondary production but resulted in a shift in its composition (**Paper II**). The annual copepod secondary production in the Barents Sea was higher than in other Arctic regions, supporting the assumption of a highly productive ecosystem. Similar to the factors influencing copepod secondary production on a spatial scale, water temperature, food availability in relation to the sea-ice retreat, and seasonal migration patterns influenced copepod secondary production, with their importance varying across seasons.

Seasonal trends in copepod secondary production

Copepod secondary production in the northern Barents Sea peaked in early summer (Figure 10, **Paper III**), similar to seasonal patterns observed in other Arctic regions (Rysgaard et al., 1999; Madsen et al., 2001; Coyle and Pinchuk, 2002; Madsen et al., 2008). Associated with the new primary production in spring and summer was the secondary production of large copepods, mainly *Calanus* spp. The peak in secondary

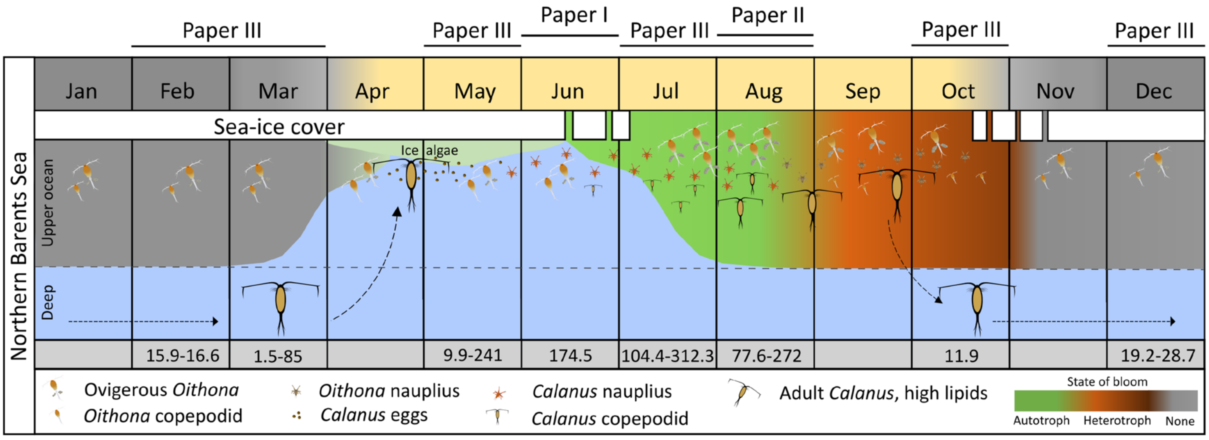

Figure 10: Copepod secondary production on the Barents Sea shelf peaked in summer (July and August) due to high production of *Calanus* spp., which ascended from diapause in spring (around May). High contribution of calanoid nauplii to copepod secondary production was observed in summer (July). Even though the secondary production of small copepods was highest in summer (August), their overall contribution to total copepod secondary production in this period was minimal. *O. similis* reproduced year-round but did not show a bi-modal life cycle like in temperate and sub-Arctic regions, as high numbers of nauplii were only observed in summer and autumn (July to October). High reproductive output of *O. similis* in summer was linked to high weight-specific egg production rates, resulting from a high percentage of ovigerous females with large clutches and high hatching success. Once the majority of *Calanus* spp. descended to hibernate at depth in autumn (around October), the contribution of small copepods to total copepod secondary production increased and remained high in winter. This seasonal shift underscores the importance of small copepods in Arctic ecosystems in winter, highlighting their role in maintaining trophic dynamics when larger species are less active.

production of *Calanus* spp. was in July in the southern parts (station P2, P3, P4) and in August in the northern part of the shelf (station P5), reaching a maximum of 250.7 mg C m^{-2} d^{-1} (**Paper III**). This is comparable to the maximum secondary production of large copepods in Disko Bay, western Greenland of 250 mg C m^{-2} d^{-1} at the end of May / beginning of June (integrating for their sampling depth of 0–50 m, based on the Huntley and Lopez, 1992 model; Madsen et al., 2001). The secondary production of *Calanus* spp. was positively correlated with chlorophyll *a* concentration (**Paper II**). This is because secondary production of broadcast-spawning copepods, e.g. *Calanus* spp., is primarily controlled by food availability (Kiørboe and Sabatini, 1995) and the life history strategies of *Calanus* spp. are tightly linked to the seasonal sea-ice algae and phytoplankton bloom cycles (Box 2, 3; Falk-Petersen et al., 2009; Daase et al., 2013; Feng et al., 2016; Feng et al., 2018). Secondary production of *Calanus* spp. by far exceeded that of small copepods in summer (maximum of 250.7 mg C m^{-2} d^{-1} compared to 9.7 mg C m^{-2} d^{-1}, respectively; **Paper I, II, III**). Under non-limiting food conditions, the production of broadcast-spawning copepods, e.g. *Calanus* spp., can be considerably higher than that of egg-carrying copepods, e.g. *Oithona similis* (Kiørboe and Sabatini, 1995). Generally, the developmental rates (time from egg to adult) of broadcast-spawning and egg-carrying copepods are the same, but broadcast spawners exhibit higher growth rates (increase in body weight over time), higher weight-specific fecundities (reproductive output relative to female body weight) and higher egg-production rates (number of eggs produced per day) than egg-carrying copepods (Kiørboe and Sabatini, 1995), which explains the higher production of *Calanus* spp. in summer compared to that of small copepods (**Paper I, II, III**). Secondary production of large copepods in the northern Barents Sea in autumn and winter was much lower, with an average of 19.6 mg C m^{-2} d^{-1} (5.2–82.5 mg C m^{-2} d^{-1}, October-March, **Paper III**). However, these winter values are still comparatively high, considering that *Calanus* spp. usually hibernate in deeper water layers in winter. There are observations of active *Calanus* in the surface layer in winter in some Arctic regions, indicating a plasticity in their diapausing behaviour (Berge et al., 2015a; Berge et al., 2020; Hobbs et al., 2020; Espinasse et al., 2022). Miller et al. (2000) suggest that individuals that were not able to build up sufficient lipid storage for diapause will remain in the surface layer. It has also been suggested that *Calanus* spp. can exit diapause before the onset of the spring bloom in case their lipid reserves get depleted (Baumgartner and Tarrant, 2017). These behaviours might explain why relatively high secondary production of *Calanus* spp. can be observed in the northern Barents Sea in winter.

Secondary production of small copepods (including *O. similis* and other small copepods, such as *Microsetella norvergica*, *Pseudocalanus* spp., *Triconia borealis*, *Oncaea* spp.) was mainly associated with the regenerated primary production in summer and autumn (**Paper III**). Interestingly, it was also high in early winter when primary production was low. Highest secondary production of small copepods in the northern Barents Sea was observed in August and December, with 9.7 mg C m^{-2} d^{-1} and 10.1 mg C m^{-2} d^{-1}, respectively (calculated using the Hirst and Lampitt, 1998 growth rate model), which was slightly lower than the maximum production of small copepods reported from Disko Bay, western Greenland in September, with 15.5 mg C m^{-2} d^{-1} (Madsen et al., 2008, integrating for their sampling depth of 0–50 m, based on the Huntley and Lopez, 1992 model). The contribution of *O. similis* to secondary production of small copepods was high in summer due to its high reproductive output, which was a result of greater numbers of ovigerous females, larger clutch sizes, and faster, more successful egg hatching compared to the rest of the year (Figure 10, **Paper III**). High food availability (Zamora-Terol et al., 2013) and water temperatures (Sabatini and Kiørboe, 1994; Drif et al., 2010; Barth-Jensen et al., 2020) in the Barents Sea in summer can explain the high reproductive output of *O. similis*. Due to its small size, *O. similis* has less lipid storage capacity than large copepods (Norrbin, 1991) and the quality of its lipids is less energetically rich (Kattner et al., 2003; Lischka and Hagen, 2007), meaning that it relies on continuous feeding to fuel reproduction, i.e. income breeding (Barth-Jensen et al., 2020). Previous studies have shown that the weight-specific egg production rate of *O. similis* is correlated with microzooplankton occurrence (Nielsen and Sabatini, 1996; Castellani et al., 2005; Castellani et al., 2007;

Zamora-Terol et al., 2013), as microzooplankton is a crucial food source that fuels the reproductive success of *O. similis*. The microbial food web is the most developed in summer in the Barents Sea (Ciambelli, 2023; Kohlbach et al., 2023), serving as an abundant food source to *O. similis*. The relative contribution of small copepods to total copepod secondary production in summer was however minimal (maximum of 9.2 % at station P2, **Paper III**). Once the majority of *Calanus* spp. had left the surface ocean in autumn to hibernate at depth, the contribution of small copepods to total copepod secondary production increased to as much as 47% (station P2, October) and remained high in winter (**Paper III**). Secondary production of small copepods in winter was characterized by a high contribution of *O. similis* copepodids and other small copepods (**Paper III**). The weight-specific egg production rates of *O. similis* were one to two orders of magnitude lower in winter and spring than in summer, due to lower numbers of ovigerous females, smaller clutches and lower egg hatching success compared to the rest of the year (Figure 10, **Paper III**). The low reproductive rates in winter where a result of a combination of low water temperatures (Ward and Hirst, 2007), low food availability and advanced age of females (Sabatini and Kiørboe, 1994). High numbers of cyclopoid nauplii observed in winter were linked to the reproduction of copepods of the family Oncaeidae. The high reproductive output of Oncaeidae is likely linked to their feeding strategy, as they are aggregate colonizing copepods and mainly feed on aggregated particles (Koski et al., 2020) and copepod faecal pellets (Møller et al., 2011). These observations confirm the assumption that the winter months are an important period for the reproduction of some small copepod species (Berge et al., 2015a; Zamora-Terol et al., 2013; Barth-Jensen et al., 2022) and for the development of juvenile stages in the Arctic.

Interannual variability of copepod secondary production

Conditions in the Barents Sea differed considerably in terms of sea-ice cover and water masses in the summers of 2018 and 2019. In August 2018, the northern Barents Sea was completely ice free and the Atlantic region was dominated by a strong Atlantic Water signal, while in August 2019, parts of the northern Barents Sea were still ice covered and water temperatures in the entire study region were overall lower. This led to differences in the microbial community structure between these two years (Kohlbach et al., 2023; Amargant-Arumi et al., 2024), although not in the quantity of primary production (Amargant-Arumi et al., 2024). Despite the large interannual variations of environmental factors, there were no significant differences in the quantity of copepod secondary production between the two years (**Paper II**). There were however significant interannual differences of the *Calanus* spp. community composition between the two years, with the smaller *C. finmarchicus* showing a higher contribution to copepod secondary production in the summer with little sea-ice cover and in habitats characterized by warmer water temperatures and a pronounced Atlantic Water signal. Under the current climate conditions, it seems that the contribution of *C. finmarchicus* to copepod secondary production in the northern Barents Sea depends on seasonally advected biomass, rather than on the year-round production of a locally established population. The larger *C. glacialis*, on the other hand, was more important in the summer with extensive sea-ice cover and in habitats with colder water temperatures, sea-ice cover and with the presence and higher contribution of diatoms to pelagic primary production (**Paper II**). The interannual variation in copepod secondary production can likely be explained by a mismatch scenario between *C. glacialis* reproduction and the phytoplankton development (Søreide et al., 2010) in the year with reduced sea-ice cover (**Paper II**). The timing of reproduction of *Calanus* spp. is crucial, as premature spawning relative to the phytoplankton development can lead to starvation of developing nauplii, while delayed spawning can prevent copepodids from accumulating enough energy storage for overwintering (Varpe et al., 2007). In the year with reduced sea-ice cover, the new generation of *C. glacialis* likely missed the early, high-quality food phase (Søreide et al., 2010; Leu et al., 2011) of the phytoplankton bloom, thus reducing its reproductive success (Søreide et al., 2010). The contribution of small copepods to total copepod secondary production was higher in the year with reduced sea-ice cover (**Paper II**). Similarly, the relative abundance of small copepods has increased in a period with higher inflow of warm, Atlantic Water into Kongsfjorden, Svalbard (Hop et al., 2006) and during warm periods in the Bering Sea (Coyle and Pinchuk, 2002; Hunt Jr et al., 2011; Stabeno et al., 2012; Eisner et al., 2014; Kimmel et al., 2018; Kimmel et al., 2023).

Annual budget of copepod secondary production

While the annual copepod secondary production of 6.6 g C m^{-2} y^{-1} in the Atlantic region (station P1) and of 12.4–13.2 g C m^{-2} y^{-1} on the continental shelf break and in the Arctic Ocean basin (stations P6, P7) was comparable to literature values, the annual copepod secondary production in the northern Barents Sea (stations P2-P5) was much higher than previously reported. This observation confirms the assumption that the northern Barents Sea is one of the most productive Arctic regions, even though the method used to estimate annual copepod secondary production likely resulted in an overestimation. The annual copepod secondary production in the northern Barents Sea was 16.2–43.4 g C m^{-2} y^{-1}, which is up to three times higher than reported from Disko Bay, western Greenland (14.4 g C m^{-2} y^{-1}; Madsen et al., 2008) and from the North Sea (5.6–14.3 g C m^{-2} y^{-1}; Nielsen and Sabatini, 1996) and up to 12 times higher than reported from Young Sound, northeast Greenland (2.6–3.6 g C m^{-2} y^{-1}; Rysgaard et al., 1999). The gross primary production in the Barents Sea can vary spatially and interannually. In the Atlantic region, the annual gross primary production is 106–134 g C m^{-2} y^{-1} and in the northern Barents Sea it is 54–67 g C m^{-2} $year^{-1}$ (simulated 1995–2007; Reigstad et al., 2011). An increase of the annual gross primary production of up to 30 % has been observed in years with reduced sea-ice cover (Sakshaug, 2004). When comparing the annual copepod secondary production to annual gross primary production in the northern Barents Sea, it becomes apparent that copepod secondary production was likely overestimated here, because it amounted to 30–65 % of the annual gross primary production. An energy transfer of 10 % from one trophic level to the next is considered an efficient trophic transfer in the food web (Lindeman, 1942), underscoring the assumption that copepod secondary production of this magnitude is unrealistic. This overestimation can be attributed to an overestimation of the production of *Calanus* spp., as the annual secondary production of small copepods amounted to only 1.0-1.7 g C m^{-2} y^{-1}, which was comparable to literature values. In Disko Bay, the production of small copepods of 1.7 g C m^{-2} y^{-1} accounted for ~12 % of the total copepod secondary production (Madsen et al., 2008). In the northern Barents Sea, the annual secondary production of small copepods varied spatially and was 10.5 % of the annual copepod secondary production at the southernmost station P2, while it was only 3 % at the northernmost station P5. Again, the Atlantic region showed a very different trend, where the production of small copepods amounted to 2.9 g C m^{-2} y^{-1} and formed 44 % of the annual copepod secondary production.

3.3 Are small copepods important in the Barents Sea ecosystem?

Small copepods can potentially play important roles in food web processes in the Barents Sea due to their high abundance (Gallienne and Robins, 2001; Turner, 2004), year-round occurrence and reproduction in the upper ocean (Madsen et al., 2008; Dvoretsky and Dvoretsky, 2009) and omnivorous feeding strategy (Turner, 2004).

In summer, small copepods seem to have a rather minor role for the energy transfer (here defined as the relative contribution of copepod secondary production in relation to primary production or microzooplankton production), in the ‘typical Arctic ecosystem’ found in the northern Barents Sea under the current climate conditions. Here, energy is effectively channelled through the food web by the classic food chain, which links diatoms, *Calanus* spp. and higher trophic levels (Scott et al., 2000; Hagen and Auel, 2001; Lee et al., 2006). The energy transfer of small copepods in the northern Barents Sea was only 0.3–1.4 % of primary production in summer, while that of large copepods was 7.2–96.1 % (**Paper II**). Similarly, small copepods in Disko Bay, western Greenland only played a minor role for the energy transfer in summer (Madsen et al., 2008).

The seasonal shift in the composition of copepod secondary production however underscores the crucial role of small copepods in Arctic marine ecosystems in winter. This was the time when they played an important role for the energy transfer to higher trophic levels, exerted top-down control on microzooplankton communities, and likely altered vertical carbon flux and served as prey for higher trophic level organisms. Primary production in the entire study area was very low in winter, and the secondary production of small copepods amounted to >100 % of primary production at some stations (data on seasonal primary production being prepared for publication by

Amargant-Arumí et al.). This indicates that additional food sources other than autotrophic phytoplankton were available in this period. Microzooplankton biomass amounted to 0.3 g C m^{-2} on the Barents Sea shelf in winter (Ciambelli, 2023). The production of microzooplankton can be roughly estimated using a published production to biomass (P/B) ratio of 0.23 (Lavrentyev et al., 2019). This resulted in microzooplankton production of 69 mg C m^{-2} d^{-1} in winter. Secondary production of small copepods amounted to 14.6 % of microzooplankton production, which highlights their important role in maintaining trophic dynamics when larger species are less active. Small copepods increase the steps between primary producers and higher trophic levels, resulting in a less direct and less efficient energy transfer through the food web (Turner, 2004; Roura et al., 2018). Consequently, in autumn and winter, trophic dynamics on the Barents Sea shelf change. It was shown that the trophic position of *O. similis*, the main contributor to the secondary production of small copepods, decreases from autumn to spring in Kongsfjorden, Svalbard (Choi et al., 2020). This shift occurs because *O. similis* feeds on consumers (protozooplankton) in autumn and on primary producers (diatoms) in spring. The potential ingestion rates of small copepods can be calculated by assuming a gross growth efficiency (production/ingestion) of 30 % (Straile, 1997). In winter, the potential ingestion rates of small copepods were 33.67 mg C m^{-2} d^{-1}, indicating that they exerted high predation pressure on the microzooplankton community, consuming as much as 49 % of its production. Even though cyclopoid copepods, such as *Oithona* spp., are often found in much higher abundance than calanoid copepods, their contribution to the diet of fish is considerably less important (Kane, 1984; Napp et al., 2000; Swalethorp et al., 2014). However, during the winter months when other food sources are scarce, small copepods can be an important part of the diet of polar cod (*Boreogadus saida*) larvae (Geoffroy and Priou, 2020). Some small copepods are aggregate colonizing and feed on particles (Koski et al., 2020) and faecal pellets (Møller et al., 2011). Vertical carbon flux in the Barents Sea in winter was of low quantity and quality (Bodur, 2024). This might indicate that small copepods in winter fed extensively on particles, resulting in very little carbon being exported.

3.4 Copepod secondary production in a future Barents Sea

The future pelagic ecosystem in the northern Barents Sea will likely resemble that of shelf ecosystems in the north-east Atlantic (Chust et al., 2014; Fossheim et al., 2015). It will be characterized by smaller individuals, more boreal species (Renaud et al., 2018; Kaiser et al., 2022) and by a higher contribution of smaller-sized *Calanus* spp. and small copepods to copepod secondary production (**Paper II**). These changes result from physiological responses of copepods to environmental change (water temperature and food availability in relation to sea ice decline) and from large scale processes, such as species range shifts and biomass advection.

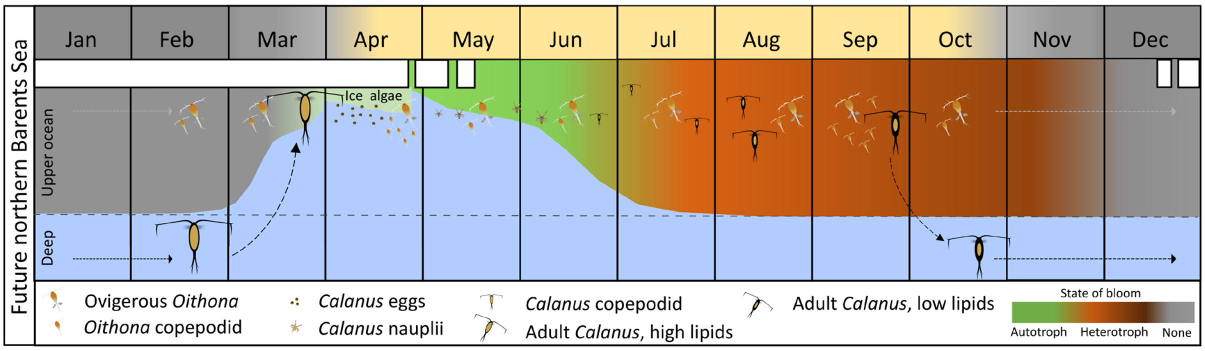

Figure 11: Future copepod secondary production in the northern Barents Sea will be characterized by a higher contribution of smaller *Calanus* spp. and small copepods and resemble that of shelf ecosystems in the north-east Atlantic. Secondary production of *Calanus finmarchicus* will likely increase due to warmer water temperatures, which might enable the species to establish a successfully reproducing population in the northern Barents Sea and due to higher biomass advection with Atlantic Water, thus locally contributing to secondary production in the Barents Sea. Secondary production of *C. glacialis*, on the other hand, will likely decrease due to the mismatch of its reproduction and the phytoplankton bloom dynamics and a northwards distribution shift of the species. Secondary production of *Oithona similis* is likely to increase due to high food availability in form of microzooplankton and warmer water temperatures, increasing its growth, fecundity and developmental rates.

Physiological responses of copepods to environmental change

Many factors can influence the developmental, growth and fecundity rates of copepods, such as water temperature, food availability and body weight. Generally, developmental and growth rates of copepods increase with temperature (Hirst and Bunker, 2003). However, developmental rates increase more rapidly, and metabolic costs are higher (Roman and Pierson, 2022), meaning that at higher temperatures, copepods reach adulthood at a smaller size, as they have less time and energy to grow larger (Kingsolver and Huey, 2008). This results in a reduction of the body size of copepods due to ocean warming (Gillooly, 2000; Daufresne et al., 2009; Evans et al., 2020).

Growth and fecundity rates of broadcast-spawning copepods, e.g. *Calanus* spp., are negatively correlated with body weight, meaning that smaller individuals exhibit higher growth and fecundity rates (Hirst and Lampitt, 1998). Thus, populations of smaller *Calanus* spp. in a future Barents Sea under non-limiting food conditions can potentially show higher turnover rates. However, the metabolic rates of the Arctic and boreal *Calanus* species react differently to warming. The egg production rate of *C. glacialis* is high between 0–2.5 °C but decreases after a threshold of 5–6 °C (Kjellerup et al., 2012; Pasternak et al., 2013; Weydmann et al., 2015), and a mismatch between the species' energetic gains and losses occurs with increasing temperatures (Alcaraz et al., 2014; Grote, 2017). The egg production rate of *C. hyperboreus* does not depend on temperature itself, but rather on the availability of lipids of the females (Henriksen et al., 2012). With increasing temperatures in the deep ocean, which has already been observed in the Greenland Sea and Eurasian Basin (Appen et al., 2015), the respiration rates of overwintering *C. hyperboreus* females will likely increase, resulting in more lipids being allocated to their basic metabolism than into reproduction. The reproductive potential and the duration of the spawning period of *C. hyperboreus* will therefore likely decrease (Schultz et al., 2020). The egg production rate of *C. finmarchicus* on the other hand, more than triples between 2.5–5 °C (Kjellerup et al., 2012) and linearly increases up to 15 °C (Campbell et al., 2001; Pasternak et al., 2013). Therefore, with increasing water temperatures, the reproductive output of the Arctic *Calanus* species will decrease, while that of the boreal *Calanus* species will increase. Furthermore, growth rates of broadcast-spawning copepods, e.g. *Calanus* spp., are mainly governed by phytoplankton availability (i.e. chlorophyll *a* concentration; Hirst and Bunker, 2003). In the Barents Sea, predictions of primary production dynamics are uncertain and differ for the southern and northern regions (Wassmann and Reigstad, 2011). Increased open water areas with higher light transmission due to sea-ice melt in the northern Barents Sea are predicted to lead to a prolonged phytoplankton growing season if nutrients are sufficient (Wassmann and Reigstad, 2011). Furthermore, under-ice blooms are predicted to occur more often in the future (Arrigo et al., 2012). Therefore, primary production in the northern Barents Sea will likely increase. In the Atlantic region, thermal stratification is predicted to increase, leading to a potential decrease in primary production due to lower nutrient availability (Hordoir et al., 2022). However, wind-driven vertical mixing can resupply nutrients to the surface ocean and promote fall blooms (Ardyna et al., 2014). Changes in the primary production regime will have impacts on the secondary production of *Calanus* spp. Not only food quantity but also the timing of *Calanus* spp. reproduction in relation to the phytoplankton bloom phenology is essential (**Paper II**). More frequent mismatch scenarios will likely decrease the reproductive potential of the Arctic *Calanus* species in the future (Figure 11). Because of the seasonal bloom phenology and the low water temperatures, *C. finmarchicus* is assumed to not be able to successfully reproduce in the Arctic at present (Hirche and Kosobokova, 2007; Ji et al., 2012; Melle et al., 2014). With increasing water temperatures and a possible extension of the productive period of primary producers, conditions for *C. finmarchicus* in a future Arctic will likely become more favourable (Freer et al., 2022) and there are indications for a successfully reproducing population in Fram Strait (Tarling et al., 2022).

The growth and fecundity rates of sac-spawning copepods, e.g. *Oithona similis*, are mainly governed by water temperature and microzooplankton availability (Nielsen and Sabatini, 1996; Castellani et al., 2005; Castellani et al., 2007; Zamora-Terol et al., 2013), while they are independent of chlorophyll *a* concentration (Hirst and Bunker, 2003) and body weight (Hirst and Lampitt, 1998). At present, the secondary production of small copepods and their importance for food web processes is the highest in the Atlantic region. With continuing Atlantification of the northern Barents Sea (Årthun et al., 2012; Wassmann et al., 2019; Gerland et al., 2023; Wold et al., 2023), their role in the future will likely increase, as a result of increasing water temperatures and higher food availability. Microzooplankton production in a future northern Barents Sea is expected to increase, as the production of smaller, heterotrophic cells was positively correlated with water temperature (Franzè and Lavrentyev, 2017).

Large-scale changes of pelagic ecosystems due to anthropogenic climate change

Ocean warming leads to large-scale shifts in the distribution range of zooplankton and fish species. Both Arctic and boreal species are shifting northwards, as the water temperatures in their current habitat exceed their species-specific temperature tolerance levels (Villarino et al., 2015). A northward shift of the distribution range of *C. finmarchicus* (Carstensen et al., 2012; Chust et al., 2014; Hop et al., 2019a), *C. glacialis* (Feng et al., 2016; Feng et al., 2018; Ershova et al., 2021) and *C. hyperboreus* (Ershova et al., 2021) has already been observed in Arctic regions. In the Barents Sea, the biomass of polar cod (*Boreogadus saida*) has declined since 2006 (Hop and Gjøsæter, 2013), while that of boreal fish species, such as capelin (*Mallotus villosus*), Atlantic cod (*Gadus morhua*) and Atlantic mackerel (*Scomber scombrus*) has increased (Fossheim et al., 2015; Kortsch et al., 2015). These geographic range shifts will lead to changes at the community level, promoting smaller species. Generally, larger species are found in colder climates at higher latitudes (Bergmann, 1848), while smaller species are found in lower latitudes (Evans et al., 2020). The increasing predation pressure on large *Calanus* due to the higher abundance of boreal fish and enhanced exposure to visual predation pressure due to sea-ice melt (Varpe et al., 2015) further selects for smaller copepods. The recent decline in winter sea-ice in the northern Barents Sea has been linked to a strengthening and warming of the Atlantic Water inflow into this region (Årthun et al., 2012). At present, up to four times the locally produced biomass of boreal zooplankton is advected through the Barents Sea Opening (Gerland et al., 2023). With increasing Atlantic Water inflow, the seasonal contribution of boreal mesozooplankton to secondary production in the Barents Sea is likely to increase due to higher biomass advection.

Alterations of the copepod community composition will lead to changes in the lipid availability on an individual and population level and therefore impact the food quality and transfer efficiency to higher trophic levels (Figure 11, Renaud et al., 2018). In ecosystems where small copepods contributed a high proportion to total copepod secondary production in summer (up to 62 % in the Atlantic region), the energy transfer was rather low, amounting to only 1.0–18.9 % of primary production. On the other hand, in ecosystems where large copepods formed the main component of copepod secondary production (86.9–97.3 %), the total energy transfer was 13.7 to >100 % of primary production (this thesis, data on seasonal primary production being prepared for publication by Amargant-Arumí et al.). Early larval stages of many fish species have a specific prey preference for calanoid nauplii, due to their high lipid content (Kane, 1984; Napp et al., 2000; Swalethorp et al., 2014; Bouchard and Fortier, 2020). In some Arctic regions, low abundance of preferred copepod prey has been linked to lower recruitment of walleye pollock (*Gadus chalcogrammus*) (Kimmel et al., 2018) and Atlantic mackerel (*Scomber scombrus*) (Lafontaine, 1999; Paradis et al., 2012). Therefore, the recruitment of ecologically and economically important fish species could be impacted in a future Barents Sea. The shift towards smaller *Calanus* might negatively influence size-selective predators, such as the little auk (*Alle alle*), that specifically targets *C. glacialis* (Kwasniewski et al., 2010; Vogedes et al., 2014; Balazy et al., 2019; Balazy et al., 2023). The prevalence of the microbial food web often promotes higher abundance of gelatinous zooplankton (Richardson, 2008), which will likely have a larger contribution to secondary production in a future Barents Sea.

3.5 Comparison of methods to determine secondary production and methodological recommendations for future studies

There are many factors that make the determination of mesozooplankton secondary production in the Arctic a challenging task. It already starts with the question: what is secondary production? Some authors define it as the generation of heterotrophic biomass solely performed by herbivores, aka the first consumers of primary production in the food web. Others (including the definition employed in this PhD thesis) define it more widely as the generation of heterotrophic biomass by organisms that are consumers of primary production, bacterial production, or of other heterotrophic organisms in the food web (Downing, 1984; Stites, 1999). Therefore, in contrast to primary production, secondary production is not confined to one trophic level but can include organisms from different trophic positions, which may also change trophic position in a seasonal context. Studies have investigated different compartments of the plankton community, from individual species to plankton groups and entire trophic levels (Lindeman, 1942; Clarke et al., 1946; Odum, 1968). In Arctic marine ecosystems, the focus lays on copepods, as they are often most important in terms of abundance and biomass and their growth rates can be estimated relatively easily (Runge and Roff, 2000). The growth rates of other common and abundant zooplankton groups in the Arctic, such as gelatinous zooplankton, Appendicularia and Chaetognatha, are more difficult to determine because little is known about their life cycle, and some groups can be difficult to sample (Runge and Roff, 2000). Almost all of the studies investigating copepod secondary production have focused on the epipelagic layer and no information is available on the production of copepods and other zooplankton in deeper waters. The population dynamics, life-history strategies, growth rates and feeding strategies of deep-sea organisms are understudied but this information is essential in order to adequately estimate their production. By excluding these zooplankton groups and depth layers, secondary production of the ecosystem is underestimated. Therefore, it is important to shift the focus on developing methods to study their population dynamics and production in the whole water column. Furthermore, most studies are descriptive in nature, rather than testing specific hypotheses to understand the driving factors of secondary production in Arctic marine ecosystems and potential implications of anthropogenic climate change (**Paper II**).

Estimates of secondary production are influenced by the approaches that are used to determine the biomass and growth rates of zooplankton, as well as by the sampling design and methodology used to study zooplankton dynamics. An establishment of a routine technique to estimate secondary production has been difficult so far, due to the application of many methods (Figure 5, Yebra et al., 2017). Additionally, the utilization of different variables to quantify secondary production (e.g. carbon, wet weight, dry weight, energy content) and units (e.g. mg C m^{-3} d^{-1}, mg C m^{-2} d^{-1}) make a comparison between studies difficult. Furthermore, the integration over different water layers (e.g. upper 50 m, upper 100 m, surface to bottom), or the total absence of an indicated sampling depth, exacerbate these problems. Development of a standardised sampling program, with unified sampling depths and units would help to compare results more easily between studies. In the following sections, some specific challenges of determining zooplankton biomass and growth rates are discussed, followed by recommendations for future studies in Arctic marine ecosystems.

Biomass estimates

There are several methods to determine zooplankton biomass. Direct measures include displacement volume, wet weight, dry weight, ash-free dry weight, elemental weight such as carbon weight, or weight of certain macromolecules, e.g. proteins, chitin, or lipids. Biomass can also be estimated indirectly from zooplankton abundance or size classes, by using biomass conversion factors (Yebra et al., 2017). Carbon content is often used in secondary production studies, as it makes a comparison between different energetic processes in the ecosystem easier. However, there are so far relatively little direct measurements of carbon content of species or specific life stages. Length-carbon weight regressions exist for many of the most common species (e.g. Ashjian et al., 2003; Sabatini and Kiørboe, 1994) but these do not consider possible seasonal changes in copepod body mass, which can be unrelated to changes in length. An example of this phenomenon can be found in **Paper III**, where the measured carbon content of large *Oithona similis* females in winter was lower than their estimated carbon content. Sampling biases, such as the unconscious selection of larger individuals can lead to biases of direct carbon measurements. Often, biomass data from more common species are used to approximate the biomass of less common species, or conversion factors are employed to convert other biomass parameters into carbon content. Moreover, there is a bias towards summer data, as these are the months where the Arctic is most accessible.

When studying trends in zooplankton biomass with traditional net sampling, one of the main challenges is to achieve the appropriate spatial resolution, as patchiness can lead to high sampling variance. In addition to patchiness, net avoidance and extrusion of zooplankton through coarse meshes can lead to an underestimation of total zooplankton biomass (Runge and Roff, 2000). In this PhD study, the use of a sampling method combining traditional single-point net sampling with different mesh sizes and modern spatial mapping, using a towed optical plankton imaging device, increased the resolution of biomass trends across the study region. This sampling design can be recommended for future studies. The imprecise approximations of biomass and sampling biases can significantly influence the determination of secondary production. In summer, sampling biases are likely to affect biomass estimates more than the individual carbon content of organisms, because carbon content is generally better known in this season. In winter, however, less information exists about the carbon content of individuals, which adds an additional challenge to accurate biomass estimation. Therefore, an effort should be made to collect carbon measurements of key species in a seasonal context in the Arctic.

In the Barents Sea and likely in Arctic marine ecosystems in general, secondary production of copepods seems to be determined primarily by the population biomass rather than by its growth rates. Biomass of large copepods in August 2018 in the three investigated depth layers (0–20, 20–50, 50–100 m at stations P1-P7) ranged from 0.02–2150.93 mg C m^{-2}, while growth rates ranged from 0.02–0.23 d^{-1}. Assuming a constant growth rate, biomass variations would result in a 124,000-fold variation in secondary production of large copepods, whereas variations in growth rate would only result in a 13-fold variation when assuming constant biomass. For small copepods, biomass ranged from 0.01–49.95 mg C m^{-2} and growth rates from 0.01–0.47 d^{-1}. Assuming a constant growth rate, biomass variations would result in an 8,800-fold variation in secondary production of small copepods, while variations in growth rate would result in a 32-fold variation when assuming constant biomass.

Copepod growth rates

Several methods have been developed to estimate copepod growth rates directly or indirectly and the choice of method depends on the research question and study system. The results from this PhD thesis (**Paper I**) show that a temperature-dependent growth rate model best describes the secondary production of predominantly herbivorous copepods, e.g. *Calanus* spp., in spring and summer, as it approximates the maximum possible growth under food saturation at certain temperatures. To estimate the secondary production of *Calanus* spp. in times of food limitation, a model should be used that includes chlorophyll *a* concentration as a proxy for food availability. The secondary production of small copepods can be calculated with a temperature-dependent model year-round, as their reproduction is not limited by phytoplankton availability. The quantity of secondary production depends heavily on the choice of the growth rate model (Liu and Hopcroft, 2006a, 2006b; Madsen et al., 2008; **Paper I**) and modelled secondary production was higher than field measurements, especially in winter (Liu and Hopcroft, 2006a, 2006b; Madsen et al., 2008; **Paper III**). In the following, I present key arguments for these observed differences.

Empirical growth rate models are often based on global synthesis of species- or group-specific field and laboratory estimates of growth and reproductive rates (e.g. Hirst and Lampitt, 1998; Hirst and Bunker, 2003). Models are an indirect method of determining secondary production, as growth is not measured directly but rather derived from environmental and biological variables. Therefore, secondary production can be estimated relatively easily without the need for additional experimental work, if details on the biology of the species are known. In Arctic marine ecosystems, modelled secondary production is often higher than *in situ* measured production (Liu and Hopcroft, 2006a, 2006b; Madsen et al., 2008; **Paper III**), which can likely be explained by an underrepresentation of growth and reproductive rates of copepods in high-latitude offshore regions and at low water temperatures in the design of the models. Furthermore, data on small copepods are limited, making the models less reliable in predicting their secondary production. However, amongst small copepods, the growth and reproductive rates of *O. similis* are the most represented. When comparing the measured and modelled growth rates of *O. similis* in a seasonal context, it became apparent that the modelled growth rates were considerably higher than the measured growth rates in the winter months (**Paper III**). Food limitation due to low microzooplankton availability (Zamora-Terol et al., 2013), a factor not included in any current model, can likely explain this discrepancy. Some models assume that copepod growth rates are governed by food concentrations, however they only include chlorophyll *a* as a proxy for food availability. As many small copepod species are omnivores, and their reproduction is uncoupled from the phytoplankton bloom, chlorophyll *a* concentration is a poor proxy for food limitation for these species (Ward and Hirst, 2007; **Paper III**). Therefore, other factors, such as particulate organic carbon or nitrogen availability or microzooplankton standing stock (Hirst and Bunker, 2003), could be included in the future development of growth rate models.

Many studies have opted for the egg incubation method due to its simple experimental design that allows the description of the growth of a species in its natural habitat by measuring its *in situ* reproductive rates. The experiments are species-specific and incubation time can be very long at low water temperatures, making this method quite time consuming (Avila et al., 2012). The premise underlying the egg incubation method is that the reproductive output of females approximates both the female and juvenile growth (Berggreen et al., 1988). However, many studies have shown that juvenile somatic growth can be higher than adult reproductive output and the egg production method therefore likely underestimates secondary production (McLaren and Leonard, 1995; Hopcroft and Roff, 1998; Hirst and McKinnon, 2001). Another premise is that secondary production only occurs during the egg-carrying period of a species. When determining secondary production of *O. similis* with the egg incubation method, almost no secondary production was observed in months where the percentage of ovigerous females was low (**Paper III**), even though these months are essential for the growth of copepodids (Lischka and Hagen, 2007; Dvoretsky and Dvoretsky, 2009; Balazy et al., 2021). Additional factors such as the number of experimental animals, the number and condition of eggs and the carbon content of females and eggs can influence the calculation of the weight-specific egg production rate and thus secondary production (**Paper III**). Given that the egg incubation method seems to underestimate and empirical growth rate models seem to overestimate copepod secondary production in Arctic marine ecosystems, the actual values likely fall within the range provided by these two methods.

Methodological recommendations for future studies

The results from this PhD thesis suggest that future studies investigating mesozooplankton secondary production in Arctic marine ecosystems should employ a combined sampling approach. Traditional single-point net sampling using different mesh sizes and modern spatial mapping methods using towed optical plankton imaging devices can increase the spatial and taxonomic resolution of secondary production measurements (**Paper I**). Hypothesis testing of central research questions, such as the effects of sea-ice reduction on mesozooplankton secondary production, can only be conducted with replicated *in situ* studies. This approach would also avoid the problem of pseudo replication (**Paper II**). Field surveys should be extended to periods that have been less studied, such as for example the transition from early to late winter to spring. Carbon weight measurements of key zooplankton species in winter are needed to adequately estimate mesozooplankton biomass year-round (**Paper III**). Additionally, the development of a copepod growth rate model that incorporates food limitation by microzooplankton standing stock and data on growth rates of small copepods at low water temperatures, is needed. This model could be designed to specifically approximate copepod secondary production in Arctic marine ecosystems, based on a comprehensive review of datasets of growth and reproductive rates from high-latitude areas, which would make the estimations of production more precise than using a global model. Additionally, modelled growth rates of key mesozooplankton species should be validated through field-based growth rate experiments at sub-zero temperatures. When choosing the egg incubation method, additional artificial cohort experiments should be performed, to adequately determine the growth rates of juveniles. And lastly, methods to determine the production of mesozooplankton groups other than copepods should be developed.

3.6 Research gaps and future perspectives

Consequences of anthropogenic climate change, such as ocean warming and acidification, sea-ice loss and increased river run-off, come hand in hand with other human-caused disturbances, such as overfishing and pollution. Therefore, Arctic zooplankton communities are facing multiple stressors at once (McKinney et al., 2015; Pörtner et al., 2019). The interaction of multiple stressors can result in synergistic, additive, or antagonistic effects on biological responses, when the effect is greater, equal, or smaller than the sum of the individual effects, respectively (Côté et al., 2016). So far, very few studies have investigated the effects of multiple stressors on the metabolic rates of zooplankton in high-latitude ecosystems (Hjorth and Nielsen, 2011; Holan et al., 2019) and this especially holds true for the consequences for early life stages (Espinel-Velasco et al., 2023). As multiple stressors can impact the growth and reproductive rates of mesozooplankton, they can lead to changes in secondary production. However, to what extent remains unknown. With short-term acclimation and long-term adaptation experiments, the response of secondary production of key mesozooplankton species to a wide temperature range and to scenarios of multiple stressors can be investigated. Field based and experimental measurements can then be used to inform ecosystem models. These models can help to upscale from spatially- and time-limited field studies to large-scale ecosystem trends.

As ship-based surveys only provide a coarse insight into the seasonal trends of mesozooplankton secondary production, it would be key to study seasonal changes in zooplankton biomass and environmental conditions more continuously, using moored instruments over an annual cycle. The collected data can then be used to study the timing and duration of peaks in secondary production, which is essential to appropriately estimate secondary production in an annual context. These endeavours could be combined with already existing long-term monitoring programs that use moored instruments, such as the Synoptic Arctic Survey, the Nansen and Amundsen Basins Observational System or the Distributed Biological Observatory.

Understanding the dynamics of mesozooplankton secondary production is not only important in light of anthropogenic climate change but also for its potential economic impact. With the increasing demand for sustainable food security, interest in the commercial harvesting of zooplankton is growing. In Norway, trials for commercial harvesting of *Calanus finmarchicus* have led to the establishment of a commercial fishery in the Norwegian economic zone and the Jan Mayen zone in the Norwegian Sea since 2019 (Nærings- og Fiskeridepartementet, 2019). However, many questions remain unanswered, such as the accurate assessment of *Calanus* stocks, the effects of *Calanus* harvesting on other trophic levels, and how to minimize bycatch.

4 Conclusions

Measurements of secondary production in Arctic marine ecosystems remain scarce, despite their importance when studying energy transfer within food webs. The primary goals of this PhD thesis were to enhance our understanding of the spatial and temporal patterns of mesozooplankton secondary production in the Barents Sea, with a special focus on the historically understudied small copepods (<2 mm in adult size), and to improve the methodologies used to study this process in Arctic marine ecosystems.

The results of this PhD thesis revealed that only the northern Barents Sea can still be considered a true 'Arctic ecosystem', where the classic food chain is most prevalent and secondary production is dominated by large *Calanus* spp. This region was highly productive and copepod secondary production exceeded that of other Arctic regions. The Atlantic region, on the other hand, exhibited very different dynamics. Here, a significant proportion of the mesozooplankton production came from organisms other than copepods and copepod secondary production was overall low, being dominated by small copepods.

Copepod secondary production exhibited clear seasonal patterns and peaked in early summer, due to the high production of *Calanus* spp. Secondary production of small copepods also peaked in summer but was an order of magnitude lower than that of *Calanus* spp. Therefore, the role of small copepods in the energy transfer in the northern Barents Sea in summer was minor. There was a seasonal shift in trophic dynamics in the Barents Sea, related to the higher relative contribution of small copepods to copepod secondary production in winter. In this previously considered unproductive season, small copepods were especially important for food web processes, showing a high contribution to the energy transfer to higher trophic levels and exerting considerable top-down control on the microzooplankton community. Interannual variations in environmental factors between two summers did not significantly alter the quantity of copepod secondary production but resulted in a shift in its composition, promoting smaller sized *Calanus* spp. and small copepods.

The spatial and temporal patterns of mesozooplankton secondary production were a result of a combination of different factors. Water temperature and food availability in relation to retreating sea ice directly influenced secondary production by impacting growth rates, while advection of mesozooplankton, predation pressure and seasonal migration patterns, influenced secondary production indirectly by impacting biomass.

The future pelagic ecosystem in the northern Barents Sea will likely resemble that of the Atlantic region, characterized by smaller individuals, more boreal species and a higher contribution of smaller-sized *Calanus* spp. and small copepods to copepod secondary production. These changes are a result of physiological responses to environmental change and of larger scale processes, such as species range shifts and biomass advection. Alterations of the mesozooplankton community can have cascading effects through the food web, by changing the availability and quality of food for higher trophic levels, which in turn will impact the recruitment of fish species and size-selective predators.

At present, there is no routine method to measure secondary production and direct and indirect methods result in a considerable spread of secondary production values. In Arctic marine ecosystems, copepod secondary production is mainly governed by biomass, as growth rates are overall low due to low water temperatures. Insufficient data on carbon weights of key species in a seasonal context leads to biases in secondary production estimation, making it essential to gather these data. Additionally, many of the commonly used global growth rate models are not ideal for the use in the Arctic, due to an underrepresentation of data from high-latitude regions in their design. Future development of a local growth rate model should include food limitation by microzooplankton availability and data on growth rates of small copepods at low water temperatures. To avoid sampling biases, future studies should employ a combined approach of traditional net sampling and spatial mapping using optical plankton imaging devices, focusing on previously understudied periods in the Arctic. In light of ongoing anthropogenic climate change, it is crucial to deepen our knowledge of the dynamics of secondary production in Arctic marine ecosystems and how the increasing importance of small copepods could influence ecosystem functioning in the future.

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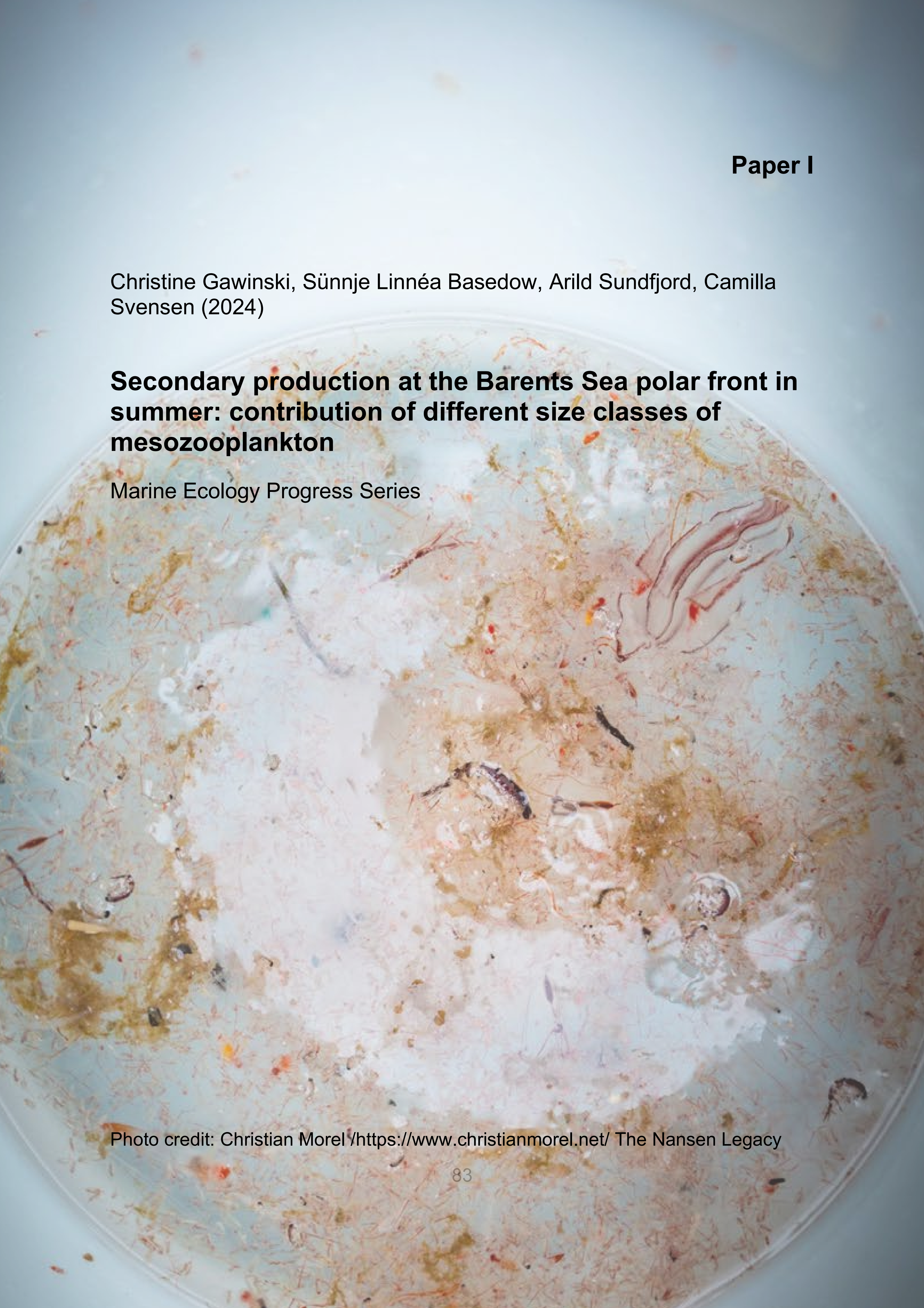

Paper I

Christine Gawinski, Sünnje Linnéa Basedow, Arild Sundfjord, Camilla Svensen (2024)

Secondary production at the Barents Sea polar front in summer: contribution of different size classes of mesozooplankton

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Secondary production at the Barents Sea polar front in summer: contribution of different size classes of mesozooplankton

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ABSTRACT: The Barents Sea polar front is characterized by high primary production following the retreat of the ice edge during spring. However, secondary production estimates of mesozooplankton across the front are scarce, despite being essential for understanding energy flow through the food web. We investigated mesozooplankton community composition and production across the Barents Sea polar front (75°–78° N) in June, covering both Atlantic and Arctic water masses with high spatial and taxonomic resolution. We highlight the contribution of small and large groups of mesozooplankton and estimate secondary production by comparing and evaluating 4 commonly used growth rate models. The zooplankton community composition and size distribution changed across the polar front. In the Atlantic region, Rotifera, Chaetognatha and Appendicularia were common, while copepods and their nauplii contributed most across the polar front and in Arctic water masses. Mesozooplankton secondary production took place mainly in the surface and was highest south of the front, declining towards Arctic waters. Considering production by copepods alone, highest values were found in the northern sector of the polar front and in the Arctic region. Young developmental stages (CI–CIV) of *Calanus* spp. and small-sized taxa contributed most to copepod production in Atlantic waters, while calanoid copepod nauplii contributed considerably to copepod production in Arctic waters. We emphasize that the production estimates were strongly influenced by the growth rate model and conclude that copepod secondary production in a summer situation with non-limiting food concentration was best described using a model that solely considers water temperature and copepod body weight.

KEY WORDS: Mesozooplankton · Copepod community composition · Density-compensated thermohaline front · Seasonal ice zone · *Calanus* spp. · *Oithona similis* · Copepod growth rate models · Laser optical plankton counter

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1. INTRODUCTION

Oceanic fronts occur at the boundaries between water masses of different physio-chemical properties such as temperature, salinity, density, nutrients, turbidity and velocity (Bakun 1997). Nutrient-rich water from below the euphotic zone can be resupplied to the surface ocean by upwelling and cross-frontal mixing (Allen et al. 2005). This is the main reason why fronts often coincide with areas of increased chlorophyll concentration and pelagic primary production (Le Fevre 1987). High numbers of zooplankton and fish larvae have been observed at fronts, due to the accumulation of individuals by convergent flows found in these regions (Franks 1992, Munk et al. 2009). In some cases, reproduction of zooplankton can be favoured, which makes oceanic fronts areas of increased secondary production (Liu et al. 2003, Derisio et al. 2014).

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Depending on the longevity of the front, larger predators are attracted, and energy is effectively channelled through the food web (Acha et al. 2004). Fronts therefore impact trophic transfer efficiency, carbon cycling in the upper layers and export rates to the benthos (Wolanski & Hamner 1988, Hunter & Price 1992, Bakun 1997). They can also act as physical boundaries to the distribution and dispersal of species (Thornhill et al. 2008).

In the Barents Sea, the confluence of warmer, more saline water of Atlantic origin and colder, less saline water of Arctic origin forms the Barents Sea polar front (Sakshaug et al. 2009). The Barents Sea polar front is a density-compensated thermohaline front, meaning that there is no horizontal density gradient that would enhance mixing or upwelling of nutrients (Fer & Drinkwater 2014, Våge et al. 2014). Thus, the front does not lead to increased primary production (Reigstad et al. 2011, Erga et al. 2014) and is therefore a dynamically 'passive' front. However, the Barents Sea polar front is often found coupled with a meltwater front that is the result of sea-ice melt during spring and summer and an important feature promoting primary production. Pelagic blooms in the frontal region occur in 2 phases, one starting near the Barents Sea polar front and progressing northwards, following the retreating ice edge and the resulting stratification (Wassmann et al. 1999). The second phase starts in the southern Barents Sea and moves northwards, resulting in a comparatively slower and less intense bloom which is initiated by stratification caused by near-surface heating from solar radiation (Loeng 1991, Wassmann et al. 1999).

The Barents Sea polar front acts as a habitat boundary for different boreal and arctic species (Hassel 1986, Owrid et al. 2000, Fossheim et al. 2006). One such example is the copepod *Calanus finmarchicus*, a boreal species that is transported into the Barents Sea with the Atlantic current (Hirche & Kosobokova 2007). *C. finmarchicus* has a 1 yr life cycle that is tightly linked to the spring phytoplankton bloom (Conover 1988, Falk-Petersen et al. 2009). Because of the late onset of the phytoplankton bloom in areas north of the polar front and a consequent mismatch with the *C. finmarchicus* reproductive cycle (Tande 1991, Melle & Skjoldal 1998, Aarflot et al. 2018), the polar front acts as a barrier to the successful reproduction of *C. finmarchicus*.

In many historical data sets, an important size fraction (200–800 µm) of the mesozooplankton community, which includes nauplii, copepodites and adults of some smaller species, is significantly underrepresented due to the use of coarse mesh sizes (Gallienne & Robins 2001). There is growing evidence for the importance of small copepods in Arctic food webs, especially the genus *Oithona*. Newer studies, using appropriate sampling gear, report high abundance, biomass and production at the Barents Sea polar front and in Arctic areas in general (Gallienne & Robins 2001, Turner 2004, Svensen et al. 2011, Zamora-Terol et al. 2013, Basedow et al. 2014, Svensen et al. 2019).

The above-cited studies have increased our knowledge of the distribution of zooplankton at the Barents Sea polar front. Despite the importance of secondary production estimates for evaluating energy transfer in marine food webs, there is still a lack of those estimates across the polar front. To our knowledge, only 2 studies have investigated secondary production across the polar front, one using a laser optical plankton counter (LOPC) in the western Barents Sea (Basedow et al. 2014) and one using a 168 µm meshed Juday net in the eastern Barents Sea (Dvoretsky & Dvoretsky 2024a).

Secondary production is defined as the increase in zooplankton biomass over a period of time and equals the sum of the product of biomass and weight-specific growth rate of each individual stage within the zooplankton population (Runge & Roff 2000). Several methods are used to estimate growth rates, including experimental approaches that determine, for example, the weight-specific egg production rate or measure growth rate directly, as well as field-based cohort-analysis and modelling approaches (Runge & Roff 2000). Technological advances of laser-based instruments to study zooplankton sizes and abundance have led to the possibility of estimating production with a high spatial resolution (Zhou et al. 2010, Basedow et al. 2014). This estimation relies on the so-called biovolume spectrum theory that assumes that biomass or biovolume in marine systems is nearly evenly distributed over logarithmic size classes and that biomass transfer between size classes can be estimated by the slope of the biovolume spectrum (Silvert & Platt 1978, Zhou 2006).

In this study, we investigated mesozooplankton secondary production and community composition with high taxonomic and spatial resolution across the Barents Sea polar front by employing a combination of traditional net sampling using WP-2 nets and GoFlo bottles and optical plankton imaging using the LOPC. To estimate secondary production, we used biomass data from traditional net sampling and optical plankton imaging in combination with empirical growth rate equations from the literature. At present, there is no clear consensus as to the most suitable growth rate model for application in polar regions, and a careful evaluation of model assumptions and shortcomings is needed before choosing which method to use and interpreting the results. Therefore, our study includes a comprehensive comparison of 4 commonly used growth rate models, namely model A: Hirst & Bunker (2003), model B: Hirst & Lampitt (1998), model C: Huntley & Lopez (1992) and model D: Zhou et al. (2010). We provide a recommendation for the most suitable model to estimate secondary production in high-latitude ecosystems during the summer. Furthermore, we address the following research questions: (1) Is the Barents Sea polar front an area of high secondary production during the summer? (2) Do secondary production and associated mesozooplankton community composition change across the Barents Sea polar front, from warm Atlantic to cold Arctic waters? (3) What are the underlying mechanisms for the observed patterns in secondary production across the front?

2. MATERIALS AND METHODS

2.1. Study area

Sampling was conducted on board the ice-enforced RV 'Helmer Hanssen' between 22 and 27 June 2011 in the area of Hopen Deep and Great Bank in the Barents Sea (Fig. 1). Station (Stn) M1 (278 m bottom depth) was chosen as a representative location for well-stratified Arctic water masses, Stns M2 (235 m bottom depth) and M3 (282 m bottom depth) were located in the polar front region, and Stn M4 (371 m bottom depth) was located in deep-mixed Atlantic waters.

2.2. Environmental data

Hydrography (salinity, temperature and resulting density) profiles were measured at the 4 stations (M1–M4) using a rosette-mounted SBE911plus sys-

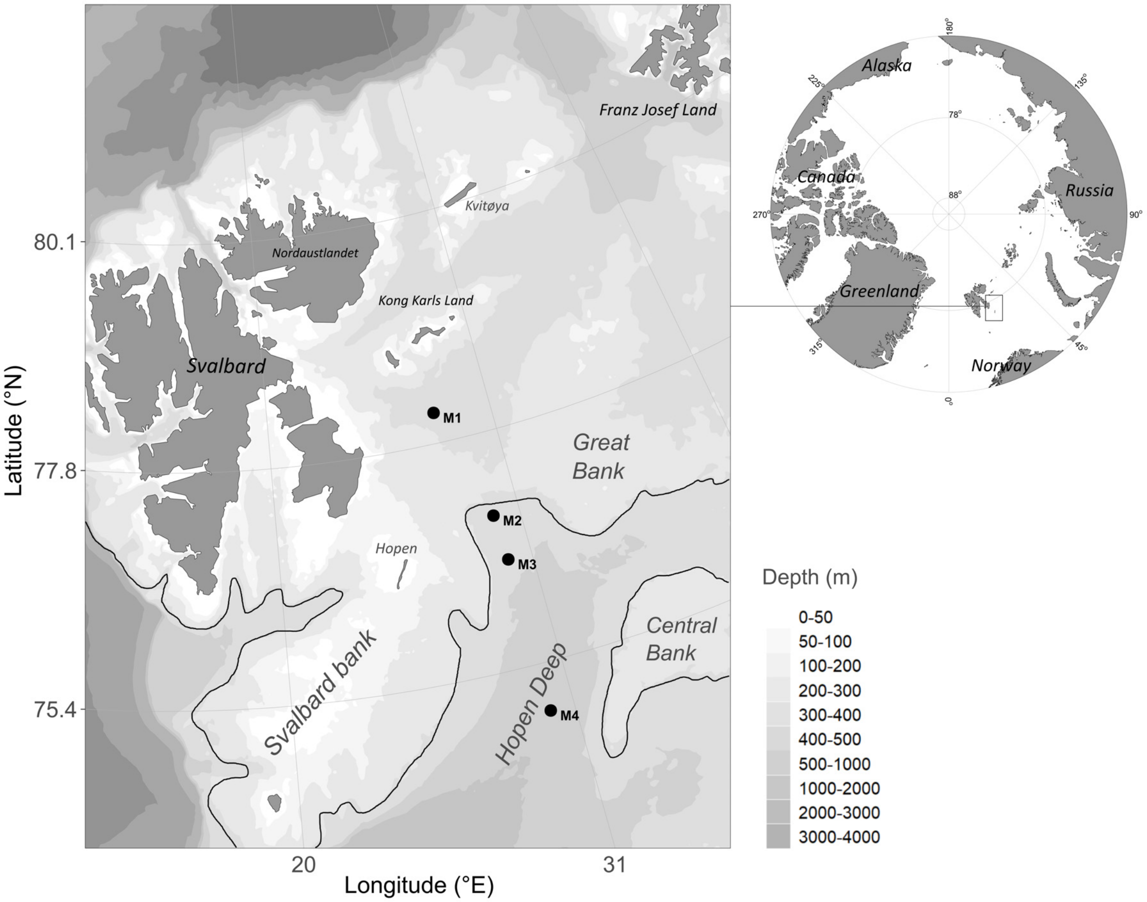

Fig. 1. Study area with the approximate location of the polar front based on the 200 m isobath indicated as a black line. Four stations (M1–M4) were sampled with a WP-2 net and GoFlo bottles, and a transect between these stations was sampled with the laser optical plankton counter (LOPC)

tem (Sea-Bird Electronics). Data were processed following standard procedures as recommended by the manufacturer and averaged to 0.5 m vertical bins before plotting. A moving vessel profiler (MVP; Brooke Ocean Technology), equipped with a CTD (Applied Microsystems Micro CTD), a fluorescence sensor (WET Labs FLRT chl *a* fluorometer) and the LOPC, was used to sample environmental data along the transect. The MVP made close-to-vertical profiles from surface to 10 m above bottom along a transect crossing the polar front. In ice-free waters south of the front, the ship was moving at 6–7 knots, while profiles were taken in MVP 'free-wheel' mode. Farther north, in waters with loose drift ice, the profiles were spaced farther apart and were taken in MVP 'continuous rpm' mode at low vessel speed (1–2 knots). For analyses of salinity, temperature and chlorophyll *a* (chl *a*), data from downward and upward profiles were used. Fluorescence data were converted into chl *a* by scaling the conversion equation supplied by the manufacturer to values obtained from pigment analyses of filtered water samples.

Water for chl *a* determination was collected with Niskin bottles mounted on a rosette at 11 fixed depths: 0, 5, 10, 20, 30, 40, 50, 60, 90, 120 and 200 m. In addition, a 12th depth was sampled at the fluorescence maximum. Triplicate sub-samples of 100–200 ml from each depth were filtered onto Whatman GF/F filters for total chl *a* and 10 µm polycarbonate filters for determination of chl *a* >10 µm. On board the ship, filters were extracted in absolute methanol in darkness for 24 h and then analysed on a Turner Designs 10-AU fluorometer (Holm-Hansen et al. 1965).

2.3. Mesozooplankton sampling

2.3.1. WP-2 net and GoFlo bottle sampling

Mesozooplankton were sampled with a WP-2 net (Hydro-Bios) with 180 µm mesh and a net opening with a diameter of 0.57 m and filtering cod-end. Filtration volume was estimated from the opening diameter and the sampling depth. Three vertical net hauls were taken during the day (around noon) and at night (around midnight) at all stations, at fixed depth intervals of 0–50, 50–100 and 100 m to bottom by using a closing mechanism. The content of the cod-end was concentrated over a 90 µm mesh on deck and preserved with buffered formaldehyde at 4% final concentration.

To increase the resolution in the surface and to quantitatively sample the small copepod species and young developmental stages, one GoFlo profile was sampled in the daytime at each station in the upper 50 m. Samples were taken from 1, 10, 20, 30, 40 and 50 m depth. The content of the water bottle (30 l) from each individual depth was concentrated over a 20 µm mesh and preserved with buffered formaldehyde at 4% final concentration.

Mesozooplankton were counted and determined to species and developmental stage under a Leica dissecting microscope at 40× magnification. *Calanus finmarchicus*, *C. glacialis* and young developmental stages of *C. hyperboreus* were distinguished to species by measuring prosome length of all counted individuals and applying size classes established by Kwasniewski et al. (2003), which are slightly modified in comparison to definitions by Unstad & Tande (1991).

By combining data of zooplankton abundance and taxonomy obtained both with the WP-2 net and the GoFlo bottles, the relative contribution of 'large' and 'small' mesozooplankton can be compared. We followed the definition of Roura et al. (2018), where a total body length of <2 mm defines small copepods. In our data set, 'small copepods' are represented by *Cyclopoida* sp. indet., *Harpacticoida* sp. indet., *Oithona atlantica, O. similis, Microsetella norvegica, Pseudocalanus* spp. and *Triconia borealis.* The group of 'large copepods' is composed of *Calanus finmarchicus, C. glacialis, C. hyperboreus* and *Metridia longa.* All other and less abundant zooplankton individuals were grouped into 'other zooplankton small' for a size <2 mm and 'other zooplankton large' for a size >2 mm. To get a quantitative representation of both large and small zooplankton across the polar front, data were combined from the WP-2 and GoFlo bottles. 'Other zooplankton small', copepod nauplii, all stages of 'small copepods', as well as all young stages (CI–CIII) of 'large copepods' were obtained from the GoFlo sampling. Data on older stages (CIV–adult) of 'large copepods' and 'other zooplankton large' were obtained from the WP-2 net sampling. To test whether there was a significant difference in copepod community composition between the day- and night-time sampling with the WP-2 net, canonical correspondence analysis was performed on fourth-root transformed abundance data from depth strata 0–50, 50–100 and 100 m to bottom sampled with the WP-2 net during day- or night-time along the transect. The interaction term (station × time of sampling) was included in the model to capture differences in copepod community composition along the transect depending on the time of the day. There was no significant difference between day- and night-time sampling with the WP-2 net (time of sampling: p = 0.94; station × time of sampling: p = 0.983). Therefore, all presented data are based on averaged data from the WP-2 day- and night-time sampling combined with GoFlo bottle sampling. Mesozooplankton abundance was converted into biomass, based on species- and stage-specific carbon weight relationships (Gawinski et al. 2024). The copepod abundance and biomass data are published on GBIF (Gawinski et al. 2023). Mesozooplankton distribution was analysed and visualized using R version 3.6.3.

2.3.2. Laser optical plankton counter (LOPC)

The LOPC is designed to count and measure particles in the water column based on laser light that passes a sampling channel and is received on a matrix of photo elements (Herman et al. 2004). The LOPC is currently no longer produced but is still used by research institutes around the world. While the LOPC is being towed through the water, zooplankton and other particles pass through the sampling channel, and their number, size and transparency are recorded. Particles can either occlude 1 or 2 diodes (called single-element particles), or 3 or more diodes (called multi-element particles, MEPs). The size of particles is measured by the peak negative change in voltage detected by each occluded diode and is defined as digital size (DS). The transparency of particles is described by the attenuation index (AI), which is based on the ratio between mean DS of all diodes that are completely occluded by a MEP, and the maximum DS a diode can have. The LOPC provides high-resolution abundance data of mesozooplankton in a size range of 0.25–4 mm. We analysed 3 size groups of particles: small (S, 0.25–0.6 mm equivalent spherical diameter ESD), medium (M, 0.6–1.5 mm ESD) and large (L, 1.5–4 mm ESD). For the medium and large group, we excluded transparent particles ($AI < 0.4$) from our abundance analyses to focus on zooplankton particles even though we may have missed a fraction of gelatinous plankton that way (Basedow et al. 2014). Mesozooplankton species were separated into the different size classes based on the definitions given by Basedow et al. (2018) (Table 1). LOPC biovolumes were converted into carbon using the regression provided by Forest et al. (2012). Data were collected along the transect and additionally at stations M1–M4, where 4–10 vertical profiles were taken in 'continuous rpm' mode at low vessel speed. The latter data were used to calculate biomass and production estimates of mesozooplankton at the stations. Only data from the downward profiles were used for mesozooplankton analyses.

LOPC particle counts were analysed and quality-controlled as described by Basedow et al. (2014, 2018). The quality of the data was good, with very few (<0.01%) incoherent multi-elements as defined by Schultes & Lopes (2009), meaning the information on the diodes occluded by MEPs was not arranged disorderly. The total number of larger particles was far below 10^6, indicating that the LOPC was not overloaded and counted the correct number of particles (Schultes & Lopes 2009). For particles <0.6–0.8 mm ESD, the LOPC does not allow differentiating zooplankton from other particles, which is possible for larger particles based on their transparency and other features. Therefore, it is often unclear if small particles are zooplankton or detritus (Basedow et al. 2018). Based on a data set from the Mediterranean Sea, Espinasse et al. (2018) developed indicators to designate the contribution of detritus to small particles, by analysing available features of particles in relation to the environment. We used these indicators to determine the contribution of non-zooplankton particles to LOPC counts during our study. For those analyses, all LOPC data, including more transparent particles with an $AI < 0.4$ are necessary and were used. In Atlantic waters south of the polar front, LOPC data were characterized by a low AI of 0.12 and low percentage (<2%) of larger MEPs, which is indicative of

Table 1. Size classification applied to data collected by the laser optical plankton counter (LOPC) at the Barents Sea polar front. Reproductive modes of the different copepod species are indicated as SS for sac spawners and BS for broadcast spawners. ESD: equivalent spherical diameter

Size class	ESD (mm)	Main zooplankton species
Small (S)	0.25–0.6	*Oithona* spp. (SS), *Microsetella norvegica* (SS), *Triconia* spp. (SS), copepod nauplii, Hydrozoa, meroplanktonic larvae, Appendicularia
Medium (M)	0.6–1.5	*Pseudocalanus* spp. (SS), *Calanus* spp. CI–CIV (BS), *Metridia longa* CI–CV (BS), Hydrozoa, Chaetognatha
Large (L)	1.5–4.0	*Calanus* spp. CV–CVI (BS), *Metridia longa* CVI (BS), Chaetognatha, juvenile and adult euphausiids

low detritus abundance. North of ca. 76.25° N, across the polar front and in Arctic waters, the data contained a high percentage (>2% or just below) of MEPs and the AI of particles was also low (0.12). In combination with the stratified waters that were observed in this region, this indicates that aggregates contributed to the particles counted by the LOPC in the region north of 76.25° N. As no distinction between particles and zooplankton could be made for size group S in this region, we did not use these data for the calculation of secondary production and excluded this area from our results section.

2.4. Secondary production estimates

Model predictions of copepod secondary production often deviate significantly from direct measurements of copepod growth rates in the field or laboratory (Liu & Hopcroft 2006a,b, Madsen et al. 2008). In addition, different growth rate models provide distinct estimates of secondary production, and each of them has its specific set of assumptions and approximations (Runge & Roff 2000; Table 2). Additionally, a validation of modelled growth rates through field-based growth rate experiments for selected key copepod species at sub-

Table 2. Comparison of 3 copepod growth rate models (A–C) and a zooplankton growth rate model (D), including an assessment of the production to biomass (P/B) ratios derived from the different models, with those documented in literature and recommendations for the use of each model. BS: broadcast-spawning; SS: sac-spawning; nd: no data; na: not applicable

	Growth rate model			
	(A) Hirst & Bunker (2003)	(B) Hirst & Lampitt (1998)	(C) Huntley & Lopez (1992)	(D) Zhou et al. (2010)
Included parameters	Temperature, copepod body weight, chl *a* concentration	Temperature, copepod body weight	Temperature	Temperature, copepod body weight, chl *a* concentration
Copepod groupings	All copepods Separate equations for SS adults & juveniles, BS adults & juveniles	All copepods Separate equations for SS adults & juveniles, BS adults & juveniles	All copepods	Mesozooplankton
Data set size	4831 measurements across 88 copepod species within 29 genera	952 measurements across 41 copepod species	181 measurements across 33 species	na[a]
Percentage of variance explained	35.7% for BS adults; 39% for BS juveniles; 11.3% for SS adults; 28.9% for SS juveniles	43.5% for BS adults, 49.0% for BS juveniles, 31.1% for SS adults, 39.9% for SS juveniles	91%	na[a]
Applicable temperature range	−2.3 to 30.6°C	−2.3 to 29.0°C	−1.7 to 30.7°C	na[a]
Applicable copepod body weight	Adults: 0.199–3260 µg C ind.$^{-1}$ Juveniles: 0.017–72.1 µg C ind.$^{-1}$	0.075–3620 µg C ind.$^{-1}$	nd	na[a]
Applicable chl *a* range	0.016–321.6 mg chl *a* l^{-1}	nd	nd	na[a]
Estimated P/B ratios	P/B ratio for total copepod community higher than literature values. Best fit for medium and large size classes, overestimation of small size class of mesozooplankton	P/B ratio for total copepod community similar to literature values. Best fit for medium and large size classes, overestimation of small size class of mesozooplankton	P/B ratio for total copepod community similar to literature values. Best fit for medium and large size classes, overestimation of small size class of mesozooplankton	P/B ratio for total copepod community lower than literature values. Best fit for small size class, underestimation of medium and large size class of mesozooplankton
Recommended use	Estimation of secondary production of large, predominantly herbivorous copepods during food-limiting conditions, e.g. fall and winter	Estimation of secondary production of large, predominantly herbivorous copepods during non-limiting food conditions, e.g. spring and summer. Year-round estimation of secondary production of small, omnivorous copepods	Not recommended in high-atitude ecosystems, due to temperature being the only factor considered and production consequently following temperature trends in the study area	Estimation of mesozooplankton production in combination with biomass data in size bins from optical plankton instruments

[a] The model of Zhou et al. (2010) originates from the model of Hirst & Bunker (2003) and incorporates the theoretical definition of zooplankton growth by Huntley & Boyd (1984)

zero temperatures is recommended for future studies, and an effort to develop a local growth rate model for high-latitude regions is needed.

Secondary production was estimated for data obtained with the LOPC sampling and with the WP2 net and GoFlo bottle sampling using 2 different methods that cover different parts of the mesozooplankton community. From the WP-2 net and GoFlo bottle sampling, we estimated secondary production for copepods only, as the applied growth rate models are not suitable for zooplankton groups other than copepods (Runge & Roff 2000). We aimed to compare and evaluate existing production models and selected the following models for estimating copepod secondary production in the Barents Sea: model A: Hirst & Bunker (2003), model B: Hirst & Lampitt (1998) and model C: Huntley & Lopez (1992). These are among the most commonly used copepod growth rate models and include important environmental and biological factors, such as temperature, chl *a* concentration and copepod body weight, that can be important in governing copepod secondary production (Runge & Roff 2000). Subsequently, we compared the production to biomass (P/B) ratios predicted by the different models to P/B ratios from the literature, to identify the model that proved most suitable for presenting the biological aspects of copepod secondary production across the Barents Sea polar front.

A different approach was applied for data acquired by the LOPC. We estimated mesozooplankton secondary production (including copepods and non-copepod mesozooplankton groups) in different size classes (small, S, 0.25–0.6 mm ESD; medium, M, 0.6–1.5 mm ESD; and large, L, 1.5–4 mm ESD), by applying a zooplankton growth rate model developed for the usage with optical plankton counters (model D: Zhou et al. 2010).

2.4.1. Copepod secondary production based on WP-2 net and GoFlo bottle sampling

Daily copepod secondary production (mg C m^{-3} d^{-1}) in the upper 50 m water column was calculated using the following formula (Runge & Roff 2000):

$$p = \Sigma B_i \times g_i \tag{1}$$

where B_i is copepod stage-specific biomass for the upper 50 m (mg C m^{-3}), obtained from the WP-2 net and GoFlo bottle sampling, and g_i is stage-specific growth rate (d^{-1}). We focused on the upper 50 m water column only, as LOPC sampling identified this to be the active mesozooplankton layer.

Ideally, the growth rates of all developmental stages of individual copepod species would be determined experimentally at *in situ* temperatures and food conditions. However, as this would be a tremendous and unrealistically labour-intensive task, different modelling approaches have been developed to estimate growth rates of copepods (Runge & Roff 2000). These models are based on literature reviews of studies that experimentally determine female fecundity and juvenile somatic growth rates of a variety of copepod species. The weight-specific growth is then related to different forcing variables of copepod production, such as temperature, body weight and chl *a* concentration. Some of the most widely used examples of growth rate models include:

Model A: Hirst & Bunker (2003), a multiple linear regression growth model that assumes that copepod growth is governed by temperature, copepod body weight and chl *a* concentration;

Model B: Hirst & Lampitt (1998), a multiple linear regression model that assumes that copepod growth is dependent on temperature and copepod body weight;

Model C: Huntley & Lopez (1992), a temperature-dependent growth rate model that assumes that copepod growth is solely determined by temperature.

Models A–C (Table S1 in the Supplement at www.int-res.com/articles/suppl/m735p077_supp.pdf) are global copepod growth rate models that can be applied to actively growing copepod populations spanning geographically from polar to tropical regions. The least covered regions in the models are polar offshore areas. Furthermore, most of the models incorporate data from egg production experiments of broadcast-spawning copepods and only include a few *in situ* measurements of juvenile copepod growth rates. Model A is based on the most extensive data set of 4831 weight-specific fecundity and juvenile growth rate measurements, followed by model B with 952 and model C with 181 measurements (Table 2). The temperature range observed during our study was −1.4 to 4.6°C, the chl *a* concentration was 0.55–1.96 mg chl *a* m^{-3} (Table S2), and the individual copepod body weight was 0.06–1317 µg C ind.$^{-1}$ (*Oithona* spp. nauplii were the lightest and *Calanus hyperboreus* adult females (AF) the heaviest). Therefore, all variables observed during our study fall well within the application range of the different models (Table 2). To calculate secondary production of broadcast-spawning and sac-spawning copepods, the respective formulas for adult and juvenile copepods of models A and B were used, while model C is applicable to all copepods (Table S1). The copepod secondary production data are published on GBIF (Gawinski et al. 2023).

2.4.2. Mesozooplankton secondary production based on LOPC data

With the advancement of optical plankton counters, efforts have been made to develop models that can predict growth rates based on biovolume spectrum theory and consider the higher particle abundance observed with optical plankton counters, compared to zooplankton abundance from traditional net sampling. One such example is model D: Zhou et al. (2010), a growth rate model that assumes that growth of zooplankton is governed by temperature, body weight and chl *a* concentration and includes a factor accounting for assimilated food input by zooplankton. This model builds upon the model of Hirst & Bunker (2003) and incorporates the definition of zooplankton growth by Huntley & Boyd (1984), which posits that growth is governed by food concentration, zooplankton assimilation efficiency and clearance rate. By combining the 2 equations and theoretically restructuring the resulting equation, the model is streamlined to require simplified input variables, namely chl *a* concentration, copepod body weight and temperature. By combining these 2 approaches, Zhou et al. (2010) argued that an overestimation of zooplankton growth at high temperatures and food concentrations is avoided. Model D has previously been used to estimate zooplankton secondary production based on the size-bin data from LOPC counts (Basedow et al. 2014). The advantages of estimating secondary production with the LOPC are high spatial resolution and the ability to detect patches of high mesozooplankton secondary production and its extent, depth range and size distribution.

Daily mesozooplankton secondary production (mg C m^{-3} d^{-1}, normalised by size bin) of size classes S, M and L, sampled with the LOPC, was calculated following the method described by Basedow et al. (2014) (their Eqs. 3 & 5). Here, production p (mg C m^{-3} d^{-1}, normalised by size bin) is given as:

$$p = g \times w \times N \tag{2}$$

where g is weight-specific growth rate (d^{-1}), w is mean weight for each size bin (mg C $ind.^{-1}$), and N is abundance (ind. m^{-3}). Weight-specific growth g (d^{-1}) for each size bin was calculated according to Zhou et al. (2010):

$$g(w, T, Chla) = 0.033\left[\frac{Chla}{(205\, e^{-0.125T})}\right] e^{0.09T} w^{-0.06} \tag{3}$$

where w is weight for each size bin (mg C $ind.^{-1}$), $Chla$ is chl *a* (mg C m^{-3}), and T is temperature (°C). The volume of particles was converted into carbon using a ratio of mg carbon = 0.0475 body volume (Gallienne & Robins 2001), and chl *a* was converted to carbon using a ratio of C:chl *a* = 50 (Basedow et al. 2014).

To compare estimates of copepod secondary production, which are based on biomass obtained from WP-2 net and GoFlo bottle sampling, with mesozooplankton secondary production based on LOPC sampling, we also estimated copepod secondary production using model D. Subsequently, copepod secondary production calculated with models A–D was grouped into 3 size classes (S_net, M_net, L_net), aligning with the size classes used in the LOPC sampling (S, M, L).

2.4.3. Comparison and evaluation of secondary production resulting from different growth rate models

The estimates of copepod secondary production differed considerably when calculated using the 4 selected models (A–D). Overall, model D resulted in the lowest total copepod secondary production values, ranging from 0.11 to 0.27 mg C m^{-3} d^{-1} (Stns M2 and M4, respectively, Table 3). The highest total copepod secondary production values were obtained using model A, with 6.48–12.27 mg C m^{-3} d^{-1} (Stns M4 and M1, respectively, Table 3), which is 24–84 times higher than using model D (Fig. 2, Table 3). Model B resulted in copepod secondary production values 10–33 times higher, and model C 6–16 times higher values, than model D. Models A and B generally showed the same trend of increasing copepod secondary production from the Atlantic to the Arctic region (models A and B in Fig. 2, Table 3), with highest copepod secondary production observed at the Arctic station (M1) for model A and at the northern station in the polar front (M2) for model B. The opposite trend was observed when using model C, with generally high copepod secondary production in the Atlantic region and in the polar front and lower in the Arctic region (model C in Fig. 2, Table 3). Model D showed highest copepod secondary production in the Atlantic region and lower but comparable copepod production across the polar front and in the Arctic region (model D in Fig. 2, Table 3). For Arctic regions, model A often overestimates the growth rates of juvenile broadcast-spawning copepods by a factor of 3–8 during periods with high chl *a* concentrations (Liu & Hopcroft 2006a,b, Madsen et al. 2008). A large spread of produc-

Table 3. Copepod and mesozooplankton biomass (mg C m^{-3}), estimated copepod and mesozooplankton secondary production (mg C m^{-3} d^{-1}) averaged for the upper 50 m water column and daily production to biomass (P/B) ratios for copepods and mesozooplankton at 4 stations. Copepod secondary production was estimated according to Hirst & Bunker (2003) (model A), Hirst & Lampitt (1998) (model B), Huntley & Lopez (1992) (model C) and Zhou et al. (2010) (model D) and was based on copepod biomass obtained with WP-2 net and GoFlo bottle sampling. Mesozooplankton secondary production was obtained from laser optical plankton counter (LOPC) counts and the model of Zhou et al. (2010). Copepods and mesozooplankton were divided into size groups (S, small: 0.25–0.6 mm; M, medium: 0.6–1.5 mm; and L, large: 1.5–4 mm) and are depicted as S_net, M_net, L_net for copepods from the WP2-net and GoFlo bottle sampling and S, M, L for mesozooplankton from the LOPC sampling. Production estimates for LOPC size group S at Stns M3, M2 and M1 were excluded due to the contribution of an unknown proportion of non-zooplankton particles

Size class	Station	Region	Biomass		Production					P/B ratio				
			Copepods	Whole meso-zoo-plankton community	Copepods				Whole meso-zoo-plankton community	Copepods				Whole meso-zoo-plankton community
			Net + GoFlo	LOPC	A	B	C	D	LOPC	A	B	C	D	LOPC
S_net / S	M4	Atlantic	4.45	44.31	0.91	0.44	0.34	0.06	0.42	0.20	0.10	0.08	0.01	0.01
	M3	Front	6.25	32.33	3.23	1.07	0.31	0.04	No data	0.52	0.17	0.05	0.01	No data
	M2	Front	4.07	30.62	2.10	0.72	0.17	0.01	No data	0.52	0.18	0.04	0.00	No data
	M1	Arctic	12.62	6.73	10.22	2.59	0.49	0.09	No data	0.81	0.21	0.04	0.01	No data
M_net / M	M4	Atlantic	17.93	24.11	5.52	2.33	1.24	0.21	0.19	0.31	0.13	0.07	0.01	0.01
	M3	Front	14.19	16.29	3.89	1.41	0.70	0.09	0.07	0.27	0.10	0.05	0.01	0.00
	M2	Front	19.79	14.45	4.94	1.81	0.83	0.06	0.06	0.25	0.09	0.04	0.00	0.00
	M1	Arctic	2.27	9.4	0.53	0.16	0.09	0.02	0.01	0.23	0.07	0.04	0.01	0.00
L_net / L	M4	Atlantic	0.42	13.44	0.05	0.03	0.03	0.00	0.08	0.12	0.08	0.08	0.00	0.01
	M3	Front	10.41	34.19	1.37	0.66	0.52	0.05	0.13	0.13	0.06	0.05	0.01	0.00
	M2	Front	19.25	11.91	2.19	1.12	0.81	0.05	0.04	0.11	0.06	0.04	0.00	0.00
	M1	Arctic	14.13	107.01	1.52	0.73	0.54	0.08	0.04	0.11	0.05	0.04	0.01	0.00
Total	M4	Atlantic	22.81	81.86	6.48	2.80	1.61	0.27	0.69	0.28	0.12	0.07	0.01	0.00
	M3	Front	30.84	82.81	8.49	3.15	1.53	0.18	No data	0.28	0.10	0.05	0.01	No data
	M2	Front	43.10	56.98	9.23	3.65	1.81	0.11	No data	0.21	0.08	0.04	0.00	No data
	M1	Arctic	29.02	123.14	12.27	3.49	1.12	0.19	No data	0.42	0.12	0.04	0.01	No data

tion values for this model can be expected, as it only explains a relatively low percentage of the variance in the data set it is built on (Hirst & Bunker 2003; Table 2). On the other hand, models B and C often seem to underestimate copepod growth rates compared to *in situ* growth rate measurements in Arctic regions (Liu & Hopcroft 2006a,b), although model B explains a higher proportion of the variance in the data set that it is built on (Hirst & Lampitt 1998; Table 2). Model C is probably less suited for Arctic areas, as secondary production by implication follows the pattern of temperature distribution in the study area and does not take copepod stage composition into consideration.

The different size groups (S_net, 0.25–0.6 mm equivalent spherical diameter [ESD]; M_net, 0.6–1.5 mm ESD; L_net, 1.5–4 mm ESD) showed similar trends in relative contribution to total copepod secondary production across models A–C (Fig. 2), but not for model D. Production of size group S_net was lowest at the Atlantic station (M4) and highest at the Arctic station (M1) for models A–C, while it was the opposite for model D. Size group M_net showed highest production at Stn M4 and lowest production at Stn M1 in all models. Size group L_net had highest production at the northernmost station in the polar front (M2) and lowest production at Stn M4 in models A–C, while for model D, production was equally high at Stns M1 and M4 and lowest at the northernmost station in the polar front (M2) (Fig. 2). The spread in secondary production values across models A–D was largest for the size classes S_net and M_net (Fig. 2) and can likely be attributed to the lack of growth rate data of small species and young developmental stages of copepods at high latitudes, and we suggest that this leads to poor predictive power of the models.

To evaluate the performance of the models, we chose to compare daily production to biomass (P/B) ratios of models A–D with P/B ratios from the literature. Alternatively, the predicted growth rates of the individual developmental stages among different copepod species could be compared to experimentally determined growth rate measurements at specific temperatures, as reported in existing literature. However, few studies have conducted these experiments at subzero temperatures, limiting the available data for such comparisons. There were clear differences in the daily

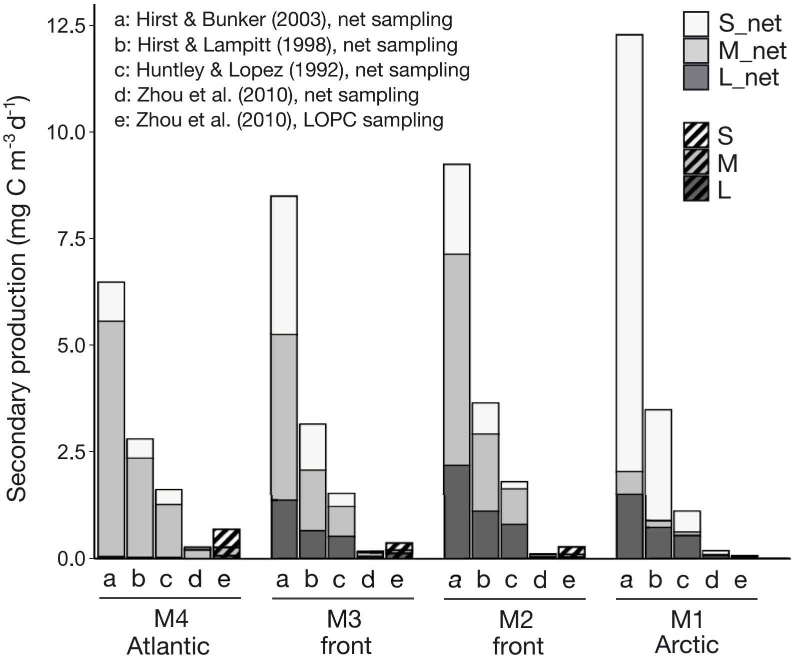

Fig. 2. Copepod (a–d) and mesozooplankton (e) secondary production estimates (mg C m^{-3} d^{-1}) averaged over the upper 50 m water column, across the 4 sampling stations (M1–M4) using 5 different methods. a–d are based on copepod biomass estimates from the WP-2 net and GoFlo bottle sampling and the following growth rate models: a: Hirst & Bunker (2003), b: Hirst & Lampitt (1998), c: Huntley & Lopez (1992) and d: Zhou et al. (2010). e is based on laser optical plankton counter (LOPC) mesozooplankton biovolume size spectra and the model of Zhou et al. (2010). Copepods and mesozooplankton were divided into size groups small (S, 0.25–0.6 mm), medium (M, 0.6–1.5 mm) and large (L, 1.5–4 mm) and are depicted as S_net, M_net, L_net for copepods from the WP2-net and GoFlo bottle sampling and S, M, L for mesozooplankton from the LOPC sampling

P/B ratios for the different models (Table 3), with model A showing the highest daily P/B ratios, followed by models B and C, and the lowest daily P/B ratios resulting from model D (Table 3). P/B ratios for specific copepod species in the Arctic are scarce. Daily P/B ratios of the large copepod *C. glacialis* (size group L) ranged between 0.03 and 0.05 d^{-1} in the Arctic (Slagstad & Tande 2007). Yearly P/B ratios of 6.5 yr^{-1} for *C. finmarchicus* and 3.25 yr^{-1} for *C. glacialis* and *C. hyperboreus* have been reported for the Barents Sea (Pedersen et al. 2021). When assuming a growth period of 150 d (June to August, as used for the annual biomass calculations in Pedersen et al. 2021), this results in daily P/B ratios of 0.04 for *C. finmarchicus* and 0.02 for *C. glacialis* and *C. hyperboreus*. Daily P/B ratios for the small copepod *Pseudocalanus* sp. (size group S) range between 0.007 and 0.043 d^{-1} (Sakshaug et al. 2009). Yearly P/B ratios of 6.5 yr^{-1} for small copepods (Pedersen et al. 2021) and 2.7 yr^{-1} for *Pseudocalanus* sp. (Sakshaug et al. 2009) have been reported. These yearly ratios result in daily P/B ratios of 0.01–0.02 (assuming a 365 d growth period). Daily P/B ratios for the total mesozooplankton community in the Barents Sea varied between 0.02 and 0.10 (Dvoretsky & Dvoretsky 2009, 2024a,b). The P/B ratios of the total copepod community and size group L_net based on models B and C in this study match the literature values, while the P/B ratios of model A were higher and those of model D were lower (Table 2). For size group S_net, models A–C gave higher P/B ratios than the ones reported in the literature, while model D gave similar results (Table 2).

Based on the observations outlined above, we suggest that the 2 temperature-dependent models, B and C, describe copepod secondary production most realistically in summer. By including a body weight factor, model B takes copepod stage composition into consideration and is therefore a better representation of copepod secondary production than model C. Early life stages of copepods grow faster than adults (Hirst & Lampitt 1998), which is not taken into consideration in the latter model. Model B approximates the maximum possible copepod growth at certain temperatures under food saturation, and we suggest it should be used to estimate copepod secondary production in Arctic regions during spring and summer months. During periods with low chl *a* concentrations, model A might be a better approximation of the growth of predominantly herbivorous copepods, e.g. *Calanus* spp., as they would likely be food limited. For small, omnivorous copepods, model B is a good approximation of growth throughout the year, as the growth of these copepods is generally more temperature limited than food limited. Based on the argumentation outlined above, the main results of copepod secondary production across the polar front are based on WP-2 net and GoFlo bottle sampling combined with model B (Table 2).

The average LOPC-derived mesozooplankton secondary production for the upper 50 m (based on LOPC counts and model D) was lower than the copepod secondary production (based on WP-2 net and GoFlo bottle sampling) estimated with models A–C, but was higher than the copepod secondary production when estimated with model D. This means that the traditional copepod growth rate models (A–C) result in higher growth rates compared to the optical plankton counter growth rate model (D). However, the LOPC showed concentrated patches of extremely high mesozooplankton secondary production along the transect, where the magnitude was comparable to the average copepod secondary production obtained with traditional net sampling and model B (see Figs. 5 & 7). If mesozooplankton secondary production in these patches were calculated with model B, these values would have been several orders of magnitude higher than copepod secondary production obtained from traditional net sampling. To evaluate the spatial distribution, depth range and patchiness of mesozooplankton secondary production across the Barents Sea polar front, we present results based on LOPC sampling combined with model D.

3. RESULTS

3.1. Hydrography and chl *a*

A thorough description of hydrography, small-scale current shear, diffusivity, suspended chl *a* biomass and dominant phytoplankton taxa at the polar front in June 2011 is provided by Wiedmann et al. (2014). Here we present a short summary of results relevant to this study.

The polar front was identified between approximately 76.3° and 77.5° N and was characterized by the confluence of Arctic water (ArW, temperature [T] < 0°C, 34.3 < salinity [S] < 34.8, Loeng 1991) and Atlantic water (AW, T > 3°C, S > 35.0, Loeng 1991). Very open drift ice with a coverage of around 30% was only observed at Stn M1 during the sampling period, while Stns M2–M4 were ice-free. The water column at M1 was characterized by a shallow, cold, low-salinity surface mixed layer, about 7 m thick. Temperatures were low throughout the water column, exceeding zero only at depths greater than 200 m (Fig. 3A). At Stn M2, a 15 m thick surface mixed layer with even lower salinity was observed, likely reflecting larger total meltwater input. Modified AW was found below 85 m. At Stn M3, an 18 m thick surface mixed layer was followed by a sharp increase in salinity and decrease in temperature, down to a thin layer with remnants of ArW (around 20–40 m depth). There was a rapid transition to AW at a depth of 50 m, with temperature peaking at 3°C at 75 m depth. Stn M4 was situated inside the AW domain, where a deep (~30 m) surface mixed layer with T > 5°C was observed.

The concentration of chl *a* across the polar front was patchy (Fig. 3C). Subsurface chl *a* maximum concentrations were found at all stations well below the mixed layer depth. The highest concentration of extracted chl *a*, 4.4 mg m^{-3}, was found in the Arctic region (Stn M1, 40 m depth), while the maximum across the front and in the Atlantic region ranged from 1.4 to 2 mg chl *a* m^{-3} (between 30 and 40 m depth). The Arctic region (Stn M1) was different from the other areas by having a bloom of larger cells >10 µm, while cells <10 µm prevailed in the rest of the study area (Table S2). Integrated mean chl *a* concentrations for the upper 50 m water column ranged from 1.96 mg chl *a* m^{-3} in the Arctic region (Stn M1) to 0.55–0.90 mg chl *a* m^{-3} across the front (Stns M2 and M3, respectively) and 0.82 mg chl *a* m^{-3} in the Atlantic region (Stn M4) (Table S2).

3.2. Mesozooplankton community composition and secondary production across the Barents Sea polar front

3.2.1. Spatial resolution of mesozooplankton distribution using LOPC sampling

High-resolution sampling with the LOPC revealed a patchy distribution of mesozooplankton across the polar front. Overall, mesozooplankton abundance was highest in the Atlantic region (Stn M4) and decreased across the polar front (Stns M3, M2), with lowest numbers observed in the Arctic region (Stn M1) (Fig. 4). Small-sized particles (zooplankton) of 0.25–0.6 mm ESD (size group S) were most abundant in the Atlantic region, where they reached maximum numbers of 560 000 ind. m^{-3} and were distributed throughout the whole water column. High numbers of small-sized particles (zooplankton and aggregates) were also observed in the northern parts of the polar front, from approximately 76.7° to 77.5° N, where they were located in the surface layers to a depth of about 100 m (Fig. 4). Medium-sized zooplankton particles of 0.6–1.5 mm ESD (size group M, Fig. 4) and large-sized zooplankton particles of 1.5–4 mm ESD (size group L, Fig. 4) were distributed more patchily and reached maximum numbers of 105 000 and 4800 ind. m^{-3}, respectively. A patch of medium-sized zooplankton with high abundance was found associated with the sub-surface chl *a* maximum in the Atlantic region. A patch of large-sized zooplankton was observed associated with an area of warmer water, located below the tongue of the polar front south of Stn M3 (Fig. 4). Along the rest of the transect, medium- and large-sized zooplankton were less abundant.

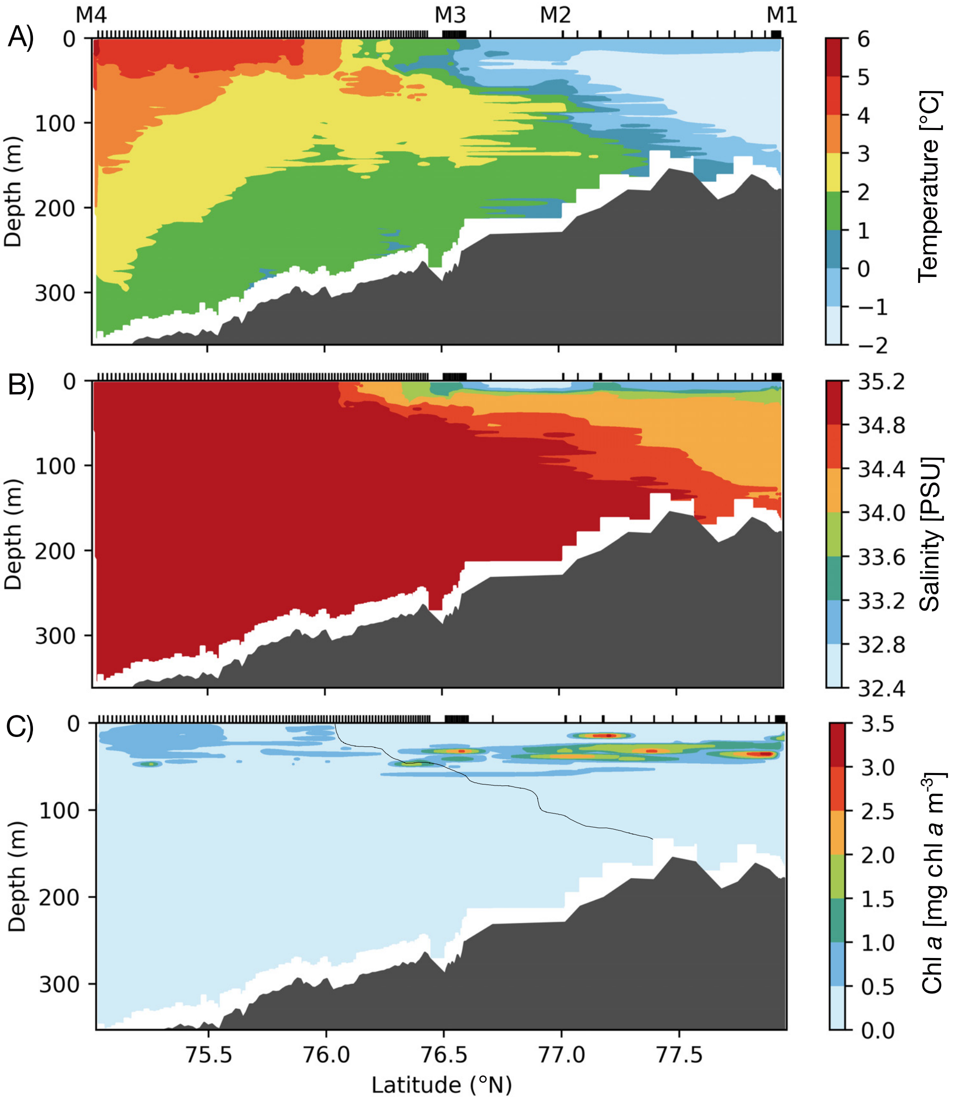

Fig. 3. Transect of (A) temperature (°C), (B) salinity (PSU) and (C) chlorophyll *a* concentration (mg chl *a* m^{-3}) across the polar front from Hopen Deep (left) to Great Bank, Barents Sea (right), in June 2011. The approximate location of the polar front based on the 34.8 isohaline is indicated with a black line. The locations of the different profiles are indicated with black dashes

3.2.2. Spatial resolution of mesozooplankton secondary production

Mesozooplankton secondary production (based on LOPC sampling combined with growth rate model D, Zhou et al. 2010) was mainly concentrated in the upper 50 m water column. Total mesozooplankton secondary production was highest in the Atlantic region and lower across the polar front and in the Arctic region (Fig. 5, mesozooplankton production values from panels A–C combined). In the Atlantic region, mesozooplankton secondary production of size group S reached a maximum of 1.2 mg C m^{-3} d^{-1} in localized patches and averaged 0.42 mg C m^{-3} d^{-1} for the upper 50 m (Stn M4, Table 3), which constituted a large proportion of the total mesozooplankton secondary production in this area (Fig. 5). For the region north of 76.35° N, we cannot report accurate mesozooplankton production values for size group S, due to an unknown contribution of non-zooplankton particles. The estimates of size group S in this area approximate the maximum possible mesozooplankton secondary production, including the unknown contribution of detritus. These values are lower than the values observed in the Atlantic region, meaning that the Atlantic region was the most productive area during our study. Mesozooplankton secondary production of size groups M and L was patchily distributed across the transect and associated with areas of high chl *a* concentrations (Fig. 5). The average mesozooplankton secondary production in the upper 50 m of size groups M and L was highest in the Atlantic region and the southern part of the polar

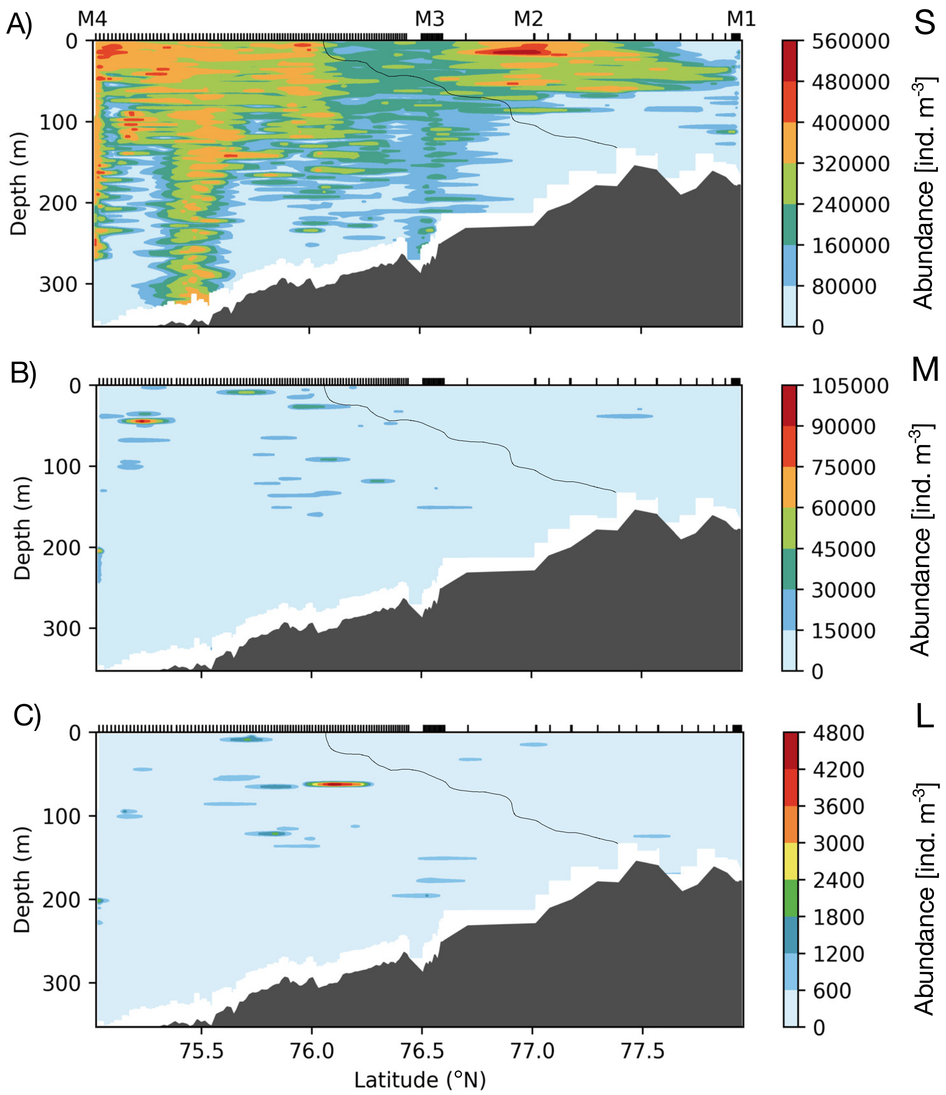

Fig. 4. Transect of mesozooplankton abundance (ind. m^{-3}) obtained with the laser optical plankton counter (LOPC) across the polar front from Hopen Deep (left) to Great Bank, Barents Sea (right). (A) Small-sized particles (S, 0.25–0.6 mm equivalent spherical diameter, ESD), (B) medium-sized particles (M, 0.6–1.5 mm ESD), (C) large-sized particles (L, 1.5–4.0 mm ESD). The approximate location of the polar front based on the 34.8 isohaline is indicated with a black line. The locations of the different LOPC profiles are marked with black dashes, and M1–M4 mark the locations where WP-2 net and GoFlo samples were taken

front, with 0.19 mg C m^{-3} d^{-1} (Stn M4, Table 3) and 0.13 mg C m^{-3} d^{-1} (Stn M3, Table 3), respectively. Some small patches of size groups M and L reached maximum values of 1.75 and 3.5 mg C m^{-3} d^{-1}, respectively.

3.2.3. Taxonomic resolution of mesozooplankton distribution using WP-2 net and GoFlo bottle sampling

Total mesozooplankton abundance from the WP-2 net and GoFlo sampling was highest in the Atlantic region (Stn M4) and decreased across the polar front towards the Arctic region (Stn M1) (Fig. 6A). The lowest mesozooplankton abundance was observed in the northern part of the polar front (Stn M2). Between 95 and 98% of all mesozooplankton individuals were found in the surface layer from 0 to 50 m depth (Fig. 6A). Total mesozooplankton biomass in the upper 50 m ranged from 22.81 mC m^{-3} in the Atlantic region (Stn M4) to 43.10 mg C m^{-3} in frontal waters (Stn M2, Table2) and was dominated by large copepods of the genus *Calanus* (Fig. 6D). Calanoid copepod nauplii contributed considerably to total mesozooplankton biomass in the Arctic region, while young developmental stages (CI–CIV) and small-sized copepods contributed most to total mesozooplankton biomass in the Atlantic region (Fig. 6E).

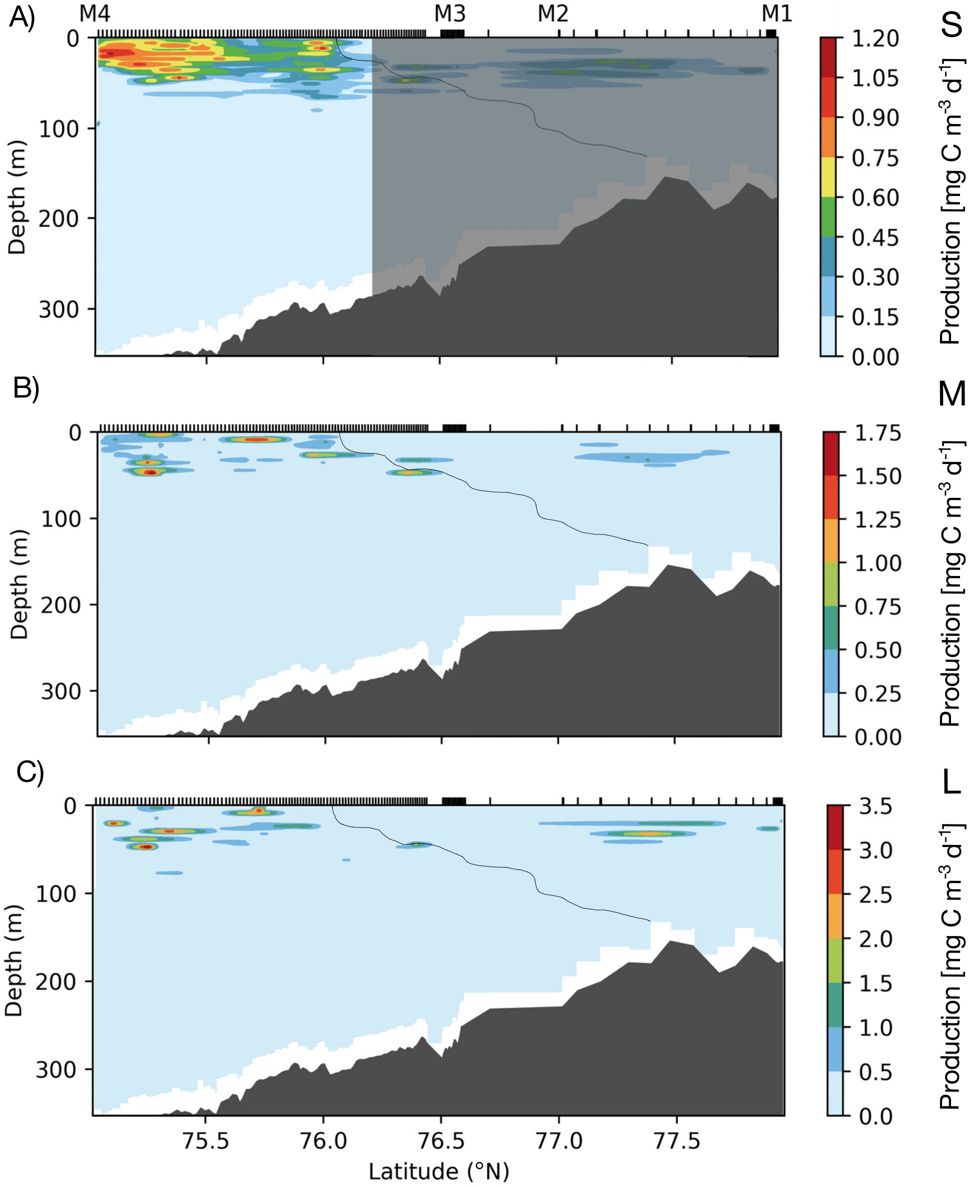

Fig. 5. Transect of mesozooplankton secondary production (mg C m^{-3} d^{-1}) across the Barents Sea polar front based on the laser optical plankton counter (LOPC) data. (A) Small-sized particles (S, 0.25–0.6 mm equivalent spherical diameter, ESD). Estimations north of 76.25° N are excluded from the results, as a possible overestimation of production, due to an unknown fraction of aggregates contributing to the LOPC counts in this region, cannot be ruled out (grey shaded area). (B) Medium-sized particles (M, 0.6–1.5 mm ESD). (C) Large-sized particles (L, 1.5–4.0 mm ESD). The approximate location of the polar front based on the 34.8 isohaline is indicated with a black line. The locations of the different LOPC profiles are marked with black dashes, and M1–M4 mark the locations where WP-2 net and GoFlo samples were taken

When considering the combined abundance of copepod and non-copepod mesozooplankton in the Atlantic region (Stn M4), Rotifera and copepod nauplii accounted for 49 and 39% of the total abundance, respectively (Fig. 6A–C). Across the polar front and in the Arctic region, copepod nauplii were the dominant mesozooplankton group, accounting for 68–71% of total abundance. Small cyclopoid and harpacticoid copepods and their nauplii were more abundant in the south, with abundance of *Oithona similis* decreasing from 3.4 × 10^{3} ind. m^{-3} in the Atlantic region (Stn M4) to 0.6 × 10^{3} ind. m^{-3} in the Arctic region (Stn M1). Large copepods were numerically dominated by *C. finmarchicus* in the south (99%) and *C. glacialis* in the north (95%, data not shown). Across the polar front, a mix of both *Calanus* species was observed (between 79 and 87% *C. finmarchicus*). *C. hyperboreus* was absent in the Atlantic region (Stn M4) and only found in very low abundance across the polar front (0.1–0.2%), while it contributed 5% to total *Calanus* spp. abun-

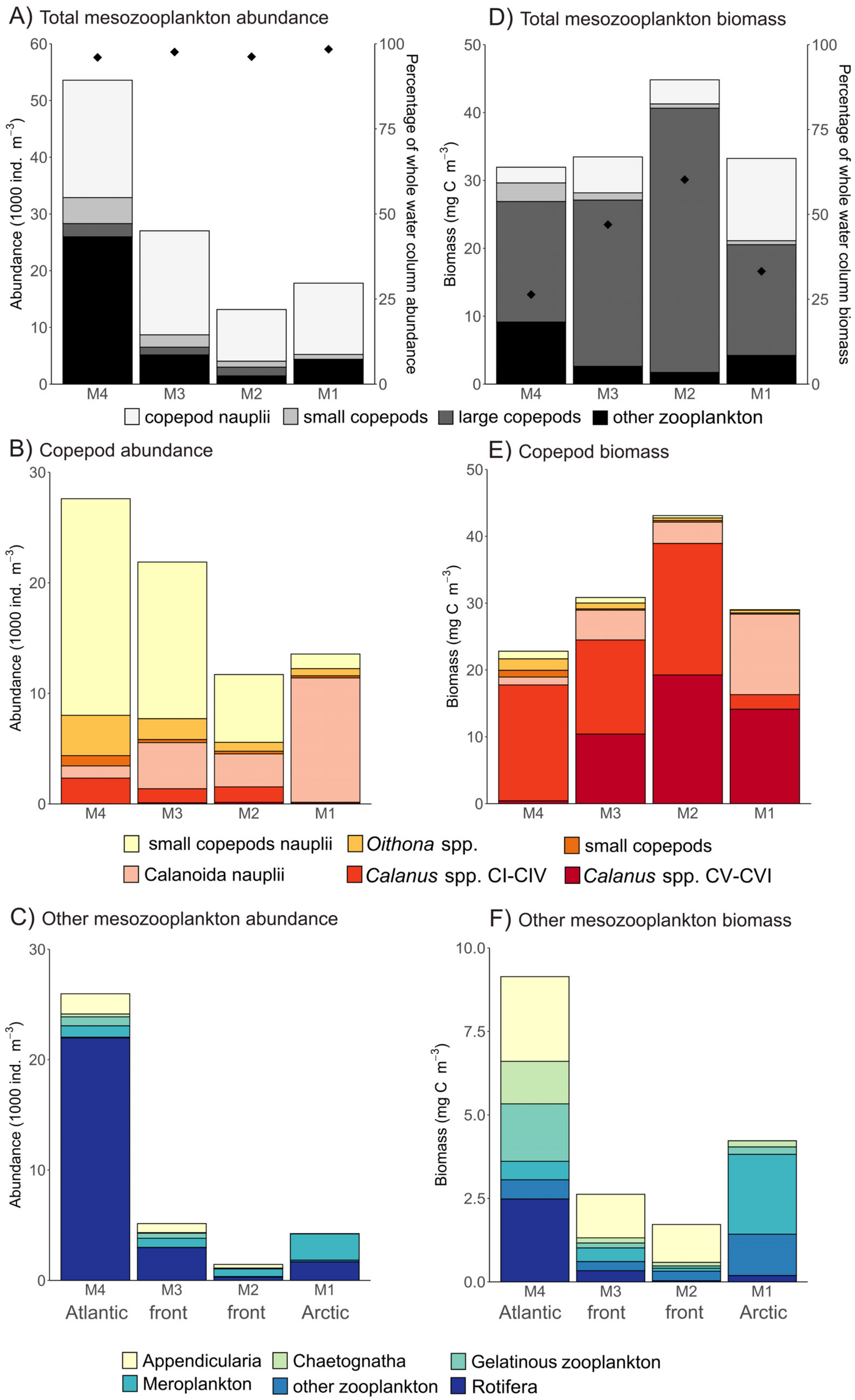

Fig. 6. Abundance (upper 50 m, 1000 ind. m^{-3}) of (A) total mesozooplankton, (B) copepods and (C) mesozooplankton other than copepods, and biomass (upper 50 m, mg C m^{-3}) of (D) total mesozooplankton, (E) copepods and (F) mesozooplankton other than copepods collected with the WP-2 net and GoFlo bottles at the sampling stations (M1–M4) across the polar front. The right axes in panels A and D indicate the percentage of the whole water column abundance and biomass that is found in the upper 50 m at each station, respectively (indicated by diamonds). Note the different scales on the y-axes

dance in the Arctic region (Stn M1). The *Calanus* community was in an early developmental state in the Arctic region, where active reproduction was observed, and the community was dominated by adults and CV copepodites (1 and 32%, respectively, Fig. 6E). Crossing the polar front into the Atlantic region, the *Calanus* community gradually showed a more advanced developmental state, and the contribution of young stage CI—CIV copepodites increased from 67 to 100 % (Stns M1 to M4). Zooplankton other than copepods contributed a high proportion to total mesozooplankton abundance in the upper 50 m. Here, Rotifera, with *Synchaeta* spp. as the main representative, and Appendicularia, with *Fritillaria borealis* as the main representative, were most abundant, with 22 × 10^3 and 1.8 × 10^3 ind. m^{-3} in the Atlantic region (Stn M4), respectively (Fig. 6C,F). Appendicularia, Chaetognatha and gelatinous zooplankton were abundant in the Atlantic region but were almost completely absent in the Arctic region. High numbers of larval stages of Polychaeta, Echinodermata and Bivalvia were observed at the Arctic region (Stn M1) and in the northern parts of the polar front (Stn M2) (Fig. 6).

3.2.4. Taxonomic resolution of copepod secondary production

Estimates of the total copepod secondary production (based on WP-2 and GoFlo sampling and model B, Hirst & Lampitt 1998) ranged from 2.80 mg C m^{-3} d^{-1} in the Atlantic region (Stn M4) to 3.65 mg C m^{-3} d^{-1} in the northern sector of the polar front (Stn M2) and 3.49 mg C m^{-3} d^{-1} in the Arctic region (Stn M1) (Table 4, Fig. 7).

Of the total copepod production, the small copepods and nauplii (size group S_net) contributed the least at Stn M4, with 0.45 mg C m^{-3} d^{-1}, but their production increased northwards, reaching a maximum of 2.59 mg C m^{-3} d^{-1} in the Arctic region (Stn M1) (Fig. 7, Table 4). In the Atlantic region, the small copepods *Oithona similis*, *Microsetella norvegica* and *Triconia borealis* and their nauplii together contributed 33.3% to copepod secondary production of size group S_net. In the rest of the transect, copepod secondary production of size group S_net was completely dominated by calanoid nauplii (96—99%). Copepod secondary production of size group M_net was highest in the Atlantic region (Stn M4) with 2.32 mg C m^{-3} d^{-1} and decreased across the polar front to a minimum of 0.16 mg C m^{-3} d^{-1} in the Arctic region (Stn M1) (Fig. 7, Table 4). Reflecting the *Calanus* spp. community composition, copepod secondary production of size group M_net was mainly comprised of *C. finmarchicus* CI—CIV copepodites in the south (Stn M4), while *C. glacialis* CI—CIV copepodites gained in importance crossing the front and were the main contributors in the Arctic region (Stn M1). Copepod secondary production of size group L_net was lowest in the Atlantic region (Stn M4) with 0.03 mg C m^{-3} d^{-1} and reached 0.74 mg C m^{-3} d^{-1} in the Arctic region (Stn M1) (Fig. 7, Table 4). The *Calanus* spp.

Table 4. Copepod secondary production estimates (prod.) in mg C m^{-3} d^{-1} for the upper 50 m water column, based on the growth rate model of Hirst & Lampitt (1998), and percentage of total copepod secondary production (% prod.) for different categories of copepods at the Atlantic station (M4), the frontal stations (M3 and M2) and the Arctic station (M1). Depicted are total copepod secondary production (all stages CI—CVI + nauplii), secondary production of copepod nauplii (Calanoida and Cyclopoida & Harpacticoida nauplii) and secondary production of copepod stages CI—CVI (small copepods CI—VI, large copepods CI—IV, large copepods CV—CVI). Size classification of the different copepod categories is depicted as S_net, M_net and L_net

		Atlantic		Front				Arctic	
		(Stn M4)		(Stn M3)		(Stn M2)		(Stn M1)	
		Prod.	% prod.	Prod.	% prod.	Prod.	% prod.	Prod.	% prod.
Copepod nauplii + CI—CVI		2.80	100	3.15	100	3.65	100	3.49	100
Copepod nauplii		0.36	12.8	1.04	33.0	0.71	19.5	2.58	73.9
	Calanoida nauplii (S_net)	0.30	10.7	1.01	32.0	0.70	19.2	2.58	74.0
	Cyclopoida, Harpacticoida nauplii (S_net)	0.06	2.1	0.03	1.0	0.01	0.3	0.00	0.0
Copepods CI—CVI		2.44	87.2	2.11	67.0	2.94	80.5	0.91	26.1
Small copepods	CI—VI (S_net)	0.09	3.2	0.04	1.3	0.01	0.3	0.01	0.2
Large copepods	CV—VI (L_net)	0.03	1.1	0.66	20.9	1.12	30.6	0.74	21.3
	CI—IV (M_net)	2.32	82.9	1.41	44.8	1.81	49.6	0.16	4.6

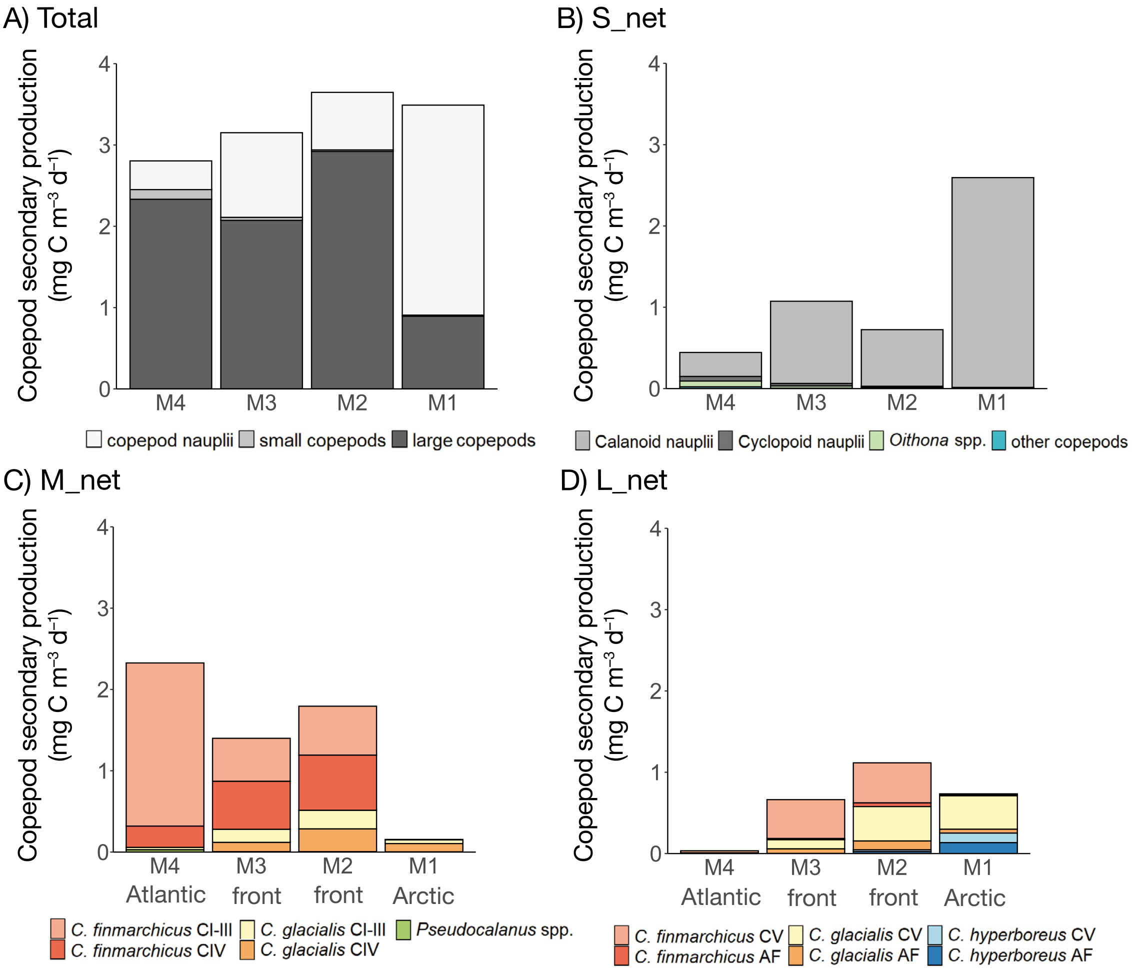

Fig. 7. Copepod secondary production estimates (averaged for the upper 50 m, mg C m^{-3} d^{-1}) based on WP-2 net and GoFlo sampling for the different size classes of copepods according to the model of Hirst & Lampitt (1998). (A) Total copepod secondary production, (B) small size class (S_net), (C) medium size class (M_net), (D) large size class (L_net). AF: adult females

community composition was reflected in the copepod secondary production of size group L_net, with *C. finmarchicus* CV and AF contributing most to copepod secondary production in the southern parts of the transect (Stns M4 and M3), while *C. glacialis* and *C. hyperboreus* CV and AF contributed most in the northern parts (Stns M2 and M1).

4. DISCUSSION

While the Barents Sea is often considered to be a highly productive area, few studies have addressed the quantity and pattern of mesozooplankton secondary production in this area, despite the undeniable importance of mesozooplankton for the energy transfer in marine food webs. In this study, we investigated mesozooplankton and specifically copepod secondary production with high taxonomic and spatial resolution across the Barents Sea polar front in summer, by utilizing a combination of traditional net sampling and optical plankton imaging techniques. The LOPC was a useful tool for detecting patches of high mesozooplankton secondary production and provided valuable information about the extent, depth range and size distribution of the productive mesozooplankton layer. We found a distinct pattern of secondary production across the front, where total mesozooplankton secondary production (including copepod and non-copepod groups) was mainly concentrated in the upper 50 m water column and was highest in the Atlantic region south of the polar front. Copepods and their nauplii were the main component of the mesozooplankton community across the whole study region. In the Atlantic region, however, high abundance and biomass of other mesozooplankton groups, such as Rotifera, Chaetognatha, and Appendicularia, were observed. Copepod secondary production was lowest in in the Atlantic region and increased towards the Arctic region. Different copepod species and life stages played an important role for copepod secondary production in distinct regions of the polar front and were influenced by varying environmental and biological factors across the study area. For our copepod secondary production estimates, we decided to use the model of Hirst & Lampitt (1998) (considering temperature and copepod body weight), because we believe that it best approximates the growth of copepods under food saturation and low temperatures found in the study area.

4.1. Is the Barents Sea polar front an area of increased secondary production?

The Barents Sea is an Arctic shelf sea known for its high productivity and contrasting production regimes in its northern parts, influenced by cold, Arctic water and its southern parts, influenced by warm, Atlantic water (Sakshaug et al. 2009). Secondary production in the study region is influenced by the advection of zooplankton biomass with the Norwegian Atlantic Current (Wassmann et al. 2006), by the interplay of sea-ice retreat, the meltwater front and the phytoplankton bloom status (Wassmann et al. 1999), and by predation pressure (Langbehn et al. 2023). Total mesozooplankton secondary production at the end of June was highest in the Atlantic region south of the Barents Sea polar front (Fig. 5), which is in accordance with results from a previous study conducted with the LOPC in the same area in summer (Basedow et al. 2014). The secondary production values of the mesozooplankton community reported by Basedow et al. (2014) for the Atlantic region in August were substantially higher than the ones reported in the present study for the end of June. During the study of Basedow et al. (2014), a late summer bloom was occurring in the Atlantic region, indicated by a maximum surface chl *a* concentration of 2.8 mg m^{-3}, which might have promoted increased levels of secondary production in the region.

Copepod secondary production during our study, on the other hand, was lowest in the Atlantic region and increased towards the north, reaching a maximum in the northern part of the polar front (Stn M2, Fig. 7). In the eastern Barents Sea, highest copepod secondary production was also recorded in the Barents Sea polar front in summer (Dvoretsky & Dvoretsky 2024a). In the present study, total copepod secondary production was 2.8 mg C m^{-3} d^{-1} in the Atlantic region, 3.15–3.65 mg C m^{-3} d^{-1} across the polar front and 3.49 mg C m^{-3} d^{-1} in the Arctic region (upper 50 m, growth rate model of Hirst & Lampitt 1998), and higher than previously reported for the Barents Sea (Dvoretsky & Dvoretsky 2009, 2012, 2024a,b; Table 5). Copepod secondary production reported in the present study was also higher than production in other Arctic regions in summer months, such as in Disko Bay, western Greenland (Madsen et al. 2001, 2008; Table 5), the Bering Sea (Kimmel et al. 2018; Table 5) and the Gulf of Alaska (Coyle & Pinchuk 2003; Table 5). Secondary production reported for the White Sea (Primakov & Berger 2007; Table 5) and Chukchi Sea (Sastri et al. 2012; Table 5) was higher, but here different methodology was used, namely the physiological method and the chitobiase essay, respectively, and the production values are therefore not directly comparable. We conclude that the north-western Barents Sea is generally a very productive region in summer, but the polar front itself is not an area with increased total mesozooplankton secondary production, but rather increased copepod secondary production.

There are at least 2 possible reasons for the high total mesozooplankton production combined with low copepod production in the Atlantic region, namely advection of zooplankton biomass, resulting in high predation risk for large copepods, and differences in food availability across the polar front. Firstly, zooplankton abundance and biomass in the Atlantic part of the Barents Sea are highest in summer and strongly influenced by the advection of organisms from the Norwegian Sea into the Barents Sea (Wold et al. 2023). During this period, the contribution of non-copepod groups to total zooplankton abundance and biomass can be high (Wold et al. 2023), which was also the case in our study. Therefore, boreal species on the one hand can seasonally contribute to local zooplankton secondary production in Barents Sea and on the other hand can impact copepod secondary production through increased predation. Specific mortality rates of *Calanus* spp. residing in the surface layers in the Atlantic region in summer were estimated at −0.35 d^{-1} and resulted from high predation pressure by hydrozoans and chaetognaths, increased natural mortality and high migration of *Calanus* spp. to deeper water layers (Basedow et al. 2014). In shallower, ice-free habitats, visually foraging fish can exert a significant predation pressure on copepods. As a result, abundance of large copepods is higher where sea-ice shades the water or the water column is deeper, allowing for an escape from visual predators through vertical migration (Langbehn et al. 2023). The pattern of lower copepod secondary production the Atlantic

Table 5. Secondary production estimates from other Arctic regions during comparable seasons. Production values of Dvoretsky & Dvoretsky (2009, 2012, 2024a,b) were recalculated from dry mass, according to their conversion factor: 1 mg dry mass = 0.4 mg carbon mass. Production values of Coyle & Pinchuk (2003) were recalculated from mg C m^{-2} d^{-1} to mg C m^{-3} d^{-1}, based on their sampling depth of 100 m. LOPC: laser optical plankton counter

Region	Season	Investigated mesozooplankton fraction	Production (mg C m^{-3} d^{-1})	Method	Source
Barents Sea, polar front	June	Total mesozooplankton Total copepods Small copepods Large copepods	0.69 2.80–3.65 0.00–2.93 0.32–1	LOPC sampling and model D Traditional net sampling & model B	This study
Barents Sea, polar front	August	Total copepods	0.32–1	Hirst et al. (2003)	Dvoretsky & Dvoretsky (2024a)
NE Barents Sea	June–July	Total mesozooplankton	0.2–0.93	Hirst et al. (2003)	Dvoretsky & Dvoretsky (2024b)
S Barents Sea	July–August	Total copepods	0.04–0.44	Model B	Dvoretsky & Dvoretsky (2012)
SE Barents Sea	August	Total copepods	0.4–2	Model B	Dvoretsky & Dvoretsky (2009)
White Sea	June	Total copepods	~6.5	Physiological method	Primakov & Berger (2007)
Disko Bay, Greenland	June	Small copepods Large copepods (*Calanus* spp.)	0.08–0.16 0.5–2.2	Model A	Madsen et al. (2001, 2008)
Gulf of Alaska	June	Total copepods	0.3–0.4	Model B	Coyle & Pinchuk (2003)
Chukchi Sea	July	Planktonic crustaceans	0.4–4.1	Chitobiase method	Sastri et al. (2012)
Bering Sea	July	Small copepods Large copepods	0.3–1.4 0.1–0.28	Combination of different growth rate equations	Kimmel et al. (2018)

region, observed in this study, can be explained by a combination of increased predation risk in the Atlantic region and higher food availability in other areas. At the time of our study, the microbial community was latitudinally structured and displayed a post-bloom state in the Atlantic region (Wiedmann et al. 2014), which probably promoted the growth of small copepods. Across the polar front, the community was in an earlier seasonal developmental state and still resembled a late bloom stage in the marginal ice zone in the Arctic region (Wiedmann et al. 2014), where reproduction of *Calanus* spp. was high. The interplay of the microbial food web and copepod secondary production is discussed in more detail in Section 4.3.

Another aspect that likely influenced the observed trends in copepod secondary production is the sampling design. Zooplankton distribution is very patchy and influenced by local eddies, meanders and biological cues (Sakshaug et al. 2009, Basedow et al. 2014, Trudnowska et al. 2016), which can result in the formation of thin patches that can stretch horizontally over several kilometres (Trudnowska et al. 2016). Similar patches were observed in the present study through the use of the LOPC (size groups M and L, Fig. 4). When studying zooplankton trends with traditional net sampling, one of the main challenges is to achieve the appropriate spatial resolution, as patchiness can lead to high sampling variance. In addition to patchiness, net avoidance and extrusion of zooplankton and the estimation of filtered volume are aspects that add complexity to an accurate assessment of zooplankton trends (Runge & Roff 2000). Our sampling design consisted of a single vertical net haul at only 4 stations, raising the possibility that zooplankton patches might have been missed using the traditional net sampling approach. Because of the high contribution of mesozooplankton groups other than copepods in the Atlantic region (Fig. 6A,C,D,F), we likely excluded a large part of total mesozooplankton secondary production with the traditional net sampling in this region, as we focused on copepods only. In the frontal and Arctic waters, however, other mesozooplankton groups were less abundant, and copepod secondary production therefore likely constituted most of the total mesozooplankton secondary production in these areas.

4.2. Particle size distribution across the polar front inferred from LOPC sampling

The polar front is an important feature in structuring the distribution pattern of different mesozooplankton species. Secondary production of small mesozooplankton (size group S, 0.25–0.6 mm ESD) was high in the Atlantic region south of the polar front, while secondary production of medium- (M, 0.6–1.5 mm ESD) and large-sized mesozooplankton (L, 1.5–4 mm ESD) was patchily distributed across the study area and associated with areas of high chl *a* concentration (Fig. 5). These findings are consistent with the results of a previous LOPC study conducted at the polar front in the area of the West Spitzbergen Shelf (Trudnowska et al. 2016). Those authors found that small mesozooplankton, e.g. *Oithona* spp., *Triconia* spp., *Acartia* spp. and copepod nauplii, frequently accumulate in areas with density discontinuities, such as horizontal density gradients associated with the meeting of hydrographically different water masses (Trudnowska et al. 2016). The formation of a meltwater layer in the upper 20 m of the water column, present across the polar front at the time of our study, likely led to the development of a horizontal density gradient that facilitated the observed differences in the distribution of the small size group (Fig. 4). Patches of medium- and large-sized mesozooplankton, such as *Calanus* spp., were associated with areas of high chl *a* concentration (Fig. 4). This trend was also observed by Trudnowska et al. (2016) at the polar front and can likely be explained by the high food availability and active aggregation of grazers. During our study, most of the secondary production measured by the LOPC was located in the upper 50 m water column. Chl *a* is one of the factors included in the growth rate model of Zhou et al. (2010) that was used to estimate production, and the measured chl *a* concentrations were low at a depth deeper than 50 m. As a consequence, the secondary production values were low in this depth range. This might lead to an underestimation of the production of small-sized copepods, as their production is not limited by chl *a* availability (Hirst & Bunker 2003). Therefore, production estimates of size group S might be underestimated to a depth of 100 m, where *Oithona similis*, the main representative of small-sized copepods in Arctic waters, is usually found (Lischka & Hagen 2005).

The LOPC counts all particles within a certain size range that are present in the water column and consequently includes not only zooplankton, but also other particles such as faecal pellets, marine snow and inorganic suspended material (Schultes & Lopes 2009). The contribution of such particles to total counts can be substantial, as observed during periods of high glacial runoff (Trudnowska et al. 2014) or high river runoff (Schultes & Lopes 2009). According to the indices developed by Espinasse et al. (2018), it can be said with high certainty that particles of size group S, observed in non-stratified AW during our study, were zooplankton, while an unknown fraction of aggregates contributed to LOPC counts in stratified waters of the polar front and the Arctic region. A simultaneous study by Wiedmann et al. (2014) found that the particulate organic carbon (POC) flux in Arctic waters was dominated by larger particles (0.5–2.8 mm ESD), which were most likely diatom aggregates and presumably contributed to the LOPC counts of size group S during our study. In Atlantic waters, a high POC flux of small particles (0.05–1.00 mm ESD) with a POC:volume ratio matching copepod faecal pellets was observed (Wiedmann et al. 2014). However, in all likelihood, these faecal pellets did not contribute to the small particles counted by the LOPC in the Atlantic region during our study, as they are fragile and therefore broken up by the MVP during towing.

4.3. Copepod secondary production related to community composition inferred from WP-2 net and GoFlo bottle sampling

The variations in the contribution of different copepod communities to total copepod secondary production can be related to temperature and food availability across the polar front, as these factors are the key drivers of secondary production (Kiørboe & Sabatini 1995). Secondary production of large, broadcast-spawning copepods is primarily controlled by food availability, while the productivity of small, sac-spawning copepods is mainly controlled by temperature (Kiørboe & Sabatini 1995). Generally, developmental rates (time from egg to adult) of broadcast-spawning and egg-carrying copepods are the same, but broadcast spawners exhibit higher growth rates (increase in body weight over time), higher weight-specific fecundities (reproductive output relative to female body weight) and higher egg-production rates (number of eggs produced per day) than egg-carrying copepods (Kiørboe & Sabatini 1995). Under non-limiting food conditions, the production of broadcast-spawning copepods can therefore be considerably higher than that of egg-carrying copepods (Kiørboe & Sabatini 1995). From our observations, we suggest that during a (late) phytoplankton bloom scenario in Arctic waters, *Calanus* spp. can outcompete small-sized copepods due to the high food availability and the low temperatures that restrict sac-spawner reproduction. In a post-bloom scenario in warm Atlantic waters, small-sized copepods play an important role in secondary production, as they profit from the warmer water temperatures (Barth-Jensen et al. 2020).

The Atlantic region (Stn M4) was in a nutrient-depleted post-bloom stage at the time of our study (Wiedmann et al. 2014), and a grazer community consisting mainly of small-sized egg-carrying copepod species and the large copepod *Calanus finmarchicus* was associated with the prevailing microbial food web (Franzè & Lavrentyev 2017). We observed high reproduction of *Oithona* spp. in Atlantic waters, which can be explained by the higher water temperatures of ca. 5°C in this region. Reproduction of *Oithona* spp. is positively correlated with increasing temperature, and potential hatching rates at the Atlantic station (M4) were at least 7 times higher than at the Arctic station (M1), when applying the hatching rate (HR) equation of Barth-Jensen et al. (2020) ($HR = 0.018T + 0.013$, assuming a temperature of 0°C at Stn M1 to avoid negative hatching rates). Small copepods live close to food saturation due to their size (Kiørboe & Sabatini 1995) and can consume a large range of prey, including ciliates, dinoflagellates, phytoplankton and faecal material (Gallienne & Robins 2001), which made their reproduction uncoupled from the phytoplankton bloom that was observed in Arctic waters. Productivity of large, broadcast-spawning copepods, e.g. *Calanus* spp., is mainly governed by food availability, and the effect is more pronounced on adult weight-specific fecundity than on juvenile growth (Kiørboe & Sabatini 1995). Assuming a gross growth efficiency (growth ingestion^{-1}) of 0.3 for metazoan zooplankton (Ikeda & Motoda 1978), the ingestion rate of the *Calanus* spp. (CI–CVI) community can be assessed. In the Atlantic region (Stn M4), 7.8 mg C m^{-3} d^{-1} was needed to sustain *Calanus* spp. (CI–CVI) secondary production. No primary production was measured in this study, but chl *a* standing stock and microzooplankton production can indicate potential food limitation. Microzooplankton biomass was 5–8 times higher in the Atlantic region compared to the Arctic region and the polar front (Table S3; Franzè & Lavrentyev 2017). The estimated microzooplankton production in the Atlantic region was 17.7 mg C m^{-3} d^{-1} (Franzè & Lavrentyev 2017) and the chl *a* standing stock was 41 mg C m^{-3} (C:chl *a* ratio = 50, Basedow et al. 2014). This relatively low standing stock might indicate that chl *a* was heavily grazed upon by the zooplankton community. The high secondary production of *C. finmarchicus* copepodites in the Atlantic region can likely be attributed to additional grazing on microzooplankton, as has previously been observed north of Svalbard (Svensen et al. 2019). *Calanus* spp. feed efficiently on diatoms but show a more varied diet outside of the spring bloom that can include a variety of proto- and microzooplankton (Cleary et al. 2017).

The polar front stations were characterized by a post-bloom phytoplankton community (Wiedmann et al. 2014). Low numbers of calanoid nauplii indicated that the mesozooplankton community was likely in a more mature state, meaning calanoid reproduction had already happened some weeks earlier. This is further affirmed by the presence of high numbers of young-stage calanoid copepodites, which are assumed to be the offspring of a late-spawning G_0 population (Arashkevich et al. 2002). The required food concentration to sustain *Calanus* spp. (CI–CVI) secondary production across the polar front was 6.9–9.8 mg C m^{-3} d^{-1}. Juvenile calanoid copepods achieve half their potential maximum growth at a chl *a* concentration of 0.6 mg m^{-3}, which is one order of magnitude lower than the food concentration adults need (Hirst & Bunker 2003). Therefore, the observed low chl *a* standing stock of 0.55–0.9 mg m^{-3} (27.5–45 mg C m^{-3}) in combination with 1.7–2.3 mg C m^{-3} d^{-1} microzooplankton production might still be sufficient to fuel copepodite growth across the front.

The Arctic region (Stn M1) was in a late peak bloom stage, with loose drift-ice still present and a phytoplankton community mainly consisting of large diatom cells (mostly of the genera *Thalassiosira* and *Chaetoceros*) (Wiedmann et al. 2014). We observed a 'classical grazer food chain', typically linked to the phytoplankton spring bloom, where large-celled diatoms are consumed by copepods of the genus *Calanus*. The contribution of calanoid nauplii to the total copepod secondary production was highest in the Arctic region, indicating local reproduction of *Calanus*, most likely of *C. glacialis*, in response to the bloom. The required food concentration to sustain *Calanus* spp. (CI–CVI) secondary production in the Arctic region was 3.0 mg C m^{-3} d^{-1}. Naupliar stages I and II of both *C. finmarchicus* and *C. glacialis* do not feed (Breteler et al. 1982, Daase et al. 2011), and the growth of the other naupliar stages is less strongly governed by food availability than adult fecundity is (Hirst & Bunker 2003). Therefore, the chl *a* standing stock of 98 mg C m^{-3} and the estimated microzooplankton production of about 2 mg C m^{-3} d^{-1} (Franzè & Lavrentyev 2017) might be sufficient to fuel copepod secondary production in the Arctic region. Because copepod nauplii show on average 2 times faster developmental rates than copepodites (Kiørboe & Sabatini 1995), their contribution to overall secondary production can be substantial. Indeed, we observed that calanoid nauplii contributed 74% to total copepod secondary production in Arctic waters. To our knowledge, this study is one of the first to highlight the importance of nauplii for secondary production at the Barents Sea polar front.

5. CONCLUSIONS

The north-western Barents Sea is characterized by high secondary production during the summer, exceeding that of other Arctic regions. Contrary to the commonly held belief that oceanic fronts universally enhance secondary production, our observations present a more nuanced perspective for the Barents Sea polar front. While copepod secondary production was highest in the northern section of the polar front and in the Arctic region north of it, the total mesozooplankton secondary production was highest in the Atlantic region located to the south of the polar front. Two main factors influenced secondary production in the study region. Firstly, the advection of mesozooplankton biomass with the Norwegian Atlantic Current played a pivotal role. Through this process, boreal mesozooplankton locally contributed to the mesozooplankton secondary production in the Atlantic region and likely exerted significant predation pressure on large copepods, resulting in decreased copepod secondary production in this region. Secondly, the interplay between the sea-ice retreat, the meltwater front and the phytoplankton bloom status emerged as another important factor impacting secondary production. These complex interactions resulted in variations in water temperature and food availability across the polar front and particularly impacted copepod secondary production dynamics throughout the study region. In the Atlantic region, young developmental stages (CI–CIV) of *Calanus* spp. contributed most to copepod secondary production. This area also stood out as the only region where small-sized copepod species contributed noticeably to copepod secondary production, due to higher water temperatures that favoured their reproduction. In the Arctic region, on the other hand, calanoid nauplii and older developmental stages (CV–CVI) contributed most to copepod secondary production. During the (late) phytoplankton bloom scenario that was observed in the Arctic region, *Calanus* spp. likely outcompeted small-sized copepods because of the high food availability and low water temperatures that restricted sac-spawner reproduction.

We demonstrate how estimates of copepod secondary production vary considerably with the chosen method to estimate copepod growth rates. However, the trends in the contribution of the different size classes to total copepod production were the same for all copepod growth rate models. During periods with high chl *a* concentrations, we recommend estimating copepod secondary production in the epipelagic layer of Arctic areas with the model of Hirst & Lampitt (1998), as it gives approximations of copepod growth rates at specific temperatures under food saturation. In periods with very low chl *a* concentrations, when large, predominantly herbivorous copepods are food limited, we recommend using a model that considers chl *a* as a food proxy, such as the model of Hirst & Bunker (2003). Secondary production of small copepods can be estimated year-round with the model of Hirst & Lampitt (1998), as growth of these copepods is more temperature- than food-limited. Combining high spatial- and taxonomic-resolution sampling using an optical plankton counter and traditional net sampling was a good approach to estimate secondary production across the Barents Sea polar front, and we recommend employing a combination of both sampling methods for future studies in high-latitude areas.

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Paper II

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Response of the copepod community to interannual differences in sea-ice cover and water masses in the northern Barents Sea

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Response of the copepod community to interannual differences in sea-ice cover and water masses in the northern Barents Sea

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The reduction of Arctic summer sea ice due to climate change can lead to increased primary production in parts of the Barents Sea if sufficient nutrients are available. Changes in the timing and magnitude of primary production may have cascading consequences for the zooplankton community and ultimately for higher trophic levels. In Arctic food webs, both small and large copepods are commonly present, but may have different life history strategies and hence different responses to environmental change. We investigated how contrasting summer sea-ice cover and water masses in the northern Barents Sea influenced the copepod community composition and secondary production of small and large copepods along a transect from 76°N to 83°N in August 2018 and August 2019. Bulk abundance, biomass, and secondary production of the total copepod community did not differ significantly between the two years. There were however significant spatial differences in the copepod community composition and production, with declining copepod abundance from Atlantic to Arctic waters and the highest copepod biomass and production on the Barents Sea shelf. The boreal *Calanus finmarchicus* showed higher abundance, biomass, and secondary production in the year with less sea-ice cover and at locations with a clear Atlantic water signal. Significant differences in the copepod community between areas in the two years could be attributed to interannual differences in sea-ice cover and Atlantic water inflow. Small copepods contributed more to secondary production in areas with no or little sea ice and their production was positively correlated to water temperature and ciliate abundance. Large copepods contributed more to secondary production in areas with extensive sea ice and their production was positively correlated with chlorophyll *a* concentration. Our results show how pelagic communities might function in a future ice-free Barents Sea, in which the main component of the communities are smaller-sized copepod species (including smaller-sized *Calanus* and small copepods), and the secondary production they generate is available in energetically less resource-rich portions.

KEYWORDS

sea-ice cover, copepod community composition, secondary production, northern Barents Sea, interannual variability, sea-ice melt

1 Introduction

One of the most noticeable consequences of ongoing climate change is the decline of Arctic summer sea ice (Pörtner et al., 2019). Sea ice is melting earlier and forming later in the season, resulting in a prolonged open water period with increased light transmission to the upper ocean (Wassmann and Reigstad, 2011). The seasonally ice-covered Barents Sea is experiencing the highest rates of warming amongst all regions of the Arctic (Isaksen et al., 2022) and it is projected to be ice-free during winter beyond the year 2061 (Onarheim and Årthun, 2017). These physical alterations have major impacts on biological processes in the Barents Sea, as sea ice constitutes a unique habitat for sea ice algae and further controls light availability and mixing in the upper ocean, which regulates the onset of phytoplankton blooms (Sakshaug et al., 1991). The blooms typically follow the northwards retreat of sea ice in spring and summer, as the melting ice creates the stratified surface layer and increased light transmittance that are necessary for bloom formation. Once surface nitrate and silicate are depleted, the phytoplankton community changes from a diatom-dominated system to one dominated by flagellates and ciliates (Rat'kova and Wassmann, 2002). Timing and quality of the bloom are critical for the biomass and reproductive success of secondary producers.

Associated with the diatom-dominated system are large, lipid-rich copepods of the genus *Calanus* that have developed a reproductive cycle that is tightly linked to the ice algae and spring phytoplankton blooms (Falk-Petersen et al., 2009). The Arctic species *Calanus hyperboreus* reproduces during winter, entirely based on internal lipid reserves that were build up during the previous growth season (Falk-Petersen et al., 2009). *C. glacialis* on the other hand usually spawns just before or during the ice algae bloom (Søreide et al., 2010), while the boreal species *C. finmarchicus* reproduces during the open water spring bloom (Hirche, 1996). Offspring of *C. hyperboreus* and *C. glacialis* are dependent on the phytoplankton spring bloom for growth and accumulation of energy reserves that are needed for diapause (Falk-Petersen et al., 2009; Søreide et al., 2010). Nauplii and young copepodids (CI-III) of *C. finmarchicus* feed during the spring bloom, while the development of older copepodids (CIV-V) is fueled by grazing on microzooplankton during the summer (Svensen et al., 2019). In late summer, *Calanus* spp. that have acquired enough lipids for diapause descend into deeper water layers to hibernate at depth until the next spring bloom (Falk-Petersen et al., 2009). While *Calanus* spp. often dominate the mesozooplankton community in terms of biomass, smaller copepods (adult body size <2 mm; Svensen et al., 2019), such as *Oithona similis*, usually dominate in terms of numbers (Gallienne and Robins, 2001; Madsen et al., 2008). These copepods are closely associated with the microbial food web occurring in late summer and autumn, as they are omnivores (Lischka and Hagen, 2007). In contrast to *Calanus* spp., they reproduce year-round, with greatest abundance of eggs and nauplii occurring during spring and summer (Ashjian et al., 2003; Madsen et al., 2008).

The reduction of summer sea-ice cover due to climate change can lead to increased primary production in parts of the Barents Sea, depending on the prevalent nutrient and stratification regimes (Randelhoff et al., 2020). With a retreat of the seasonal ice zone northwards, regions previously covered by ice will likely experience a prolonged phytoplankton growing season and higher primary production, if sufficient nutrients are available. The southern edge of the seasonal ice zone is expected to become less productive due to increased thermal stratification and the resulting decrease in nutrients supplied to the surface layers (Wassmann and Reigstad, 2011). These changes will likely affect the zooplankton community by altering the composition of the grazers. In the Bering Sea, large-sized *Calanus* spp. were found to be more abundant during cold periods with extensive sea-ice cover (Coyle and Pinchuk, 2002; Hunt et al., 2011; Stabeno et al., 2012; Eisner et al., 2014; Kimmel et al., 2018, Kimmel et al., 2023), while small copepods (e.g. *Oithona* spp. and *Pseudocalanus* spp.) were more abundant during warm periods with less sea-ice cover (Stabeno et al., 2012; Kimmel et al., 2018, Kimmel et al., 2023). Similar observations have been made in Svalbard fjords and the northern Barents Sea, where higher abundance of small copepods has been linked to warmer periods (Balazy et al., 2018) and the abundance of *Calanus* spp. was influenced by Atlantic water inflow and sea-ice cover (Dalpadado et al., 2003; Daase and Eiane, 2007; Blachowiak-Samolyk et al., 2008; Dalpadado et al., 2012; Stige et al., 2019).

Secondary production is key in understanding how climate related changes, such as a reduction of sea ice, may impact the transfer of energy in Arctic marine food webs. Secondary production refers to the biomass produced by consumers, such as copepods, in a given unit of time (e.g., mg C m^{-2} d^{-1}). The Barents Sea is a highly productive fishing ground and *Calanus* spp. are a crucial food source for many small and juvenile planktivorous fish such as the Barents Sea capelin (*Mallotus villosus*), Atlantic herring (*Clupea harengus*) and polar cod (*Boreogadus saida*) (Hassel et al., 1991; Huse and Toresen, 1996; Bouchard et al., 2017). Small copepods, such as *O. similis* and *Pseudocalanus* spp. are food for fish larvae and other larger zooplankton, such as krill, amphipods, chaetognaths, ctenophores, and hydrozoans (Turner, 2004). Eggs and nauplii of both small and large copepods form a substantial part of the diet of the early larval stages of polar cod. Here, small copepods are especially important to polar cod larvae hatching during the winter months, when other food sources are scarce (Geoffroy and Priou, 2020). In the Bering Sea, sea-ice concentration was found to impact secondary production of *Calanus* spp., which was low during warm periods with less sea-ice cover (Kimmel et al., 2018, Kimmel et al., 2023). In the Barents Sea previous research on secondary production has mainly focused on the southern regions close to the polar front (Basedow et al., 2014; Dvoretsky and Dvoretsky, 2024a) and the eastern Barents Sea (Dvoretsky and Dvoretsky, 2009; Dvoretsky and Dvoretsky, 2024b) and primarily on large *Calanus* spp. (Slagstad et al., 2011). Gaining insights into the effects of sea-ice reduction on copepod secondary production in the Barents Sea is of great social and economic significance, especially since interannual sea-ice concentrations in the northern Barents Sea are highly variable due to climate change (Efstathiou et al., 2022).

In the present study, we evaluate how a reduction in sea-ice cover influenced the copepod community composition and their secondary production in the upper 100 m of the northern Barents Sea. We further examined the relationship between copepod secondary production and environmental and biological drivers, such as hydrography, protist community composition and bacterial and primary production. Zooplankton samples were collected in August 2018, a year with reduced sea-ice cover, and in August 2019, a year with extensive sea-ice cover along a transect spanning 76-83° N. We address the following research questions through direct hypothesis testing: Did differences in sea-ice cover between the two years (I) affect the total copepod secondary production and (II) change the contribution of different species to the total copepod secondary production? Additionally, we explore whether patterns in community composition or secondary production correlated with other environmental or biological factors through multivariate descriptive analyses.

We expect the total copepod secondary production to be higher in the summer with reduced sea-ice cover (2018) due to an extended period of primary production. However, this would likely be accompanied by a change in the copepod community composition, because diatom blooms terminate earlier in a year with reduced sea-ice cover and the community of primary producers becomes dominated by flagellates and ciliates earlier in the season, which favors the growth of small copepods (e.g. *O. similis*) (Gallienne and Robins, 2001). We therefore hypothesize that small copepods will contribute more to the total copepod secondary production during the summer with reduced sea-ice cover (2018), whereas large copepods (e.g. *Calanus* spp.) will contribute more when the summer sea-ice cover is more extensive (2019). Furthermore, we expect the quantity and relative contribution of small copepod production to total copepod production to be higher in habitats with higher water temperatures and a higher abundance of ciliates and dinoflagellates. Conversely, in habitats characterized by colder water temperatures and higher concentrations of chlorophyll *a*, which are typically associated with increased phytoplankton biomass and greater diatom abundance, we expect the production of large *Calanus* spp. and their contribution to total copepod production to be higher.

2 Material and methods

2.1 Study area

Samples and measurements were collected in the northern Barents Sea as part of The Nansen Legacy project, during cruises of RV *Kronprins Haakon* in August 2018 (06.-23.08.2018) and August 2019 (05.-27.08.2019). The study sections, where stations were located, covered an environmental gradient from Atlantic to Arctic waters (76°-83° N, Table 1; Figures 1A, C). Samples were collected at 8 stations in 2018 and 6 stations in 2019 and were categorized according to their locations. Station P1 was in Atlantic waters south of the polar front and is seen as a representative of 'Atlantic' environmental conditions. Stations P2-P5 were located north of the polar front on the Barents Sea shelf and are seen as representing 'Barents Sea shelf' conditions and stations P7, PICE1 and SICE2-3 were located in the deeper Arctic Ocean basin, representing 'Arctic Ocean basin' conditions. Stations P1-P5 were visited in both years, and among these stations P4 and P5 were in ice-free waters at the time of sampling in 2018 and in ice-covered waters during sampling in 2019 (Table 1). PICE1 and SICE2-3, only visited in 2018, were also ice covered, as well as P7, which was only visited in 2019.

2.2 Zooplankton sampling

Zooplankton was collected with stratified net hauls using two separate MultiNet® Type Midi (HYDRO-BIOS Apparatebau GmbH, net opening 0.25 m^2), one with 64 µm and one with 180 µm mesh size net bags. The depth intervals for the shallow shelf stations were: bottom-200, 200-100, 100-50, 50-20 and 20-0 m. Where bottom depth exceeded 600 m, zooplankton was collected from the following depth strata: bottom-600, 600-200, 200-50, 50-20, 20-0 m. The 180 µm net was hauled with a speed of 0.5 m s^{-1} and the 64 µm with a speed of 0.3 m s^{-1} to warrant optimal water filtering. All samples were processed immediately upon retrieval of the nets. The samples were concentrated on 64 µm and 180 µm sieves respectively, gently flushed with filtered sea water, and stored in 125 mL bottles with 4% formaldehyde-seawater solution free from acid. Due to unpredictable failures of water flow meters installed in the plankton nets used, the volume of filtered water was calculated based on a regression equation describing the

TABLE 1 Location and bottom depth at the stations where zooplankton samples were collected in August 2018 and August 2019.

2018 station #	Date of sampling	Latitude	Longitude	Bottom depth (m)	Ice covered on day of sampling	Days since ice retreat (< 15% sea ice concentration)	comments	2019 station #	Date of sampling	Latitude	Longitude	Bottom depth (m)	Ice covered on day of sampling	Days since ice retreat (< 15% sea ice concentration)	comments
P1	Aug 09	76.00	31.23	325	no	219	always ice free	P1	Aug 08	76.00	31.22	325	no	92	11 days of loose drift ice in May
P2	Aug 10	77.50	34.00	192	no	88		P2	Aug 12	77.50	33.99	186	no	43	
P3	Aug 12	78.75	34.00	305	no	83		P3	Aug 13	78.75	34.00	307	no	45	
P4	Aug 14	79.75	34.00	335	no	73		P4	Aug 14	79.69	34.23	353	yes	32	loose drift ice 6 days before and 2 days after sampling
P5	Aug 15	80.50	34.00	163	no	79		P5	Aug 15	80.50	33.99	163	yes	0	ice covered for another 16 days
PICE1	Aug 17	83.35	31.58	3930	yes	0	always ice covered								
SICE2	Aug 19	83.34	29.30	3920	yes	0	always ice covered								
SICE3	Aug 20	83.23	25.87	3911	yes	0	always ice covered								
								P7	Aug 21	81.93	29.14	3300	yes	0	always ice covered

The presence of ice cover (yes/no) and the number of days that have passed since the ice retreated from each station are indicated.

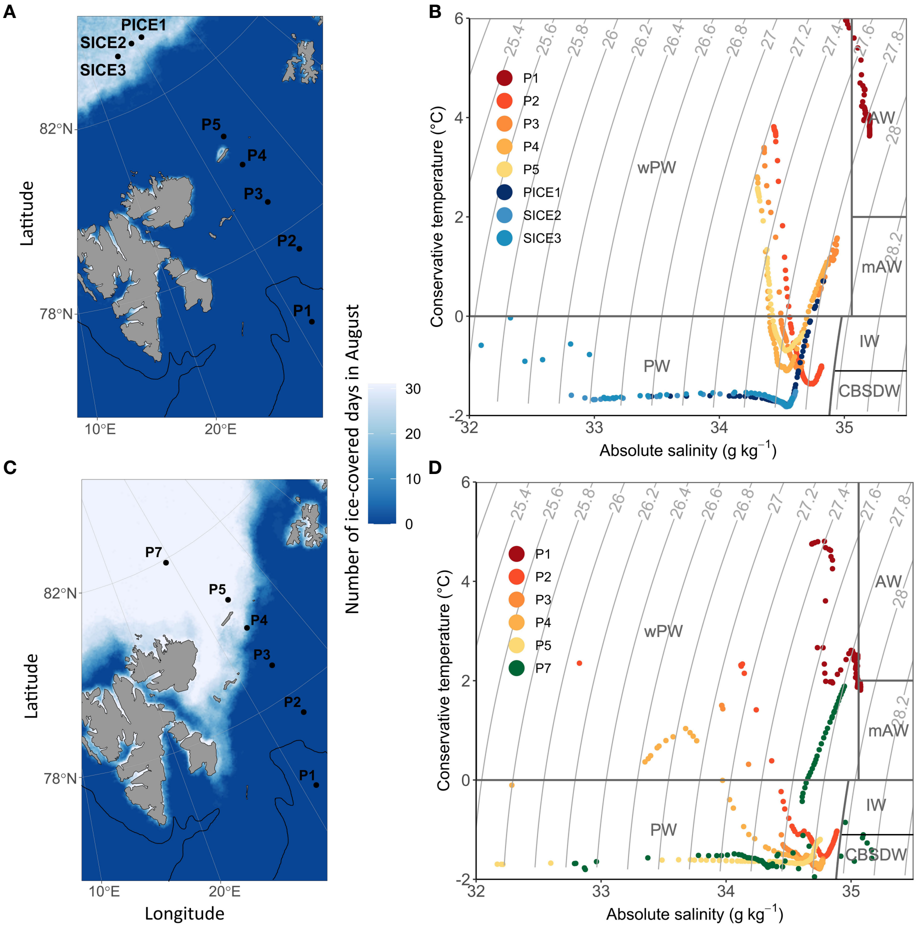

FIGURE 1
Location of the sampling stations and sea-ice cover during the sampling period (indicated as number of ice-covered days during August) in 2018 **(A)** and 2019 **(C)**. The approximate location of the polar front based on the 200 m isobath is indicated with a black line. During the sampling campaign in 2018, sea ice was only present at stations PICE1 and SICE2-3 in the Arctic Ocean basin. During the 2019 sampling campaign, sea ice was present at P4, P5 and P7. **(B)** shows a t-s-plot of water masses in 2018 and **(D)** in 2019 (PW, Polar Water; IW, Intermediate Water; CBSDW, Cold Barents Sea Dense Water; wPW, warm Polar Water; AW, Atlantic Water; mAW, modified Atlantic Water, following definitions by Sundfjord et al., 2020).

relationship between the volume of water filtered through the net and depth strata:

$$\text{Volume filtered } (m^3) = -1.2682 + 0,3298 * (\text{lower layer depth } [m] - \text{upper layer depth } [m]) \; (N = 537, \; R2 = 0.789, \; p = 0.000)\,.$$

The equation is based on a data set consisting of numerous zooplankton collections using MultiNet plankton nets conducted in the Barents Sea area, e.g. from projects 'On Thin Ice', 'Cabanera', 'MariClim'. This model equation is valid for depth strata ranging from 20 m to 400 m. For water layers <20 m, the volume of filtered water was calculated based on the relationship: Volume filtered (m^3) = net opening area * (lower layer depth [m] - upper layer depth [m]), assuming the filtration efficiency declared by the manufacturer (in the range of 90%).

Zooplankton samples were analyzed under an Olympus SZX7 dissecting microscope (OM Digital Solutions GmbH) equipped with an ocular micrometer following methods described in Postel et al. (2000) and Kwasniewski et al. (2010). In the first step, the zooplankton sample was filtered from the preservative solution of formaldehyde, suspended in a beaker with fresh water and then all large zooplankton (total length >5 mm) were removed, identified, and counted in their entirety. Smaller zooplankton (total size <5 mm) were identified and counted from sub-samples taken from a fixed sample volume using a macro pipette. In this case, at least five subsamples were analyzed in detail, assuming that the number of organisms identified and counted was not less than 500 individuals. If the number of individuals in 5 subsamples was smaller, further subsamples were taken until at least 500 zooplankton individuals from the smaller than 5 mm fraction were identified and counted. All zooplankton individuals were identified to the lowest possible taxonomic level, also specifying developmental stage (copepodid stage for copepods). The remaining sample was scanned to detect rare species and developmental stages. The species distinction between *Calanus finmarchicus*, *C. glacialis* and younger developmental stages of *C. hyperboreus* was made based on the length of the prosome, using the size classes established in the study by Kwasniewski et al. (2003). This approach likely introduces some bias in our data, as studies using molecular tools have shown a high but regionally variable overlap in prosome lengths of *C. finmarchicus* and *C. glacialis*, which often leads to an underestimation of *C. glacialis* (e.g., Gabrielsen et al., 2012; Choquet et al., 2018). However, as the results of molecular species analysis for our study region are currently not available to us and the vast majority of ecological studies of zooplankton to date, including studies on species distribution patterns, are based on using size classes to distinguish between *Calanus* species (e.g. Unstad and Tande, 1991; Hirche et al., 1994; Basedow et al., 2004; Kosobokova and Hirche, 2009; Kosobokova et al., 2011; Wold et al., 2023), our data should nevertheless provide insights into *Calanus* species distribution in comparison with previous observations. We followed Roura et al. (2018), who defines small copepods as those having adult body size of <2 mm. Consequently, abundance of 'small copepods' was represented by *Acartia longiremis*, *Centropages hamatus*, Harpacticoida spp. indet., *Oithona atlantica*, *O. similis*, *Microcalanus* spp., *Microsetella norvegica*, *Neomormonilla* spp., *Oncaea* spp., *Pseudocalanus* spp., *Scolecithricella minor* and *Triconia borealis*. Abundance of 'large copepods' was represented by Aetideidae, *C. finmarchicus*, *C. glacialis*, *C. hyperboreus*, *Gaetanus tenuispinus*, *Heterorhabdus norvegicus*, *Metridia longa*, *Scaphocalanus brevicornis* and *Paraeuchaeta* spp. The samples from the 64 µm and 180 µm gauze nets were analyzed separately, and the analytical results were then combined. Abundance data of copepod nauplii, all stages of 'small copepods', as well as all early developmental stages (CI-CIII) of 'large copepods', were obtained from the 64 µm net results. Abundance data of older developmental stages (CIV-adult) of 'large copepods' were based on 180 µm net results. Copepod abundance was converted into biomass, based on species and stage-specific carbon mass relationships (Supplementary Table 1). Copepod stage specific carbon mass was obtained from literature if available. For copepod species and life stages for which no published carbon mass was available, a conversion factor of 0.4 (individual dry weight to carbon weight) was used (Peters and Downing, 1984). For further analyses, we only used data on copepod abundance (ind. m^{-2}) and biomass (mg C m^{-2}) integrated for the upper 100 m at individual stations (including three net sampling depth strata: 0-20, 20-50 and 50-100/50-200 m). In the case where samples were taken over a depth range of 50-200 m (P7, PICE1, SICE2, SICE3), the abundance in the 50-100 m depth strata was calculated as one third of the abundance of the 50-200 m depth strata, assuming an even distribution of zooplankton in this layer of water. While this approach might potentially lead to an underestimation of copepod production in these depth strata, a comparison using one third or the total abundance or biomass in the 50-200 m depth layer indicated that it had minimal impact in our study and did not change the main results or conclusions. This is due to the comparatively low abundance and biomass in the deep layers of the Arctic Ocean basin (P7, PICE1, SICE2, SICE3).

2.3 Secondary production calculation

Daily copepod secondary production p (mg C m^{-2} d^{-1}) in the upper 100 m was calculated using the following Equation 1, (Runge and Roff, 2000):

$$p = \sum Bi \times gi \tag{1}$$

Where Bi is copepod stage specific biomass for the upper 100 m (mg C m^{-2}) and gi stage specific growth rate (d^{-1}).

Here, gi was determined for nauplii, copepodids and adults of individual broadcast-spawning and sac-spawning copepod species using the multiple linear regression model of Hirst and Lampitt (1998), taking temperature and body weight into consideration (Table 2; Supplementary Table 1: distinction of broadcast- and sac-spawning copepod species). We chose the Hirst and Lampitt (1998) growth model, as it reflects the physiological performances of copepods at low water temperatures relatively realistically and has been used in previous studies on copepod secondary production in Arctic regions (e.g. Liu and Hopcroft, 2006; Madsen et al., 2008). This global model can be used to calculate growth rates of actively growing copepod populations in the epipelagic layer of polar to tropical regions (Hirst and Lampitt, 1998). The present study focuses solely on the upper 100 m water column, as copepods found in this depth range are assumed to be active. We are aware that some copepods below 100 m will be active and hence contribute to the total copepod production in the ecosystem. Therefore, our production estimates may be considered conservative. An alternative approach would be to estimate production for the entire water column – hence also to include the deeper communities. However, we believe this would significantly overestimate the production estimates. Diapause plays a crucial role in the life cycle of *Calanus* spp., where individuals that have acquired enough lipids descend into deeper water layers in late summer, to hibernate at depth until the next spring bloom (Falk-Petersen et al., 2009). Therefore, including hibernating individuals below 100 m (Ashjian et al., 2003) would overestimate secondary production. The majority of small copepod species, such as *Oithona* spp. and *Pseudocalanus* spp., can be found above a depth of 150 m in summer months in Arctic waters, with highest abundance recorded in the upper 50 m water column (Lischka and Hagen, 2005; Madsen et al., 2008; Darnis and Fortier, 2014). Mesopelagic, omnivorous copepods, such as *Metridia longa* and *Microcalanus* spp., and carnivorous copepods, such as *Paraeuchaeta* spp., are only sporadically found in the upper

TABLE 2 Equations used to calculate stage specific growth rates of sac spawning and broadcast spawning copepods, after Hirst and Lampitt (1998).

sac spawners	nauplii + copepodids	$log_{10}g = -1.4647 + 0.0358[T]$
	adults	$log_{10}g = -1.7726 + 0.0385[T]$
broadcast spawners	nauplii + copepodids	$log_{10}g = 0.0111[T] - 0.2917[log_{10}BW] - 0.6447$
	adults	$log_{10}g = 0.6516 - 0.5244[log_{10}BW]$

100 m (Darnis and Fortier, 2014) and are therefore not the focus of the present study. Furthermore, currently there is a shortage of models that can accurately estimate the growth rates of these kind of copepods (Kobari et al., 2019). We therefore decided to use the first approach of estimating secondary production for the upper 100 m only, with a potential underestimation of production – rather than to include all depth layers and risk an overestimation of the production.

2.4 Supplementary physical and biological data

In addition to sea-ice cover, multiple other biological and environmental factors can influence the copepod community composition and their production, such as water temperature and salinity (e.g. Daase and Eiane, 2007; Trudnowska et al., 2016; Balazy et al., 2018), the protist community composition (e.g. Levinsen et al., 2000; Leu et al., 2011) and primary production (e.g. Svensen et al., 2019). We therefore included data on water column temperature and salinity, chlorophyll *a* concentration, protist abundance, primary production, and bacterial production rates, collected during the same cruises as part of The Nansen Legacy project, in our statistical analyses. Detailed sampling procedures for the environmental and biological properties measured can be found in The Nansen Legacy sampling protocol (The Nansen Legacy, 2020).

2.4.1 Sea-ice concentration

A dataset containing daily sea-ice concentrations for each of the sampling stations in 2018 and 2019 was obtained from the data portal of the Norwegian Polar Institute (Steer and Divine, 2023). Daily sea-ice concentrations were derived from a 6.25 km resolution gridded sea-ice concentration product based on AMSR-E and AMSR2 passive microwave sensors. The satellite derived sea-ice concentration dataset was complemented with local sea-ice concentration from visual bridge-based sea ice observations, conducted following ASSIST Ice Watch protocol during some of the Nansen Legacy cruises to the study area. To visualize the sea-ice cover during the study period, AMSR2 sea-ice concentration data were obtained from the data archive of the University Bremen (Spreen et al., 2008) for the Svalbard region for each day in August 2018 and August 2019. The data was then processed by classifying each grid cell (3.125 km grid spacing) in the Barents Sea as either ice-free (0) or ice-covered (1) based on a threshold of less than 15 % sea-ice coverage representing ice-free conditions. Finally, the number of ice-covered days for each grid cell was determined by summing up the number of days classified as ice-covered, giving a range between 0-31 days of ice cover in August.

2.4.2 Hydrography

Data on hydrography of the sampling area was obtained from the Svalbard Integrated Arctic Earth Observing System (SIOS) data portal (Ingvaldsen, 2022; Reigstad, 2022). The data, consisting of depth profiles of water column salinity and temperature, were obtained using a rosette-mounted conductivity-temperature-depth (CTD) sensors mounted on the SBE911+ probe from Sea-Bird Electronics. Data were processed following standard procedures as recommended by the manufacturer and were averaged to 1 m vertical bins before plotting. We applied the suggested water mass definitions for the central and northern Barents Sea (Sundfjord et al., 2020), based on conservative temperature CT, absolute salinity SA and potential density values, following TEOS-10 convention.

2.4.3 Chlorophyll *a*

Values of acid-corrected chlorophyll *a* concentration at the stations along the transect were obtained from the SIOS data portal (Vader, 2022a, Vader, 2022b). Water for the measurements was collected with 10 L Niskin bottles mounted on a CTD rosette at nine depths: 5, 10, 20, 30, 40, 50, 60, 90 m and at the fluorescence maximum. Chlorophyll *a* was extracted with methanol using GF/F filters following the Holm-Hansen and Riemann (1978) procedure and its concentration was measured on board, using a Turner Design AU10 fluorometer.

2.4.4 Protist abundance

Abundance data of pelagic marine protists (cells L^{-1}) at the study stations were obtained from the SIOS data portal (Assmy et al., 2022a, Assmy et al., 2022b). Samples were collected with Niskin bottles mounted on a CTD rosette at depths: 5, 10, 30, 60, 90 m and at deep chlorophyll maximum. The samples were preserved using a mixture of glutaraldehyde and hexamethylenetetramine-buffered formalin at final concentrations of 0.1% and 1%, respectively. The organisms were identified and counted under an inverted microscope according to the Utermöhl method (Utermöhl, 1958).

2.4.5 Primary production

Primary production rates at selected stations (2018: P1, P2, P4, PICE; 2019: P1, P4, P5, P7) were estimated by measuring ^{14}C uptake during *in situ* incubations. Water was collected from a CTD rosette at 10, 20, 40, 60, 90 m and at the fluorescence maximum. The samples were stored in a dark and cold environment until processing, no longer than one hour. Two 250 mL polystyrene incubation bottles, one clear and one dark, were filled with water from each depth. $NaH_{14}CO_3$ was added to each incubation bottle to a final activity of 0.1 mCi/mL. Two 250 µL subsamples of each incubation bottle were fixed with 250 µL pure ethanolamine to quantify total added carbon. Both bottles were then incubated at their corresponding sampling depths, attached to a freely drifting mooring rig. After 18 to 24 hours, the bottles were recovered, and their contents filtered onto 25 mm Whatman GF/F filters at low vacuum pressure. The filters were transferred to 20 mL scintillation vials, and 750 µL concentrated HCl was added to remove the unincorporated inorganic carbon. The samples were stored in the dark until analysis, at which point 10 mL of scintillation cocktail (Ecolume) was added before analysis in a scintillation counter (Tricarb). Samples were counted for 10 minutes.

2.4.6 Bacterial production

Bacterial production rates at selected stations (2018: P1-P5, PICE; 2019: P1-P5, P7) were measured using the method of 3H-leucine incorporation according to Smith and Azam (1992). In short, four replicates of 1.5 mL of seawater, collected at depths of 5, 10, 20, 40, 60, 90, 120 m and at maximum fluorescence using Niskin bottles mounted on a CTD rosette, were distributed in 2 mL Eppendorf vials. To one replicate, 80 µL of 100% trichloroacetic acid (TCA) were immediately added to serve as control. All replicates were incubated with 3H-leucine (25-nM final concentrations) for 2h at *in situ* temperature (temperature measured at the sampling depth) and stopped through addition of 80 µL of 100% TCA. For the analysis, samples were first centrifuged for 10 min at 14,800 rpm and subsequently washed with 5% TCA (repeated three times). 5 mL of scintillation liquid (Ultima Gold) was added after the final step and the radioactivity in the samples was counted on a Perkin Elmer Liquid Scintillation Analyzer Tri-Carb, 2800TR. The measured leucine incorporation was converted to µg carbon incorporated per L per hour according to Simon et al. (1992). Datasets for bacterial production measurements in August 2018 and August 2019 can be found at NMDC (Müller, 2023a, Müller, 2023b).

2.5 Statistical analyses

Data on copepod abundance (ind. m^{-2}), biomass (µg C m^{-2}) and secondary production (µg C m^{-2} d^{-1}) were aggregated at different taxonomic resolutions, combining across all developmental stages, using the following groupings: Calanoida nauplii, *Calanus finmarchicus*, *C. glacialis*, *C. hyperboreus*, *Microcalanus* spp., *Pseudocalanus* spp., Cyclopoida nauplii, *Oithona* spp., other Cyclopoida (including predominantly *Triconia borealis*), *Microsetella norvegica* and 'other copepods' (Table 3, representative species and life stages used in the grouping). Data was tested for normal distribution using the Shapiro-Wilk test. Prior to the analysis, data on abundance were fourth root transformed and data on biomass and secondary production were $\log_{10}(x+1)$ transformed to approximate the normal distribution and stabilize variances. All statistical analyses of the copepod community were performed on abundance, biomass, and secondary production data from three depth strata (0-20, 20-50, 50-100 m) at stations along the study transect in 2018 and 2019. Because of non-replicated zooplankton tows, we used the different depth strata as replicates within each station, to be able to perform statistical tests on the dataset.

To test whether bulk abundance, biomass, and secondary production of the total copepod community and of individual copepod species differed significantly between the two years (2018 and 2019) and locations (stations P1, P2, P3, P4, P5, which were sampled in both years), two-ways Analyses of Variance (ANOVA) were performed for the dominant copepod species mentioned above.

To test whether there was a significant difference in copepod community composition between the two years (2018 and 2019) and locations (stations P1, P2, P3, P4, P5), a permutation test was performed for a Constrained Correspondence Analysis (CCA) on abundance data and for a Redundancy Analysis (RDA) on biomass and secondary production data. Due to the nature of the data, a CCA was chosen for the abundance data (count data appropriate for Chi-square distances) and an RDA for biomass and secondary production data (both continuous variables appropriate for Euclidean distances). The explanatory variables in the CCA and RDAs included year and location. The interaction term (year x location) was included in the model to capture interannual differences of the copepod community along the transect. The significance of the overall model and individual terms were obtained by permutation testing (1000 permutations) at a significance level of $\alpha = 0.05$.

To test the effect of environmental variables on the copepod community composition at stations in the two years, a CCA was performed on abundance data, whereas an RDA was performed on biomass and secondary production data. Included stations were P1-P5, P7, PICE1, SICE2, SICE3. The explanatory variables in the CCA and RDAs were selected based on ecological relevance and included water temperature (conservative temperature, °C) and salinity (absolute salinity, g kg^{-1}), number of ice-free days, and integrated chlorophyll *a* concentration (mg Chl a m^{-2} for the upper 100 m water column). Because temperature and number of ice-free days were highly correlated, the temperature residuals were extracted

TABLE 3 Copepod groupings used for the statistical analyses, with representative species and life stages.

Groupings used in the statistical analyses	Main copepod species and life stages
Calanoida nauplii	*Calanus* spp., *Pseudocalanus* spp. and other Calanoida nauplii
Calanus finmarchicus	*Calanus finmarchicus* CI-CVI
C. glacialis	*C. glacialis* CI-CVI
C. hyperboreus	*C. hyperboreus* CI-CVI
Microcalanus spp.	*Microcalanus* spp. CI-CVI
Pseudocalanus spp.	*Pseudocalanus* spp. CI-CVI
Cyclopoida nauplii	*Oithona* spp. and other Cyclopoida nauplii
Oithona spp.	*Oithona similis* CI-CVI, *Oithona atlantica* CI-CVI
other Cyclopoida	*Triconia borealis*, *Oncaea* spp. CI-CVI
Microsetella norvegica	*Microsetella norvegica* CI-CVI
other copepods	Aetideidae, *Acartia longiremis*, *Centropages hamatus*, *Gaetanus tenuispinus*, *Heterorhabdus norvegicus*, Harpacticoida spp. indet., *Neomormonilla* spp., *Metridia longa*, *Scaphocalanus brevicornis*, *Scolecithricella minor*, *Paraeuchaeta* spp.

using a linear model relating temperature to ice-free days. These temperature residuals were further used in the analyses and were representative of temperature variations within the water column decoupled from the spatial trend in sea-ice cover. Using temperature residuals also ensured that secondary production was not correlated with the same temperature data set that was used in the secondary production calculations. Model assumptions (linearity, variance heterogeneity and normality) were checked via exploratory data analyses and regression diagnostics. Salinity was square root transformed and number of ice-free days was $\log_{10}(x+1)$ transformed, due to their skewed distributions. The significance of the overall model and individual terms were obtained by permutation testing (1000 permutations) at a significance level of $\alpha = 0.05$.

In the constrained multivariate analysis, we could only include salinity, temperature, integrated chlorophyll *a*, and number of ice-free days as explanatory variables, due to missing values of other biological and environmental drivers at some of the sampling stations. However, primary production rate, bacterial production rate, ciliate abundance, dinoflagellate abundance and diatom abundance can be of high ecological relevance to secondary production. To explore the relationship between copepod secondary production and these additional environmental and biological drivers, a Principal Component Analysis (PCA) was performed on the copepod secondary production variables, and the explanatory variables were then superimposed on the biplot by relating these to the principal components (PC1, PC2).

All data processing, statistical analyses and visualizations were performed using R version 4.2.2. The multivariate ordination analyses and permutation tests were performed with R package Vegan (Oksanen et al., 2023). Station maps were plotted in R using the GGOceanmaps package (Vihtakari, 2022) and Bathymetry data from the National Geophysical Data Center (NOAA National Geophysical Data Center 2009).

3 Results

3.1 Physical properties: sea ice and hydrography

Sea-ice cover and water mass distribution in the study area varied between the two years. In August 2018, the ice edge was at 83°N, while it extended as far south as 80°N in 2019 (Figures 1A, C). Analysis of the sea-ice concentration in the Barents Sea in the weeks prior to the sampling campaigns revealed that in 2018 the Atlantic station P1 had been ice-free (defined as consecutive days with < 15% sea ice concentration) for 219 days, while it had only been ice-free for 92 days in 2019 (Table 1). The Barents Sea shelf stations P2, P3, P4 and P5 north of the polar front had been ice-free respectively for 88, 83, 73 and 79 days in 2018 and 43, 45, 32 and 0 days in 2019 (Table 1). All stations in the Arctic Ocean basin in 2018 (PICE1, SICE2, SICE3) and 2019 (P7) were ice covered in August (Table 1). In 2018, the sea ice in the study area started to melt around mid-May and did not form again until approximately mid-December. In 2019, on the other hand, the sea ice started to melt roughly by the end of June and formed again by the beginning of October (Amargant-Arumí et al., 2024).

The upper 100 m water column was warmer and more saline in 2018 than in 2019. In 2018, Atlantic Water was only observed at station P1, while this water mass was not present there in 2019 and was substituted with warm Polar Water (Figures 1B, D). Stations P2, P3, P4 and P5 north of the polar front were characterized by warm Polar Water in the surface layers and Polar Water in deeper layers in both years. In 2019, both temperature and salinity of the water masses decreased from south to north over the Barents Sea shelf. The Arctic Ocean basin stations in 2018 (PICE1, SICE2-3) and 2019 (P7) were characterized by Polar Water in the surface layers and warm Polar Water in deeper layers (Figures 1B, D).

3.2 Copepod community composition

3.2.1 Copepod depth distribution

In general, the majority of the copepods were found in the upper 100 m of the water column. At the Atlantic station P1, 85% of the entire copepod community was found in the upper 100 m in 2018, and 95% in 2019 (Figures 2A, B, diamonds representing the percentage of the copepod community that resided in the upper 100 m). On the Barents Sea shelf (stations P2-P5) approximately 66-91% of the entire copepod community was in the upper 100 m in 2018 and 84-94% in 2019 (Figures 2A, B). In the Arctic Ocean basin between 47-57% of the whole copepod community were found in the upper 100 m in 2018 (stations PICE1, SICE2-3) and 49% in 2019 (station P7, Figures 2A, B). It should be recalled that the stations in the Arctic Ocean basin were located in much deeper areas of the ocean. Of the *Calanus* population at the Atlantic station P1, 4% was found in the upper 100 m of water in 2018, while it was as much as 40% in 2019 (data not shown). On the Barents Sea shelf, 51-94% of the *Calanus* spp. community was found in the upper 100 m in 2018 and 68-94% in 2019 (data not shown). In the Arctic Ocean basin, between 72-100% of the *Calanus* spp. community was in the upper 100 m in 2018 (stations PICE1, SICE2-3) and 92% in 2019 (P7, data not shown). As the present study focuses solely on the secondary production occurring in the upper 100 m water column, e.g. does not considering *Calanus* spp. below 100 m in hibernation, the focus of the following chapters lays exclusively on the depth range of 0-100 m.

3.2.2 Copepod abundance

Copepod abundance in the upper 100 m was highest at the Atlantic station P1 in both years and amounted to 1052 and 1023 x 10^3 ind. m^{-2} in 2018 and 2019, respectively. The copepod community was numerically dominated by small copepods and cyclopoid nauplii (Figures 2A, B). The small copepod *Microsetella norvegica* and its nauplii were found almost exclusively at the Atlantic station P1. The total abundance of this species, including nauplii, was 225 x 10^3 ind. m^{-2} in 2018 and 40 x 10^3 ind. m^{-2} in 2019. The large copepods *Calanus* spp. reached abundance of 0.4 x 10^3 ind. m^{-2} in 2018 and 5 x 10^3 ind. m^{-2} in 2019, representing less than 0.5% of total copepod abundance in both years. Other large copepods, e.g. *Metridia longa*, were virtually absent at station P1

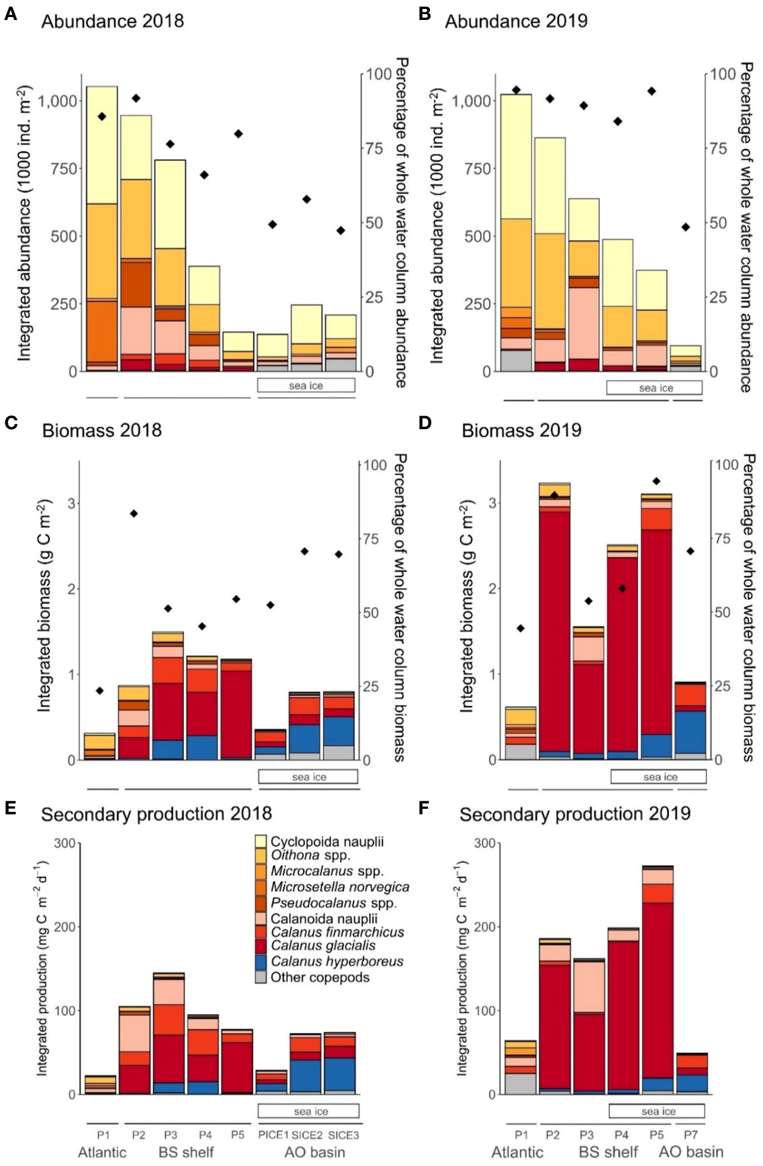

FIGURE 2

Abundance (upper panels), biomass (middle panels) and secondary production (lower panels) of dominating copepods within the upper 100 m layer at the southernmost station P1 (Atlantic), on the Barents Sea shelf (BS shelf) and in the Arctic Ocean basin (AO basin) in 2018 (left side graphs) and 2019 (right side graphs). Integrated abundance (1000 ind. m^{-2}) in 2018 (panel **(A)**) and 2019 (panel **(B)**), integrated biomass (g C m^{-2}) in 2018 (panel **(C)**) and 2019 (panel **(D)**) and integrated secondary production (mg C m^{-2} d^{-1}) in 2018 (panel **(E)**) and 2019 (panel **(F)**) with proportions for individual copepod groups shown in the legend. Diamonds represent the percentage of the copepod community abundance (panels **(A, B)**) and biomass (panels **(C, D)**) that was located in the upper 100 m. Solid lines below the figure panels indicate the respective regions of the study section. Sea-ice cover is indicated with white rectangles under the graphs.

in 2018, whereas they represented up to 4% of the total copepod abundance at this station in 2019.

On the Barents Sea shelf (stations P2-P5) copepod abundance ranged between 145-946 x 10^3 ind. m^{-2} in 2018 and 374-863 x 10^3 ind. m^{-2} in 2019. The community was numerically dominated by small copepods and copepod nauplii in both years (Figures 2A, B). *Calanus* spp. and especially individuals in the size range of *C. glacialis*, contributed more to total abundance there. In terms of abundance, *Calanus* spp. made up 6-12% of the copepod community in 2018 (18-62 x 10^3 ind. m^{-2}) and accounted for 4-7% (16-44 x 10^3 ind. m^{-2}) in 2019. The species composition of the *Calanus* complex differed between the two years. *C. finmarchicus* made up 31-67% of the *Calanus* abundance on the Barents Sea shelf in 2018 and 1-17% in 2019. C. *glacialis* made up 29-68% in 2018 and 73-97% in 2019. C. *hyperboreus* made up 0.5-5% in 2018 and 1-10% in 2019. Copepod nauplii made up more than half of the total abundance of Copepoda on the shelf in both years, with cyclopoid nauplii being more abundant than calanoid nauplii. The only exception was station P3 in 2019, where the highest nauplii abundance was recorded (420 x 10^3 ind. m^{-2}) and the nauplii assemblage was dominated by calanoid nauplii, with 63% contribution to total nauplii abundance.

In the Arctic Ocean basin copepod abundance in the upper 100 m of the ocean was low in both years, ranging from 137-246 x 10^3 ind. m^{-2} in 2018 (stations PICE1 and SICE2, respectively) and 95 x 10^3 ind. m^{-2} in 2019 (station P7) (Figures 2A, B). This was only a fraction (9-23%) of the abundance found at the Atlantic station P1. The copepod community in both years consisted mainly of copepod nauplii (48-76% of total abundance) and small copepods (24-46% of total abundance), while large copepods played a minor role (0-6% of the total abundance). As for *Calanus* spp., *C. finmarchicus* accounted for approximately 60-70% in both years, while *C. hyperboreus* only accounted for 7-26% in 2018 and 34% in 2019.

3.2.3 Copepod biomass

In both years, the copepod biomass in the upper 100 m was highest on the Barents Sea shelf and lower at the Atlantic station and in the Arctic Ocean basin. The copepod biomass at the Atlantic station P1 amounted to 0.31 g C m^{-2} in 2018 and 0.61 g C m^{-2} in 2019. In 2018, *Oithona* spp., *Microsetella norvegica* (Figures 2C, D) and the nauplii of both small copepods contributed most to the copepod biomass. In 2019, the copepod biomass consisted mainly of *Oithona* spp., other small copepods (e.g. *Pseudocalanus* spp., *Triconia borealis*, *Microcalanus* spp., *Microsetella norvegica*) and *Metridia longa* (other copepods in Figures 2C, D).

Copepod biomass was the highest on the Barents Sea shelf, with a maximum of 1.50 g C m^{-2} at station P3 in 2018 and a maximum of 3.21 g C m^{-2} at station P2 in 2019. The main component of copepod biomass on the Barents Sea shelf was *Calanus* spp. in both years, except at the southernmost station P2 in 2018, where small copepods and copepod nauplii together accounted for 55% of the total copepod biomass, and station P3 in 2019, where calanoid nauplii constituted 18%. *Calanus* in the size range of *C. finmarchicus* made up 8-34% of *Calanus* spp. biomass on the Barents Sea shelf in 2018 and 24-44% in 2019. C. *glacialis* made up 48-90% in 2018 and 82-96% in 2019. C. *hyperboreus* made up 2-27% in 2018 and 2-9% in 2019 (Figures 2C, D).

Copepod biomass was considerably lower in the Arctic Ocean basin than in the south, with 0.06-0.80 g C m^{-2} in 2018 and 0.90 g C m^{-2} in 2019. Here the biomass was mainly composed of *Calanus* spp. and other large copepods and *C. hyperboreus* contributed up to 60% in *Calanus* spp. biomass in both years (Figures 2C, D).

3.2.4 Copepod secondary production

The secondary production of copepods in the upper 100 m was highest on the Barents Sea shelf and lower at the Atlantic station P1 and at stations in the Arctic Ocean basin. At the Atlantic station P1, total estimated secondary production was 22.3 and 64.3 mg C m^{-2} d^{-1} in 2018 and 2019, respectively. Small copepods (13.8 and 19.3 mg C m^{-2} d^{-1} 2018 and 2019, respectively) and their nauplii (1.8 and 1.4 mg C m^{-2} d^{-1} 2018 and 2019, respectively) contributed considerably to the total copepod secondary production (Figures 2E, F). The production of large copepods at the Atlantic station was only 1.9 mg C m^{-2} d^{-1} in 2018 while it was 32.7 mg C m^{-2} d^{-1} in 2019.

The total estimated secondary production on the Barents Sea shelf ranged between 77.6-144.8 mg C m^{-2} d^{-1} in 2018 and 162.1-272.2 mg C m^{-2} d^{-1} in 2019. There was a change between years in the relative contribution of different groups to total secondary production of copepods on the Barents Sea shelf. In 2018, copepod nauplii and small copepods accounted for a large part of the production in the southern-most part of the Barents Sea shelf (stations P2), while *Calanus* spp. accounted for the majority of production in the remaining northern part (stations P3, P4, P5). In 2019, *Calanus* spp. accounted for most of the copepod secondary production at all stations except station P3, where calanoid nauplii had a higher share in production, amounting to 37.2% (Figures 2E, F). *C. finmarchicus* made up 13-39% of *Calanus* spp. production on the Barents Sea shelf in 2018 and 0.2-9% in 2019. C. *glacialis* made up 41-83% in 2018 and 83-97% in 2019. C. *hyperboreus* made up 2-19% in 2018 and 2-6% in 2019 (Figures 2C, D).

The secondary production of copepods in the Arctic Ocean basin ranged from 28.9-74.0 mg C m^{-2} d^{-1} in 2018 to 49.2 mg C m^{-2} d^{-1} in 2019 and resulted mainly from the production of *Calanus* spp. (72-89% in 2018, 89% in 2019) (Figures 2E, F).

3.3 Distribution of copepod communities in relation to ecological drivers

3.3.1 Differences in bulk abundance, biomass, and secondary production

There were no significant differences in mean abundance, biomass, and secondary production of the bulk copepod community between the two years (2018, 2019). In contrast, the mean abundance of the bulk copepod community was significantly different between locations (upper 100 m, stations P1-P5, two-way ANOVA, p <0.001, Supplementary Table 2). Post-hoc testing showed that the mean abundance decreased from south to north (Supplementary Figure 1A).

The only copepod species for which significant interannual differences were found was *C. finmarchicus*. The mean abundance, biomass, and secondary production of *C. finmarchicus* were significantly different between the two years (abundance, p <0.001; biomass, p = 0.007; secondary production, p = 0.001, Supplementary Table 2) and the interaction between year and location had a significant effect (abundance, p = 0.018; biomass, p = 0.003; secondary production, p = 0.002, Supplementary Table 2). Post-hoc testing showed that the mean abundance, biomass, and secondary production of *C. finmarchicus* were higher in 2018 than in 2019 at station P2, P3 and P4 (Supplementary Figures 1, panels 7A–C).

Significant differences between locations were found for *Calanus* spp. and the small copepods *Oithona similis* and *Microsetella norvegica*. The mean biomass of the large copepods *Calanus* spp. was significantly different between the locations (biomass, p = 0.03, Supplementary Table 2). Post-hoc testing showed that the mean bulk biomass of *Calanus* spp. was lower at the Atlantic station P1 than at the Barents Sea shelf stations P2-P5 (Supplementary Figures 1, panel 5B). The mean bulk abundance, biomass, and secondary production of *Oithona* spp., *Pseudocalanus* spp., *Microcalanus* spp., *Microsetella norvegica* and remaining small copepods combined were significantly different between locations (abundance, p = 0.006; biomass, p = 0.003, secondary production, p < 0.001, Supplementary Table 2). Post-hoc testing showed that the mean bulk abundance, biomass, and secondary production of small copepods decreased from south to north (Supplementary Figures 1, panels 10A–C). The mean abundance, biomass, and secondary production of the small copepods *O. similis* and *M. norvegica* varied significantly with location (*O. similis* abundance, p = 0.038; *O. similis* biomass, p = 0.020; *O. similis* secondary production, p = 0.018 and *M. norvegica* abundance, p = 0.013; *M. norvegica* biomass, p = 0.013; *M. norvegica* production, p = 0.002, Supplementary Table 2). Post-hoc testing showed that the mean abundance, biomass, and secondary production of both copepods decreased from south to north.

3.3.2 Copepod community composition

Multivariate analyses showed that there was no significant difference in terms of mean abundance, biomass, and secondary production of the copepod community between the two years (Table 4). The copepod community differed significantly in terms of mean abundance, biomass, and secondary production between locations (permutation test for stations P1-P5, using copepod groupings in Table 3, CCA abundance, p = 0.001; RDA biomass, p = 0.001; RDA production, p = 0.001, Table 4). Mean abundance, biomass, and secondary production of the copepod community differed significantly when testing for the interaction between year and location simultaneously (CCA abundance, p = 0.004; RDA biomass, p = 0.011; RDA production, p = 0.049, Table 4).

TABLE 4 Results of permutation testing of the copepod community in the upper 100 m (three depth strata 0-20, 20-50, 50-100 m) in relation to the two study years (2018 and 2019) and locations (stations P1-P5).

	Factor	Variance explained (%)	p-value
Abundance	Model (Year, Location)	59.86	0.001 (**)
	Year	1.31	0.455
	Location	45.28	0.001 (***)
	Year x location	13.27	0.004 (**)
Biomass	Model (Year, Location)	61.96	0.001 (***)
	Year	1.05	0.588
	Location	50.27	0.001 (***)
	Year x location	10.64	0.011 (*)
Production	Model (Year, Location)	58.49	0.001 (***)
	Year	2.70	0.257
	Location	41.30	0.001 (***)
	Year x location	14.49	0.049 (*)

Permutation testing was performed for a Constrained Correspondence Analysis (CCA) on copepod abundance data and for a Redundancy Analysis (RDA) on copepod biomass and copepod secondary production data. Copepods were grouped into Calanoida nauplii, *Calanus finmarchicus, C. glacialis, C. hyperboreus, Microcalanus* spp., *Pseudocalanus* spp., Cyclopoida nauplii, *Oithona* spp., other Cyclopoida, *Microsetella norvegica*, other copepods. Significance codes are indicated as '***' 0.001, '**' 0.01, '*' 0.05.

The constrained ordination models that explained the differences in copepod community abundance (Figure 3A; CCA, p <0.01), biomass (Figure 3B; RDA, p <0.01) and secondary production (Figure 3C; RDA, p <0.01) between locations within and between the two years included salinity, temperature, chlorophyll *a* and number of ice-free days as explanatory variables. Of the explanatory variables, only number of ice-free days was significant (p = 0.001, for abundance, biomass, secondary production, Table 5). The CCA explained 27.16% of total variation in the abundance data (Table 5), with the first axis accounting for 18.05% and the second axis for 4.81%. The RDA explained 27.43% of total variation in the biomass data (Table 5), with the first axis accounting for 19.38% and the second axis for 5.15%. The RDA accounted for 28.77% of total variation in the secondary production data (Table 5), with the first axis accounting for 20.35% and the second axis for 5.72% of the explained variability. The first axis of the CCA and of the two RDAs was significant (p = 0.001, for abundance, biomass, secondary production) and was primarily related to ice-free days, which contributed most to the observed variation. The second axis of the CCA and of the two RDAs was related to higher temperature and salinity on one end (Atlantic Water) and higher chlorophyll *a* concentrations on the other end, but was not significant. Samples clustered by characteristic geographical area, with the Atlantic station P1, the Barents Sea shelf stations (P2-P5) and the Arctic Ocean basin stations (PICE1, SICE2-3, P7) separating within the ordination plane. There was no clear distinction between samples from 2018 and 2019 in the ordination (Figures 3A–C). Copepod abundance, biomass, and secondary production were positively correlated with chlorophyll *a* at the Barents Sea shelf stations and positively correlated with salinity and temperature at the Atlantic station. A negative correlation was found between copepod abundance, biomass and secondary production and number of ice-free days for the Arctic Ocean basin stations. The analyses showed that the abundance, biomass, and secondary production of *Microsetella norvegica*, *Pseudocalanus* spp. and *Oithona* spp. were positively correlated with number of ice-free days, water temperature and salinity. The abundance, biomass, and secondary production of *Calanus glacialis* was positively correlated with chlorophyll *a* concentration. The abundance, biomass, and secondary production of *C. hyperboreus, Microcalanus* spp. and other copepods (e.g. *Metridia longa*, *Paraeuchaeta* spp.) was negatively correlated with number of ice-free days (Figures 3A–C). This shows that distinct copepod communities were found in the southern and northern parts of the study transect (spread along the first axis), with *M. norvegica*, *Pseudocalanus* spp., *Oithona* spp. and *C. glacialis* being characteristic for the Atlantic and shelf community, and *C. hyperboreus, C. finmarchicus, Microcalanus* spp., *M. longa*, and *Paraeuchaeta* spp. characteristic for the Arctic Ocean basin community. The communities were either located in Atlantic

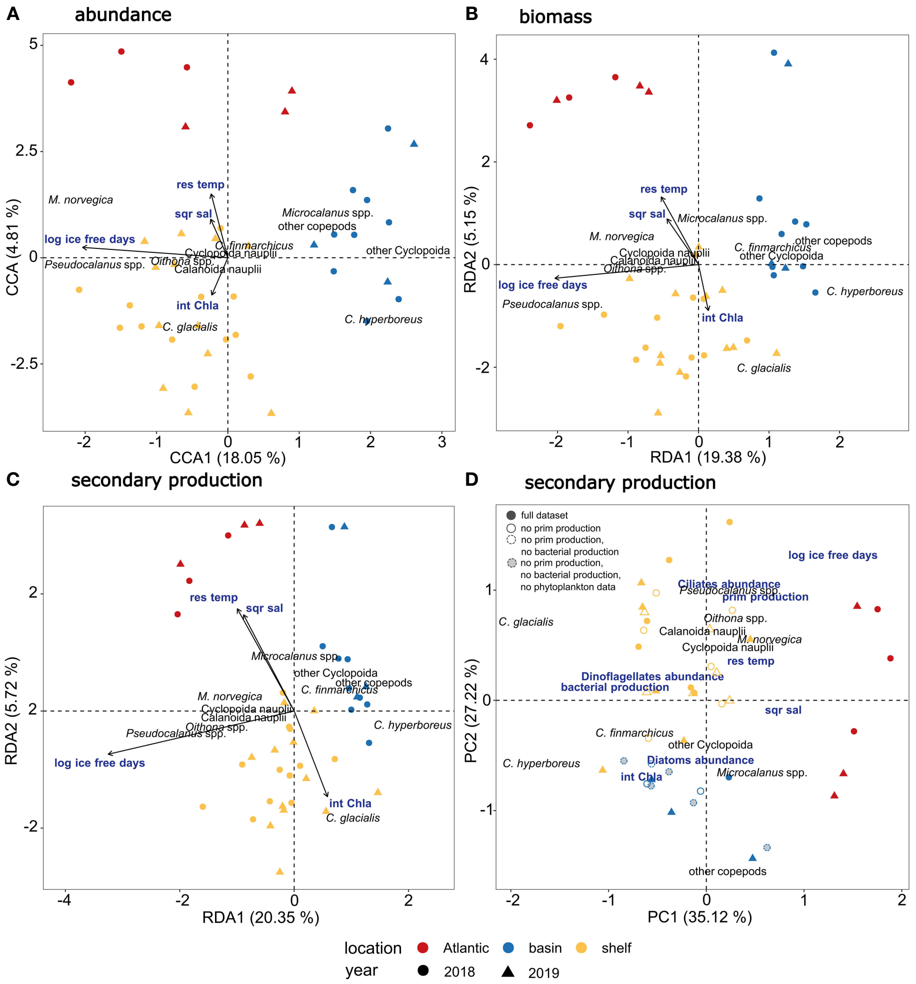

FIGURE 3
Multivariate analyses of copepod communities in relation to environmental and biological factors. **(A)** Triplot showing relationship between copepod abundance (based on fourth root transformed abundance data expressed as ind. M^{-2} in three depth strata from 0-20, 20-50, 50-100 m) and environmental factors (int Chl *a* = integrated chlorophyll *a* concentration, sqr sal = square root transformed salinity, res temp = residuals of temperature and log ice free days = log transformed number of ice-free days) using Constrained Correspondence Analysis (CCA). **(B)** Triplot showing relationship between copepod biomass (based on $\log_{10}(x+1)$ transformed biomass data expressed as µg C m^{-2}) and environmental factors using Redundancy Analysis (RDA). **(C)** Triplot showing relationship between copepod secondary production (based on $\log_{10}(x+1)$ transformed secondary production data expressed as µg C m^{-2} d^{-1}) and environmental factors using Redundancy Analysis (RDA). **(D)** Biplot showing Principal Component Analysis of copepod secondary production with overlaid potential drivers of secondary production, including log-transformed number of ice-free days, square root transformed salinity, residuals of temperature, integrated chlorophyll *a* concentration, bacterial production, primary production, abundance of ciliates, dinoflagellates, and diatoms. Solid filled symbols indicate samples with full dataset of environmental and biological variables, symbols with solid lines indicate that primary production was not measured, symbols with dashed lines indicate that primary production and bacterial production were not measured, grey-filled symbols with dashed lines indicate that primary production, bacterial production, and phytoplankton community composition were not measured.

waters with low phytoplankton biomass, i.e. low integrated chlorophyll *a*, or in other water masses with higher phytoplankton biomass (sample points spread along the second axis).

A Principal Component Analysis (PCA) revealed that the secondary production of small copepods (e.g. *Oithona* spp., *Pseudocalanus* spp., *M. norvegica*) on the Barents Sea shelf and in the Atlantic region was positively correlated with number of ice-free days and was furthermore associated with a higher primary production rate and ciliate abundance (Figure 3D). The secondary production of *C. finmarchicus* and *C. hyperboreus* and other copepods in the Arctic Ocean basin was positively correlated with integrated chlorophyll *a* values, and also associated with higher diatom abundance. The high secondary production of *C. glacialis* on the Barents Sea shelf was associated with a higher bacterial production rate and higher dinoflagellate abundance. Both the bacterial production rate and dinoflagellate abundance were negatively correlated with salinity and temperature (Figure 3D). Hence, different environmental drivers seemed to influence the copepod communities in the southern and northern parts of the study area.

TABLE 5 Results of permutation testing of the copepod community in the upper 100 m (three depth strata 0-20, 20-50, 50-100 m) at stations P1-5, P7, PICE1, SICE2 and SICE3 in relation to environmental and biological variables (int_Chla = integrated chlorophyll a concentration, res_temp = residuals of temperature, log_ice_free_days = log transformed number of ice-free days and sqr_sal = square root transformed salinity.

	Factor	Variance explained (%)	p-value
Abundance	Model (int_Chla, res_temp, log_ice_free_days, sqr_sal)	27.16	0.001***
	int_Chla	2.18	0.360
	res_temp	3.77	0.091.
	log_ice_free_days	17.52	0.001***
	sqr_sal	3.69	0.106
Biomass	Model (int_Chla, res_temp, log_ice_free_days, sqr_sal)	27.43	0.001***
	int_Chla	1.87	0.447
	res_temp	3.96	0.053.
	log_ice_free_days	18.31	0.001***
	sqr_sal	3.29	0.124
Production	Model (int_Chla, res_temp, log_ice_free_days, sqr_sal)	28.77	0.001***
	int_Chla	2.22	0.324
	res_temp	3.97	0.080.
	log_ice_free_days	18.50	0.001***
	sqr_sal	4.11	0.058.

Copepods were grouped into Calanoida nauplii, *Calanus finmarchicus, C. glacialis, C. hyperboreus, Microcalanus* spp., *Pseudocalanus* spp., Cyclopoida nauplii, *Oithona* spp., other Cyclopoida, Microsetella norvegica, other copepods. Significance codes are indicated as '***' 0.001, '.' 0.1.

4 Discussion

4.1 Effect of interannual variation of sea-ice cover on copepod secondary production

Since the cold climate period in the late 1970s, the Barents Sea has undergone a warming trend (Bagøien et al., 2020), marked by notable interannual and multidecadal variability, resulting in an overall sea surface temperature increase of about 1.5°C (Mohamed et al., 2022). In this perspective, the two investigated years were both relatively warm years, although on a generally slightly cooling trend since the record warm year 2016 (Bagøien et al., 2020). There were differences in environmental drivers in the Barents Sea between the two years of study, which influenced the pelagic community and its production. Most notably, in August 2018, there was no sea-ice cover across the Barents Sea shelf and the hydrography in the southernmost part of the section was shaped by Atlantic water masses. In 2019, parts of the Barents Sea shelf were still ice-covered and water temperature at the study stations was overall lower. In the ice-free summer of 2018, the microbial community in the study area was in a late post-bloom stage, while in 2019, remnants of a marginal ice-zone bloom were still observed (Kohlbach et al., 2023; Amargant-Arumí et al., 2024). Even though the microbial community in 2018 was in a later seasonal succession stage than in 2019, both communities sustained comparable primary production averaged across the transect (Amargant-Arumí et al., 2024). To understand how climate change affects the entire pelagic ecosystem, it is crucial to understand how this energy is transferred to higher trophic levels. The Barents Sea as a highly productive fishing ground and depends on copepods as key food sources for many fish species (Hassel et al., 1991; Huse and Toresen, 1996; Bouchard et et al., 2017). It is therefore important to understand how the productivity patterns of copepods may be altered by changes in environmental conditions. Despite the contrasting sea-ice regimes in the two years, we did not find any statistically significant interannual differences in the mean copepod secondary production (Table 4), even though a comparison of the total integrated copepod biomass and secondary production between the two years (integrated for the upper 100 m) suggested that both were higher in 2019 than 2018 (Figures 2C–F). Instead, we found that spatial rather than interannual differences dominated the variation of copepod secondary production across the study region. Integrated bulk copepod secondary production for the upper 100 m ranged between 22.3-64.3 mg C m^{-2} d^{-1} in the Atlantic region, 77.6-272.2 mg C m^{-2} d^{-1} on the Barents Sea shelf and 28.9-74.0 mg C m^{-2} d^{-1} in the Arctic Ocean basin (Figures 2E, F). These values are comparable to data reported for the eastern Barents Sea (13.6-128 mg C m^{-2} d^{-1}, assuming a dry mass to carbon mass relationship of 0.4 and integrating for the upper 100 m, Dvoretsky and Dvoretsky, 2024a) and the Barents Sea polar front (mean 70 ± 8.8 mg C m^{-2} d^{-1}, for the whole water column, Dvoretsky and Dvoretsky, 2024b).

One possible explanation for the absence of interannual variability in the analyzed dataset is that potential interannual differences may have been masked by natural heterogeneity in the depth and spatial distribution of copepods, which is a natural feature of zooplankton and not an effect of climate change. Although the distribution of copepods within the three distinguished depth layers (0-20, 20-50, 50-100 m) did not differ much (Supplementary Figures 2-4 for copepod abundance, biomass and secondary production, respectively), similarly to the zooplankton distribution in the same region described by Wold et al. (2023), the within-group variability of copepod occurrence data across different depth layers at a station was nevertheless high. This reduced the power of the analyses and potentially masked interannual variability. Furthermore, using depth layers as replicates introduces pseudoreplication, which may lead to optimistic estimates affecting the statistical inference. But the large variance observed within stations implies that effect size must be large for significant effects to emerge. To address these challenges, a sampling plan which involves replicate sampling with vertical resolution across multiple stations within each region would be crucial, enabling the inclusion of depth as a predictor in the statistical model to correct for potential differences between depths. Unfortunately, this is a very challenging sampling plan both at sea and in the laboratory and could not be implemented, even for such a large-scale research program as The Nansen Legacy. Further sampling efforts are needed to conclusively answer the important question of the effect of sea-ice reduction on the bulk copepod secondary production and should ideally focus on specific regions to investigate long-term trends. Despite its potential, this approach would require long-term monitoring and additional resources, posing practical challenges. At present we can discuss the question of the effects of interannual variation in sea-ice cover on copepod production based on results from short-term studies such as the present one, which, despite their limitations, provide new insights into how copepod communities respond to changes in water masses and sea ice cover.

It has previously been suggested that as the Arctic continues to warm and sea ice declines, large copepods may become less important for copepod secondary production, while the proportion of small copepods in the copepod community increases (Kimmel et al., 2018, Kimmel et al., 2023) and our observations support this notion. We found significant differences in the copepod community composition and production when comparing individual sampling sites between the two years. These changes could mainly be linked to differences in sea-ice cover at the stations between the two years. Small copepods showed the highest contribution to total copepod production at the warmer stations, but *Calanus* spp. was overall the largest contributor to secondary production in both years. The differences in community composition and secondary production of small and large copepods in 2018 and 2019 were consequences of the interplay of the sea-ice retreat, the phytoplankton bloom status and Atlantic water inflow. In the following we discuss each of these factors in the context of copepod community production.

4.2 Higher water temperature and the specific structuring of the microbial food web promoted secondary production of small copepods

Daily secondary production rates of 1.0-9.7 mg C m^{-2} d^{-1} for small copepods on the Barents Sea shelf are in good agreement with secondary production rates previously recorded in other Arctic regions. The maximum secondary production of small copepods in Disko Bay, western Greenland, in the upper 50 m water column was estimated as 15.5 mg C m^{-2} d^{-1} in October (Madsen et al., 2008). Secondary production values of 2.7-16.1 mg C m^{-2} d^{-1} were reported for small copepods in Ura Bay, when aggregating Dvoretsky and Dvoretsky (2012) mean daily secondary production rates of different copepod species and converting them to carbon mass, using a conversion factor of 0.4 (Peters and Downing, 1984). When comparing the integrated secondary production of small copepods reported in the present study to the integrated primary production in 2018, it becomes apparent that small copepods played a moderate role for carbon transport to higher trophic levels. At the Atlantic station P1, the integrated primary production in the upper 100 m was 632 mg C m^{-2} d^{-1} (Amargant-Arumí et al., 2024) and secondary production of small copepods was 13.8 mg C m^{-2} d^{-1}, which equals an energy transfer of 2.2%. On the Barents Sea shelf, integrated primary production was between 652-710 mg C m^{-2} d^{-1} (stations P4 and P2, respectively, Amargant-Arumí et al., 2024) and secondary production of small copepods was 4.3-9.7 mg C m^{-2} d^{-1} (stations P4 and P2, respectively), equal to an energy transfer of 0.6-1.4%.

There were no significant interannual differences in secondary production of small copepods, but variations were observed between locations, with highest production occurring in warm waters in the southernmost part of the transect. In 2018, water temperatures in the study area were overall higher, less sea-ice was present and chlorophyll *a* concentrations were low (Kohlbach et al., 2023). In August 2018, the protist community was in a late-summer oligotrophic state, dominated by small-sized autotrophic and heterotrophic protists, predominantly flagellates and ciliates (Kohlbach et al., 2023). Highest primary production in 2018 was observed at the southernmost station of the transect (P1), where the growth of small pico- and nano-flagellated cells was sustained by nutrient input through Atlantic Water inflow (Amargant-Arumí et al., 2024). Along the rest of the transect, primary production was overall low and no latitudinal structuring of the microbial community was observed (Amargant-Arumí et al., 2024). In 2019, on the other hand, the microbial community was latitudinally structured (Kohlbach et al., 2023), with highest primary and bacterial production occurring close to the sea-ice edge (around station P4, Amargant-Arumí et al., 2024). With increasing distance to the ice-edge, higher nutrient and chlorophyll *a* concentrations were observed at deeper water layers at the southern stations. The southernmost station P1 was dominated by late-summer protist communities, including high numbers of ciliates in both years (Kohlbach et al., 2023). Our analyses showed that secondary production of small copepods (e.g. *Oithona* spp.) had a positive relationship with the number of ice-free days, which was strongly correlated with the overall water temperature in the study area (Figure 3). A positive relationship between secondary production of *O. similis* and temperature has previously been demonstrated by Balazy et al. (2021). This can be explained by the fact that egg hatching and developmental rates of copepods are positively correlated with temperature, resulting in higher secondary production at higher temperature (Nielsen et al., 2002; Dvoretsky and Dvoretsky, 2009). The development and growth of small copepods appears to depend more directly on water temperature than that of large copepods, whose production is more food dependent. Because of their size, small copepods live in conditions close to food saturation (Kiørboe and Sabatini, 1995). Furthermore, species of the genus *Oithona* prey upon a larger variety of prey items including dinoflagellates, phytoplankton, and faecal material (Gallienne and Robins, 2001), with a preference for swimming prey particles such as ciliates (Svensen and Kiørboe, 2000; Zamora-Terol et al., 2013). This makes them able to sustain higher productivity in low chlorophyll *a* conditions (Sabatini and Kiørboe, 1994), as has been observed in this study in 2018 and explains the positive correlation of secondary production with ciliate abundance that we observed. In the Bering Sea, both the abundance and secondary production of the small copepods *Oithona* spp. and *Pseudocalanus* spp. were higher during a warm period (2001–2005) compared to a cold period (2007–2011) (Hunt et al., 2011; Stabeno et al., 2012; Eisner et al., 2014; Kimmel et al., 2018). In the Barents Sea, higher abundance of small copepods has previously been linked to higher water temperatures (Trudnowska et al., 2016; Balazy et al., 2018).

4.3 Water mass distribution shaped the spatial pattern of secondary production of *Calanus finmarchicus*

The daily secondary production rates of large copepods in the range of 50.8-250.7 mg C m^{-2} d^{-1} for the Barents Sea shelf reported in this study are in good agreement with secondary production previously recorded in other Arctic regions. The highest secondary production rates for *Calanus* spp. of 250 mg C m^{-2} d^{-1} have been estimated in Disko Bay, western Greenland, in the upper 50 m water column in May/June (Madsen et al., 2001). Dvoretsky and Dvoretsky (2012) reported secondary production values of 13.3-14.0 mg C m^{-2} d^{-1} for large copepods in Ura Bay (low copepod biomass in coastal Barents Sea area). When comparing the integrated secondary production of large copepods to the integrated primary production in 2019 it becomes apparent that large copepods were especially important for energy transfer to higher trophic levels in the marginal ice zone. On the Barents Sea shelf, integrated primary production in the upper 100 m was 261-551 mg C m^{-2} d^{-1} (stations P5 and P4, respectively) and secondary production of large copepods was 182.8-250.7mg C m^{-2} d^{-1} (stations P4 and P5, respectively), equivalent to an energy transfer of 33.2-96.1%. At the Atlantic station P1, energy transfer only equaled 10%, based on an integrated primary production of 340 mg C m^{-2} d^{-1} and secondary production of large copepods of 32.7 mg C m^{-2} d^{-1}.

We observed overall higher abundance, biomass, and secondary production of *Calanus* in the size range of the boreal species *C. finmarchicus* in the year that was characterized by presence of Atlantic Water in the southern part of the study area (2018). The recent Arctic winter sea-ice retreat in the Barents Sea has been linked to a strengthening of the Atlantic water inflow into this region and warming of the water masses (Årthun et al., 2012) i.e. 'Atlantification'. As a result of this event, an increasing number of organisms from boreal regions can be advected into the Arctic (Freer et al., 2022). Currently, low water temperatures prevent the boreal species *C. finmarchicus* from establishing a population that can successfully reproduce in the Arctic Ocean (Ji et al., 2012). However, this may change with continued ocean warming and a prolonged retreat of the ice edge (Tarling et al., 2022). A modelling study by Slagstad et al. (2015) showed that with rising water temperature and increasing Atlantic water inflow, the production areas of *C. finmarchicus* will steadily expand into the Greenland Sea, northern Barents Sea, and western Kara Sea. Likewise, warming and an extended growth season due to earlier sea-ice retreat have been suggested to increase the suitability of pelagic habitats in the Fram Strait for *C. finmarchicus* (Freer et al., 2022; Tarling et al., 2022). The large fraction of smaller *Calanus* found on the Barents Sea shelf in our study indicates an advection of *C. finmarchicus* onto the shelf from the southern Barents Sea (Gluchowska et al., 2017), while those in the Arctic Ocean basin are transported into this region with the West Spitsbergen Current (Basedow et al., 2018).

4.4 Differences in sea-ice cover influenced *Calanus glacialis* reproduction

Significantly higher secondary production of the larger *Calanus* (i.e. *C. glacialis*) was observed in the year with extensive sea-ice cover (2019), when chlorophyll *a* concentrations were higher and the protist community was in a late-bloom stage and showed a dominance of autotrophs and large-celled phytoplankton, in particular diatoms (Kohlbach et al., 2023). Highest primary production in 2019 was found at station P5 closest to the ice edge on the Barents Sea shelf. The marginal ice zone bloom had a typical south-to-north progression, where primary production shifted into deeper water layers in the southern parts of the study area (Amargant-Arumí et al., 2024). The sea-ice breakup in 2019 was at the beginning of July, compared to mid-May in 2018, and likely resulted in a longer ice-algae season and an extended spring bloom in 2019 (Kohlbach et al., 2023). This was supported by high numbers of calanoid nauplii observed close to the ice edge at station P3 in 2019, and the presence of CI and CII at the stations south of P3, that may indicate that reproduction took place some weeks earlier. Overall, higher abundance of older *Calanus* copepodids in 2018 compared to 2019 indicated that reproduction in 2018 had started earlier than in 2019. In 2018 biomass and secondary production of *C. glacialis* (i.e. the larger size fraction of the *Calanus* population) on the Barents Sea shelf were however generally lower than in 2019, possibly due to a mismatch between the reproduction of the species and the bloom phenology, and consequently lower recruitment. The life history strategy of *C. glacialis* is tightly linked to the distribution and timing of sea-ice cover and the resulting timing of the ice-algae and phytoplankton blooms (Falk-Petersen et al., 2009; Daase et al., 2013; Feng et al., 2016, Feng et al., 2018). The nutritional quality of both ice algae and phytoplankton is highest at the beginning of the bloom (Søreide et al., 2010; Leu et al., 2011) and *C. glacialis* females can increase their reproductive output if an ice algae bloom is available to fuel egg maturation, while they must rely to a large extent on internal energy reserves from the previous feeding season in the absence of an ice algae bloom (Søreide et al., 2010). The reduction of sea-ice thickness and extent alters the current primary production regime, shortening the growth period of ice algae and advancing the onset of the open water phytoplankton growth season (Arrigo et al., 2008; Søreide et al., 2010). At sub-zero temperatures, the species' nauplii require about three weeks to develop to the first naupliar stage that feeds (Daase et al., 2011). If the phytoplankton bloom occurs shortly after the ice algae bloom, the new generation may miss the early, high-quality food phase of the bloom, thus reducing the reproductive success.

C. glacialis secondary production was higher in the ice-covered northern parts of the study area in 2019. However, this trend was not significant, likely due to high within-group variance compared to the number of replicates in this study. Our observations nevertheless agree with previous studies showing elevated secondary production of large *Calanus* spp. during a cold period (2007–2011) compared to a warm period with reduced sea-ice cover (2001–2005) in the Bering Sea (Hunt et al., 2011; Stabeno et al., 2012; Eisner et al., 2014; Kimmel et al., 2018, Kimmel et al., 2023).

While a mismatch scenario between *C. glacialis* reproduction and the phytoplankton bloom may explain the interannual variation in the local *Calanus* population in the Barents Sea, there is so far little evidence that sea-ice loss has been detrimental to *Calanus* populations in other parts of the European Arctic. Studies from Svalbard fjords suggest that warming and sea-ice loss benefit *C. glacialis* populations (Hatlebakk et al., 2022). Life history models by Feng et al. (2016); Feng et al. (2018) showed that early ice retreat, warming, increased phytoplankton food availability and prolonged growth season overall create favorable conditions for *C. glacialis* development, leading to a northward expansion of well prospering populations of the species as the sea ice retreats. This has been confirmed by observations from the polar basin, indicating a northwards expansion of *C. glacialis* (Kvile et al., 2019; Ershova et al., 2021).

It should be noted that due to the identification of *C. finmarchicus* and *C. glacialis* based on size alone, there is a possibility of an underestimation of *C. glacialis* abundance, as the prosome lengths of the early developmental stages of the two species may overlap for populations thriving in convergence areas. Additionally, because we only looked at communities within the upper 100 m of the water column for this study, we may also have missed parts of the *Calanus* population that have likely already descended to greater depths at this time of the year. However, including diapausing *Calanus* spp. in production estimates would likely result in an overestimation of secondary production in this area. Also, even if some *Calanus* spp. in the two years might have been misidentified, the conclusion that secondary production of large copepods in 2018 was mainly driven by *Calanus* within the size range of *C. finmarchicus* and in 2019 by *Calanus* within the size range of *C. glacialis*, would remain the same, as the differences in secondary production between the two years were pronounced.

While our data indicates that differences in bloom phenology and food availability between the two years may explain the observed changes in community composition from larger to smaller species, the presence of sea ice itself and its effect on visual predation risk may have played an important role. A recent study from the Barents Sea suggests that the prevalence of large copepods in deeper troughs and under sea ice is best explained by top-down control (Langbehn et al., 2023). Large copepods, such as *Calanus* spp., experience a reduced visual predation risk and subsequent increased survival rate where sea ice shades the water. The increased predation risk in open waters can therefore shift the community to a dominance of smaller species (Aarflot et al., 2019; Langbehn et al., 2023), which is also in accordance with our observations.

4.5 Changes in copepod secondary production and the marine food web

Even though our results suggest that the total secondary production in a year with less sea-ice cover is not different from a year with extended sea-ice cover, we speculate that the shift towards smaller organisms may affect the food quality and availability for planktivorous organisms, ultimately leading to food web changes. In terms of biomass, calanoid copepods are the major component of the mesozooplankton community in the Arctic (Falk-Petersen et al., 2009), due to their high lipid content that can account for 50-70% of their dry mass (Falk-Petersen et al., 2009). The lipid content of *Calanus* spp. is size rather than species specific and a shift in dominance from larger to smaller *Calanus* individuals would lead to a reduction in lipid production at the individual level, but not necessary on population level, if overall turn-over rates increase (Renaud et al., 2018). Early larval stages of many fish species, such as Atlantic herring (*Clupea harengus*), Atlantic cod (*Gadus morhua*), haddock (*Melanogrammus aeglefinus*), Alaska pollock (*Gadus chalcogrammus)* and polar cod (*Boreogadus saida*) have a specific prey preference for calanoid nauplii, due to their high lipid content in comparison to other copepod nauplii (Kane, 1984; Napp et al., 2000; Swalethorp et al., 2014; Bouchard and Fortier, 2020). Even though cyclopoid copepods, such as those of *Oithona* spp., are often found in much higher abundance than calanoid copepods, their contribution to the diet of these fish species is considerably less important (Kane, 1984; Napp et al., 2000; Swalethorp et al., 2014). In some Arctic regions, low abundance of preferred prey (e.g. *Calanus* spp., *Pseudocalanus* spp., and *Temora longicornis*) has been linked to lower recruitment of pollock (Kimmel et al., 2018) and mackerel (Lafontaine, 1999; Paradis et al., 2012). Similar to the observed trends in other regions of the Arctic, we hypothesize that the recruitment of commercially and ecologically important fish species in the Barents Sea, such as polar cod, capelin, and Atlantic herring, may be lower in years with increased water temperature and reduced summer sea-ice, due to a shift towards a more generalist diet based on smaller-sized, less lipid-rich copepods.

Zooplankton groups other than copepods can be important both in terms of abundance and biomass in the Barents Sea. Meroplankton, e.g. Bivalvia and Echinodermata larvae, emerged across the study transect in summer (Wold et al., 2023) and high abundance of arrow worms (*Parasagitta elegans*), pteropods (*Limacina helicina*) and gelatinous zooplankton were observed (Van Engeland et al., 2023; Wold et al., 2023). In the present study, we focus solely on copepod secondary production, given the pivotal role of copepods in transferring energy to higher trophic levels in Barents Sea food webs (Pedersen et al., 2021). Most of the secondary production research has focused on copepods, as the majority of available growth rate models are tailored specifically to this group. Due to the complicated life cycle of some non-copepod groups, especially gelatinous zooplankton, determination of their growth rates can be difficult (Postel et al., 2000). Therefore, total secondary production in the study area is likely higher, especially in the Atlantic region and the Arctic Ocean basin, where the contribution of non-zooplankton groups was found to be larger than in the Arctic parts of the study area (Van Engeland et al., 2023; Wold et al., 2023). Copepods can also impact the biological carbon pump through feeding on phytoplankton and aggregates, as well as through fecal pellet production (Jumars et al., 1989). Larger, current-feeding copepods, such as *Calanus* spp., can increase the flux of particulate organic carbon (POC) through efficient grazing and production of large, fast sinking fecal pellets (e.g. Riser et al., 2008). Many small copepod taxa are particle-feeders and can decrease POC export efficiency through feeding on organic particles (e.g. Koski et al., 2020; Koski and Lombard, 2022; Mooney et al., 2023). A shift of the copepod community towards smaller-sized species will possibly be reflected in a compositional and quantitative change of the vertical flux in the Barents Sea. Indications supporting this hypothesis are the lower vertical flux in the study area in 2018 with no attenuation with depth, while the vertical flux in 2019 was higher and showed a strong attenuation profile (Amargant-Arumí et al., 2024).

5 Conclusions

The Barents Sea, known for its high productivity, sustains a substantial commercial fishery. Despite declining sea-ice, the impact on lower trophic levels' productivity is still under debate. In particular, the impact of environmental change on copepod secondary production is not well understood at present. We expected to find higher total bulk copepod secondary production in a summer with reduced sea-ice cover, due to a hypothesized extended period of primary production and consequently higher food availability. However, our observations did not support this hypothesis. Instead, we found that spatial rather than interannual differences dominated the observed variation of copepod secondary production in the Barents Sea. Here, Atlantic waters in summer were characterized by a high contribution of small copepods to total copepod secondary production, as they benefited from higher water temperatures and a more abundant microbial food web in this region. Copepod secondary production on the northern Barents Sea shelf, the study focus area, was overall highest and mainly driven by large *Calanus* spp. Our study shows that if environmental conditions (e.g. the presence of sea ice or water temperature) change to an appropriate extent in a habitat from year to year, this will affect the copepod community composition and its production. There were significant interannual differences of the *Calanus* spp. community composition between the two years, with the smaller *C. finmarchicus* being more important for total copepod secondary production during the summer with less sea-ice cover and in habitats characterized by higher water temperatures and a pronounced Atlantic water signal. The larger *C. glacialis*, on the other hand, was more important in the summer with extensive sea-ice cover and in habitats with lower water temperatures, sea-ice cover and with the presence and higher contribution of diatoms to pelagic primary production.

Due to high spatial heterogeneity in copepod distribution and consequently high variability in secondary production, we still cannot conclude with high confidence which effect the sea-ice decline will have on bulk copepod secondary production in the Barents Sea. Despite its limitations, our study provides important insight into the copepod community response to changes in water masses and sea-ice cover. The results of our study confirm the observations that, as a result of Arctic warming and reduced sea ice, large copepods may become less important and smaller-sized copepod species (including smaller-sized Calanus and small copepods) more important components of pelagic communities, which will have consequences for the secondary production of copepods, as well as for the role of copepods in food webs, biogeochemical cycles, including the biological carbon pump, and other functions performed by them in the ecosystem.

Data availability statement

The original contributions presented in the study are included in the article/Supplementary Material. Further inquiries can be directed to the corresponding author.

Ethics statement

The manuscript presents research on animals that do not require ethical approval for their study.

Author contributions

CG: Writing – review & editing, Writing – original draft, Visualization, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. MD: Writing – review & editing, Writing – original draft, Visualization, Supervision, Methodology, Conceptualization. RP: Writing – review & editing, Visualization, Supervision, Software, Methodology, Formal analysis, Data curation, Conceptualization. MA-A: Writing – review & editing, Formal analysis, Data curation, Conceptualization. OM: Writing – review & editing, Formal analysis, Data curation, Conceptualization. AW: Writing – review & editing, Investigation, Data curation, Conceptualization. MO: Writing – review & editing, Formal analysis, Data curation. SK: Writing – review & editing, Writing – original draft, Supervision, Methodology, Formal analysis, Data curation. CS: Writing – review & editing, Writing – original draft, Supervision, Methodology, Funding acquisition, Data curation, Conceptualization.

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Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

Publisher's note

Supplementary material

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fmars.2024.1308542/full#supplementary-material

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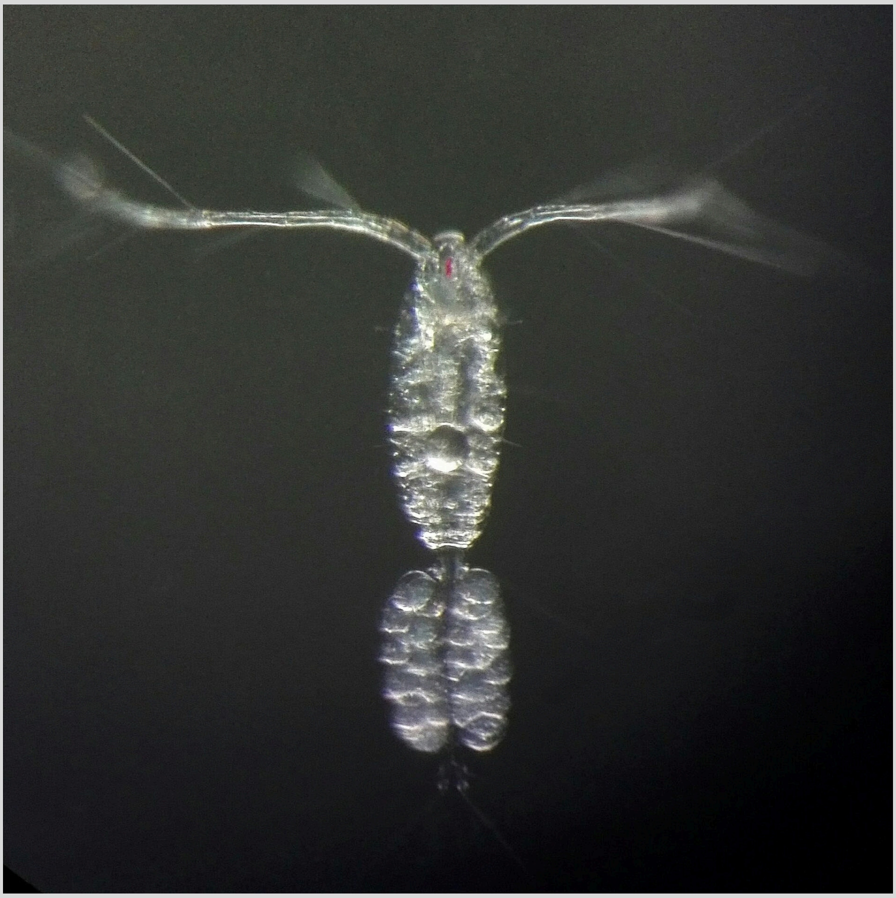
Paper III

Christine Gawinski, Sławomir Kwaśniewski, Elisabeth Halvorsen, Malin Daase, Camilla Svensen (2024)

Seasonality of *Oithona similis* population dynamics, reproductive characteristics, and contribution to copepod secondary production in the northern Barents Sea

Manuscript draft



Appendix

Web of Science literature search

To evaluate how secondary production research has evolved in 2010s and 2020s, I conducted a Web-of-Science literature search of papers with the term ‘secondary production’, in the author key words or in the title. Publications in the time period from September 2008 through May 2024 were included in this analysis. To ensure that the listed papers actually dealt with secondary production, the abstracts of all hits were carefully studied. Each paper was categorized using the same criteria as Benke (2010), namely habitat (terrestrial, marine, freshwater) and animal type (zooplankton, benthic invertebrate, vertebrate). Furthermore, I was interested in the proportion of secondary production research conducted in polar regions and did a refined search of all listed papers that had one or more of the key word combinations: ‘Arctic’, ‘Barents Sea’, ‘Svalbard’, ‘Kara Sea’, ‘Laptev Sea’, ‘East Siberian Sea’, ‘Chucki Sea’, ‘Beaufort Sea’, ‘Canadian Archipelago’, ‘Baffin Bay’, ‘Greenland Sea’, ‘Fram Strait’, ‘Arctic Ocean’, ‘Antarctic’, ‘Weddell Sea’, ‘Lazarev Sea’, ‘Riiser-Larsen Sea’, ‘Cosmonauts Sea’, ‘Cooperation Sea’, ‘Davis Sea’, ‘Mawson Sea’, ‘D’Urville Sea’, ‘Somov Sea’, ‘Ross Sea’, ‘Amundsen Sea’, ‘Bellingshausen Sea’. I did the same refined search with hits from the period studied by Benke (2010).

A total of 460 hits were found in the time period of September 2008 through May 2024, of which 395 were relevant secondary production studies. This search strategy likely led to an underestimation of studies, as papers were missed that did not include the term secondary production in the title or keywords, or used different terms to describe secondary production, such as copepod production, zooplankton production, etc. However, it should nevertheless give reasonable information about the publication pattern concerning this topic.