UiT The Arctic University of Norway

Institute of Arctic and Marine Biology

Population dynamics and production of small, marine copepods in highly seasonal Arctic and sub-Arctic environments

Coralie Barth-Jensen

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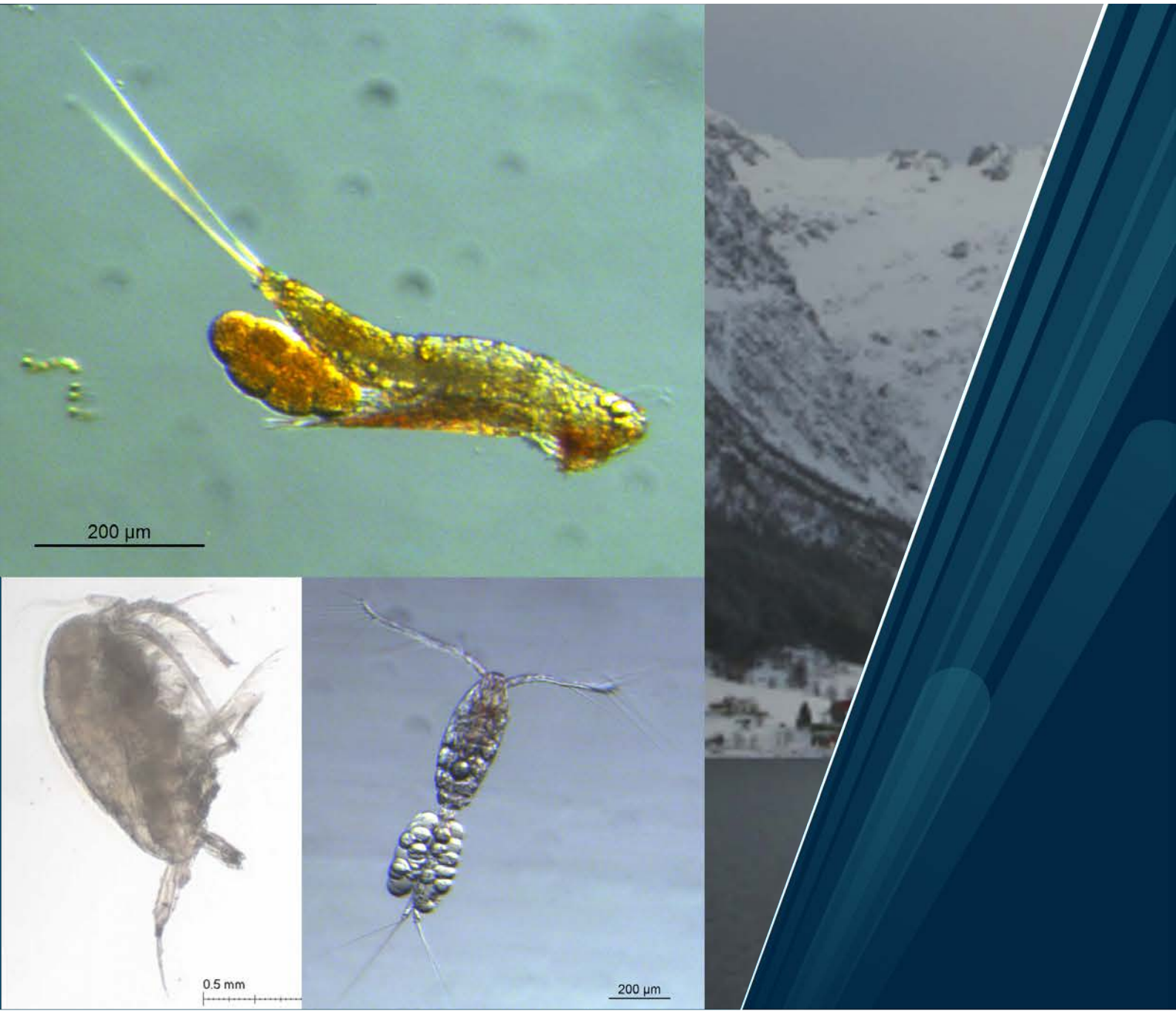

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Acknowledgements

“I've learned that people will forget what you said, people will forget what you did, but people will never forget how you made them feel.”

Maya Angelou

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Summary

Small copepods (≤ 2 mm body length) are one of the most abundant mesozooplankton in Arctic and sub-Arctic marine ecosystems. The abundance of small copepods has generally been underestimated in zooplankton studies due to the common use of nets with a mesh size ≥ 180 µm, which poorly retain small copepods. The use of finer mesh size helped to gain new insights into the biology and physiology of small copepods, which, in turn, started to raise awareness of the ecological role of small copepods in marine ecosystems. Small copepods link the microzooplankton to higher trophic levels and affect biogeochemical cycles in marine ecosystems. Investigating small copepods can therefore improve our understanding of the food web interactions and carbon flux within the ecosystems. However, the quantification of the impact of small copepods on any ecological process is difficult because of the limited knowledge available on their metabolic rates. Metabolic rates are temperature-dependent and include, e.g., growth rates, respiration rates, ingestion rates, and excretion rates. The growth rates are essential to quantify the secondary production rate of a species and are used to understand the carbon flow through the food web. For copepods, female growth rates are assumed to be their egg production rates, which are calculated using the temperature-dependent egg hatching rate. The aim of this thesis is to investigate the egg hatching rate, population dynamics, and secondary production rate of some of the less-known small copepods species. Three species were chosen among the most abundant small copepods in high-latitude ecosystems to reflect the diversity of life histories found within the small copepod community: *Oithona similis*, *Microsetella norvegica*, and *Microcalanus pusillus*.

For this thesis, we first investigated the temperature response of the egg hatching rates and egg hatching success of *Oithona similis*, *Microsetella norvegica*, and *Microcalanus pusillus* at low temperatures (**Paper I**). Then, the biomass and population dynamics of these three copepods were described for Arctic and sub-Arctic ecosystems (**Paper II and III**). The combination of the collected data enabled the estimation of the production rates of *O. similis*, *M. norvegica*, and *M. pusillus* in three sub-Arctic fjords (**Paper III**). The obtained production rates were compared to those of two common large copepod species, *Calanus finmarchicus* and *Metridia longa* (**Paper III**).

The temperature dependency of the egg hatching rate of small copepods is species-specific and can differ widely even among similar-sized species. The egg hatching rate was slower for the egg-carrying species *O. similis* and *M. norvegica* compared to free-spawning *M. pusillus*. The egg hatching rate of *M. norvegica* shows an unusual plateau at temperatures higher than 8°C, which may indicate a narrow thermal plasticity of the species and a possible local temperature adaptation or genetic differentiation of the populations. In comparison to the hatching rates, the egg hatching successes were markedly different among species and not dependent on temperatures except for *M. norvegica*. The higher hatching success of *M. norvegica* between 5°C and 8°C reinforces the possibility of narrow thermal plasticity of *M. norvegica* Arctic populations. These differences in the temperature response illustrate the error that can derive from the use of one species to model other small copepod species.

The population dynamics of the three studied species also showed different patterns. *M. norvegica* has a time-limited reproduction resulting in a short but intense reproductive season

and overwintering as adults. In contrast, *O. similis* and *M. pusillus* have continuous reproduction, where winter is used as recruitment period for a second generation. The phenology of each species seems to partially reflect the species' thermal adaptability of the and the advantages attributed to their particular life histories (such as the reduction of potential inter-specific competition and the lowering of predation pressure during winter). The success of *M. norvegica* in high-latitude ecosystems might rely on its feeding on specific food sources that are not preferred by other species and on its vertical migration to warmer surface waters during its reproductive period. The success of *O. similis* and *M. pusillus* may be partly due to their affinity to low temperatures and ability to produce and recruit two generations a year.

One of the most important findings of this thesis is the high biomass and production revealed by the quantitative sampling of the small copepods. The biomass and production of small copepods could be equal to or even higher than that of large copepods, regardless of the season. However, large spatial and interannual variations were observed. This study stresses the necessity to include appropriate sampling gear targeting small copepods in zooplankton studies. In Balsfjord, the small copepod production could equal 0.3 to 27% of the primary production. Therefore, small copepods have a significant role in the food web and carbon cycling of high-latitude fjords.

This study answers the growing demand for data on the metabolic rates of small copepods needed to calculate their impact on different ecological processes, such as carbon cycling and the trophic interactions in marine food webs. The findings of this thesis advance the knowledge of the various life-history strategies and the production potential of small copepods in high-latitude ecosystems.

List of papers

This synthesis is based on the following papers and are referred to in the text as **Paper I-III**.

Paper I

Barth-Jensen C, Koski M, Varpe Ø, Glad P, Wangensteen OS, Præbel K, Svensen C (2020) Temperature-dependent egg production and egg hatching rates of small egg-carrying and broadcast-spawning copepods *Oithona similis, Microsetella norvegica* and *Microcalanus pusillus*. Journal of Plankton Research 42:564-580

Paper II

Barth-Jensen C, Daase M, Ormańczyk MR, Varpe Ø, Kwaśniewski S, Svensen C (2022) High abundances of small copepods early developmental stages and nauplii strengthen the perception of a non-dormant Arctic winter. Polar Biology 45:675-690

Paper III

Barth-Jensen C, Svensen C, Varpe Ø, Coguiec E, Glad P, Beroujon T, Kristiansen S, Koski M. High contribution of small copepods to zooplankton secondary production in Norwegian high-latitude coastal fjord ecosystems. Manuscript

Author contributions

	Paper I	Paper II	Paper III
Concept and idea	CBJ, CS	CBJ, CS	CBJ, CS
Study design and methods	CBJ, CS, KP, OSW	CBJ, CS, MD	CBJ, CS, PG
Data gathering and interpretation	CBJ, PG, OSW, ØV	CBJ, CS, MD, MRO, SK1, ØV	CBJ, CS, EC, PG, SK2, TB, ØV
Manuscript preparation	CBJ, CS, ØV, MK, KP	CBJ, CS, MD, ØV, SK1, MRO	CBJ, CS, EC MK, ØV

CBJ = Coralie Barth-Jensen

CS = Camilla Svensen

EC = Estelle Coguiec

KP = Kim Præbel

MD = Malin Daase

MK = Marja Koski

MRO = Mateusz R. Ormańczyk

OSW = Owen S. Wangensteen

SK1 = Sławomir Kwaśniewski

SK2 = Svein Kristiansen

TB = Théo Beroujon

PG = Peter Glad

ØV = Øystein Varpe

Supervisors

Professor Camilla Svensen, Department of Arctic and Marine Biology, Faculty of Bioscience, Fisheries and Economics, UiT the Arctic University of Norway, Tromsø, Norway

Professor Peter Thor, Department of Aquatic Resources, Swedish University of Agricultural Sciences, Lysekil, Sweden

Professor Maria Koski, National Institute for Aquatic Resources, Technical University of Denmark, Kongens Lyngby, Denmark

Professor Øystein Varpe, Department of Biological Sciences, University of Bergen, and Norwegian Institute for Nature Research, Bergen, Norway, and The University Centre in Svalbard (UNIS), Longyearbyen, Norway

1 Introduction

1.1 Copepods in Arctic food webs

Arctic and sub-Arctic marine ecosystems are characterized as highly seasonal and cold, with the potential presence of seasonal or year-round ice cover. The phenology of the primary producers in these high-latitude ecosystems is shaped by the extreme oscillations of light regime from the 24-hour winter darkness (polar night) to the 24-hour summer daylight (midnight sun). In spring, the onset of the phytoplankton bloom is prompted by a combination of light conditions and stratification of the water column, leading to a relatively short and high primary production peak (Archer et al. 2000, Wassmann 2011, Juul-Pedersen et al. 2015). Following the spring bloom, the present seasonal development of the primary production includes a lower summer production and a potential autumn peak if the environmental conditions are favorable. However, the anthropogenically induced temperature increase is a main driver of changes within the Arctic marine ecosystem, including the loss of sea ice, a longer open water season, and the warming of the water column (Stroeve et al. 2012, Edwards 2017, Balazy et al. 2021). Current climate projection models predict an increase of +0.4°C decade^{-1} of surface water temperatures in the Barents Sea until 2100 (Alexander et al. 2018). These changes can potentially affect both the phenology of primary producers as well as the life-history patterns of Arctic grazing species.

High-latitude copepod communities are the main grazers of primary producers because of their overall abundance and diversity. Copepods, as poikilothermic ectotherms, have already started to respond on a population level to the increase of water temperatures, demonstrated by the ongoing poleward movement of Atlantic and Arctic copepods (Beaugrand et al. 2002, Feng et al. 2018, Evans et al. 2019, Campbell et al. 2021). A change in the ratio of small to large copepods, already observed in some Arctic copepod communities, will likely have cascading effects through the whole food web (Węsławski et al. 2009, Balazy et al. 2018, Møller & Nielsen 2019, Bouchard & Fortier 2020). Copepods are prey to carnivorous zooplankton, fishes, sea birds, and mammals, which gives copepods a key role in the energy flux in the Arctic (Falk-Petersen et al. 1990, Saito & Kiørboe 2001, Pedersen et al. 2008, Falk-Petersen et al. 2009, Descamps et al. 2022).

Small copepods have a large impact on the microzooplankton and bacterioplankton, the carbon flux and other nutrient cycles, which makes small copepods essential for modelling food webs and carbon flux (Titelman et al. 2008, Seuthe et al. 2010, Mayor et al. 2020, Koski & Lombard 2022). Physiological responses related to climate change brings uncertainty already for well-studied species, shown by divergent views on the resilience of the Arctic *C. glacialis* in the future Arctic (Renaud et al. 2018, Ashlock et al. 2021). Large copepods can have lower optimum temperatures and lower metabolic rates, which makes them physiologically less efficient at higher temperatures (Pasternak et al. 2013, Balazy et al. 2021). Large copepods also rely on a match between their reproductive strategies and the early spring bloom, which can make them vulnerable to a timing mismatch between the spring phytoplankton bloom and their peak reproduction (Søreide et al. 2010, Ashlock et al. 2021, Campbell et al. 2021). However, the knowledge gap for biological and metabolic rates is larger for small copepods than for large copepods, making future predictions hazardous. Hence, longer open water seasons and increasing water temperatures may affect the physiology and phenology of primary

Table 1. Generalization of life-history traits and function differences between large and small copepods at high latitudes.

Trait or field observation	**Small copepods**	**Large copepods**	**References**
Populations abundances	High	Medium-Low	Madsen et al. 2008, Arendt et al. 2013
Individual biomass	Medium or Low	High	Madsen et al. 2001, Lischka & Hagen 2007
Lipid reserves	Small	Large	Falk-Petersen et al. 1987, Norrbin et al. 1990, Auel & Hagen 2005, Lee et al. 2006
Relevance of species to the energy transfer to higher trophic levels	Low	High	Hopkins et al. 1989
Diapause	No	Can occur depending on species	Tande 1982, Norrbin 1994
Trophic group	Omnivorous and flux-feeder	Mainly herbivorous or carnivorous, can switch to other prey if needed	Wickstead 1962, Auel & Hagen 2005, Søreide et al. 2008, Cleary et al. 2016, Cleary et al. 2017
Reproduction type	Income breeding	Capital breeding and income breeding	Varpe et al. 2009, Varpe & Ejsmond 2018
Weight-specific metabolic rates (e.g. respiration, feeding)	High	Low	Hansen et al. 1997, Kiørboe & Hirst 2014

and secondary producers on the individual, species, and population levels, but, as of now, large insecurities stem from insufficient knowledge of individual species.

The Arctic copepod populations are composed of large and lipid-rich species, such as the primarily herbivorous *Calanus* spp. and the carnivorous *Paraeuchaeta* spp., and smaller and less energy-rich species, such as *Oithona* spp., *Pseudocalanus* spp., and *Microcalanus* spp. (Hop et al. 2021, Box 1). The copepod community can also be separated into true Arctic species, i.e., species that are endemic to the Arctic, such as *Calanus glacialis, Neocalanus plumchrus* and *Pseudocalanus minutus*, and boreal and cosmopolitan species that are advected into the Arctic from the Fram Strait or the Bering Strait, such as *Calanus finmarchicus, Calanus marshallae*, and *Oithona similis* (Plourde et al. 2005,

Pasternak et al. 2013, Ershova et al. 2016, Ashlock et al. 2021). True Arctic species are generally lipid-rich and thrive at lower temperatures but may have a less performant metabolism at higher temperatures, while boreal species are smaller than true Arctic species of the same genus and may not survive in all parts of the Arctic due to their preference of warmer waters (Pasternak et al. 2013, Ershova et al. 2016, Ershova et al. 2017, Ashlock et al. 2021, Table 1). Cosmopolitan species are also smaller than Arctic species and have broad thermal adaptability but do not necessarily have their temperature optimum at low temperatures (Nielsen et al. 2002, Balazy et al. 2021). The use of the term "cosmopolitan" should be subjected to caution, as recent genetic analyses revealed that it had been erroneously used for some species (e.g., Cornils et al. 2017, Box 2). My thesis aims to investigate the role of some of the less-known small and abundant cosmopolitan species in Arctic and sub-Arctic ecosystems.

Box 1: Size matters

Copepods are a diverse group of species that have species-specific and ontological stage differences in body sizes, ranging from egg sizes of a few micrometers to large adults of several millimeters (WoRMS Editorial Board 2022). In trait-based ecology, body size is a "master trait", which is a trait that "transcends several functions and are major determinants of zooplankton ecological strategies" (Litchman et al. 2013). Therefore, size matters when comparing species-specific biological rates, and size differences must be considered when comparing species. Body size, or volume, limits the amount of lipids that can be stored, which itself governs the possibility that a species is able to hibernate or produce eggs only from stored lipid reserves, i.e., capital-breeding (Norrbin 1991, Varpe & Ejsmond 2018, Table 1). Body size also governs biological processes such as metabolic rates (e.g., fecundity, ingestion rate, respiration rate), which have an allometric relation to body size (Kiørboe & Sabatini 1995, Hansen et al. 1997, Roa & Quioñes 1998, Kiørboe & Hirst 2014).

Body length of a copepod can be defined as the prosome length or the total length. The threshold used to distinguish between small and large species is usually 1 mm (Turner 2004) or 2 mm (Roura et al. 2018, Hop et al. 2019), and can refer to the adult size or the size of each life stage. This means that one species can belong to the small size group in its early life stages before switching to the large size group (Turner 2004). However, the consensus is to refer to the female body size when dividing species into small and large copepods.

Box 2: Cosmopolitanism or species complex?

Cosmopolitan species refers to species that have a large habitat and latitude range (Blanco-Bercial et al. 2011). They are usually eurythermal and euryhaline species, i.e., they have a wide tolerance range to temperature and salinity, respectively. Cosmopolitan species are thought to be relatively common in marine ecosystems and include several small copepod species such as *Oithona similis, Acartia tonsa,* and *Microsetella norvegica* (Knowlton 1993, Nielsen et al. 2002, Drillet et al. 2011, Koski et al. 2014). However, recent studies of some of the copepod "species" termed cosmopolitan revealed that they are not one species but species complexes (Klautau et al. 1999, Aarbakke et al. 2014, Lajus et al. 2015, Cornils et al. 2017). Species complexes are groups of sibling or cryptic species, i.e., species morphologically similar or even identical that may be reproductively isolated (Calow 2009).

Previously, distinguishing cryptic or sibling species was a major challenge, as visual identification was the only tool available for the determination of a species. This complex task requires meticulous dissection of a specimen. For example, the visual differentiation of the sibling species *Microcalanus pusillus* and *M. pygmaeus* relies on the detection of serrations on the terminal spines on the second and fourth exopods, and on the antennule to prosome length ratio (Koszteyn et al. 1991). In addition, a detailed morphological study may not be sufficient due to the lack of a unique feature for each species, as it is the case for *C. finmarchicus* and *C. glacialis* (Choquet et al. 2018). Fortunately, molecular analyses are becoming more popular with the increasing availability of analyzing instruments and the decreasing associated costs (Ershova et al. 2021). These analyses compare the sequences of DNA fragments from a single specimen or a community to a reference library, which contains the sequences of specific DNA fragments. The reliability of molecular identification permits to avoid the human bias of visual identification, but missing sequences in the reference libraries can prevent the identification of some species (Wangensteen et al. 2018).

Although cosmopolitan species exist, several species lack a genetic study of their populations, leaving doubt as to the extent of cosmopolitanism within the marine realm (Blanco-Bercial et al. 2011, Darling & Carlton 2018). Are cosmopolitan species more an exception than previously thought? The increase in studies focusing on the genetics of populations will likely challenge our current knowledge of species, including their biogeographical boundaries and physiological tolerances. Therefore, caution needs to be applied when using the metabolic or physiological rate of a species from different regions to another to avoid some erroneous conclusions. Local adaptation has been verified on several copepod species, where populations from separate regions behave differently when subjected to the same environmental forcing, such as a temperature change (Lonsdale & Levinton 1986, Hong & Shurin 2015). Similarly, sibling species can also display different thermal adaptations (Drillet et al. 2008, Titelman et al. 2008, Hopcroft & Kosobokova 2010, Ershova et al. 2016). Future studies should investigate if, in some instance, local adaptation might be an artefact of the current misrepresentation of some species as cosmopolitan instead of a complex of sibling species.

1.2 Small copepods - Knowns and unknowns

Small copepods (female body size ≤ 2 mm) are usually the most abundant mesozooplankton group in Arctic and boreal ecosystems and can constitute a substantial portion of the zooplankton biomass (Ussing 1938, Digby 1954, Pasternak et al. 2000, Svensen et al. 2011, Basedow et al. 2014, Darnis & Fortier 2014, Middelbo et al. 2019). Similar to the larger copepods, small copepods also link both primary producers and the microbial food web to higher trophic levels (Seuthe et al. 2010, Roura et al. 2018, Zeldis & Décima 2019, Table 1). However, small copepods have not been historically recognized as major prey in the diet of post-larval and adult fishes, though recent studies challenge this view (Hopkins et al. 1989, Saito & Kiørboe 2001, Pedersen et al. 2008, Tang et al. 2011, Mitsuzawa et al. 2017, Table 1). One of the main reasons the study of the large lipid-rich species took precedence over that of smaller copepods might be that relatively little is known of the ecological role of small copepods (Figure 1). For example, the number of publications having "*C. finmarchicus*" in their titles, abstracts, or keywords has grown exponentially over the last 60 years (Figure 1). The number of publications focusing on the large *M. longa* and the small *O. similis* has also increased in recent years, but less than *C. finmarchicus*. Research on *Microcalanus* spp. and *Microsetella* spp. has only accelerated in the last 20 years (Figure 1). The study of these two species is challenged by the failure to rear them in the laboratory, limiting the possibility of learning more about them. However, a better understanding of the biology and metabolism of small copepods is essential to improve our ability to make accurate future predictions in the face of climate change.

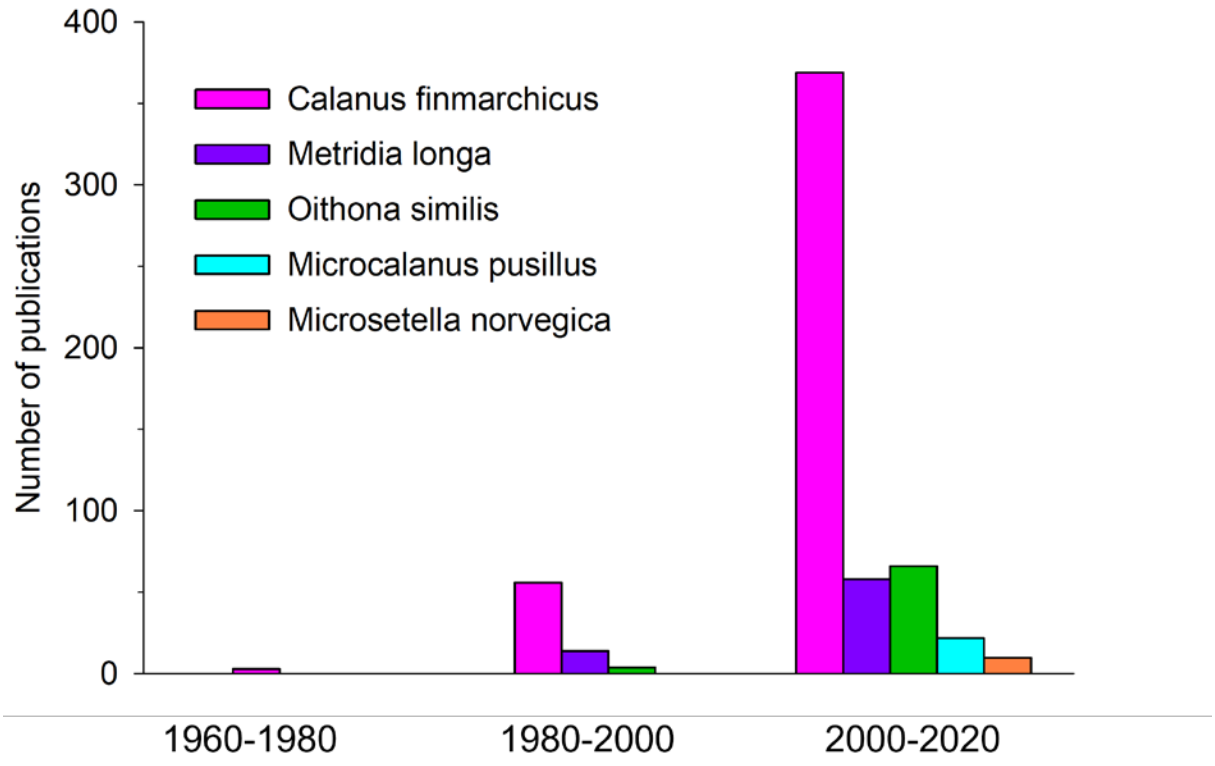

Figure 1. Total number of scientific publications between 1960 and 2020 that contain in their title, abstract or keywords both the word "Arctic" and the full name of one of the following species:" Calanus finmarchicus*",* "Metridia longa*",* "Oithona similis*",* "Microcalanus pusillus*" or* "Microsetella norvegica*". The data collection for this graph was conducted on the 30/09/2022 on the search engine Web of Science (www.webofscience.com).*

The knowledge gap is large for metabolic rates of small copepod species, such as respiration rate, excretion rate, ingestion rate, and growth rate, especially at low temperatures (Nielsen & Andersen 2002, Madsen et al. 2008). Additionally, high-latitude studies are relatively scarce compared to that of large copepods but are needed to describe the seasonal population structures and overwintering strategies of small copepods (Svensen et al. 2011, Dvoretsky & Dvoretsky 2015). These knowledge gaps hinder the description and quantification of small copepods contributions to different ecosystem processes, including secondary production and carbon cycling. For example, studies assessing the contribution of small copepods invariably report that their secondary production is significant and should be considered (Castellani 2001, Basedow et al. 2014). However, the secondary production of less-studied species is assessed by using the reproductive rates of similar-sized species or species of the same taxonomic order, which is likely erroneous (Nielsen & Andersen 2002, Madsen et al. 2008, Andersen et al. 2011). Another example shows that the contributions of small copepods to the carbon cycling are largely underestimated (Cleary et al. 2016, Steinberg 2017, Roura et al. 2018, Koski et al. 2021). Mayor et al. (2020) suggested that population dynamics and metabolic rates of small copepods must be included to model the biological carbon pump. Knowledge relative to the small copepod community is key to predict the future of the Arctic marine ecosystem functioning. It is essential to better our understanding of the role of small copepods in the pelagic food web and nutrient cycling of high-latitude ecosystems.

1.3 Main biological traits of *Oithona similis*, *Microsetella norvegica* and *Microcalanus pusillus*

Three species were targeted for this study to include the diversity found in the life history of small copepods: *O. similis*, *M. norvegica*, and *M. pusillus* (Figure 2, Table 2). These species are among the most abundant copepods in Arctic and sub-Arctic marine ecosystems (Ashjian et al. 2003, Dvoretsky & Dvoretsky 2009a, Apollonio 2013, Arendt et al. 2013). All three copepod species are comparable in terms of body size but have different life-history traits (e.g., spawning strategy, trophic regime, feeding strategy; Table 2).

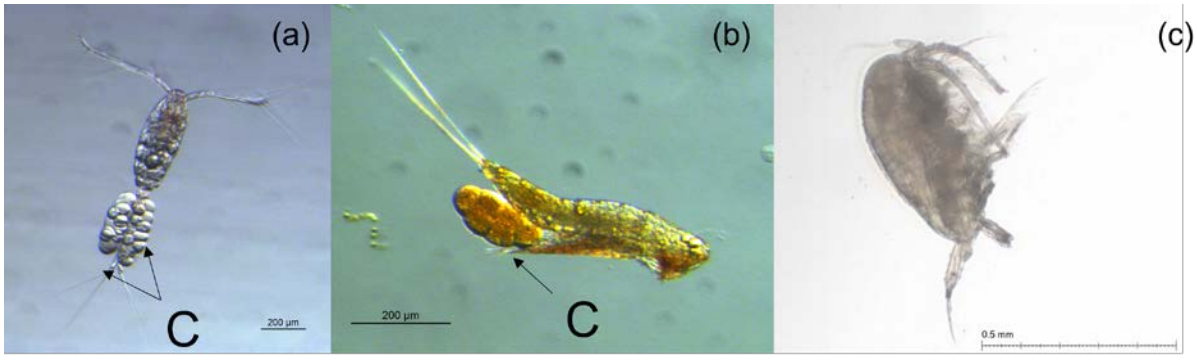

Figure 2. Pictures of (a) Oithona similis*, (b)* Microsetella norvegica*, and (c)* Microcalanus pusillus*. A scale is given for length reference (a, b: 200 µm; c: 500 µm). The arrows point to the eggs sacs, and the sum of eggs inside that egg sacs define the size of the clutch (C). Photos by Coralie Barth-Jensen.*

Table 2. Comparison of the main biological traits of O. similis, M. norvegica *and* M. pusillus*. Modified from (Benedetti 2015).*

Species name	*Oithona similis*	*Microsetella norvegica*	*Microcalanus pusillus*	References
Order	Cyclopoida	Harpacticoida	Calanoida	WoRMS Editorial Board 2022
Family	Oithonidae	Ectinosomatidae	Clausocalanidae	WoRMS Editorial Board 2022
Female prosome length (mm)	0.7-0.95	0.3-0.76, average ≈ 0.5*	0.6-0.7	Dvoretskii 2007, Koski et al. 2007, WoRMS Editorial Board 2022
Female carbon content (µg C)	0.32 – 0.61	0.32 – 0.51	0.76 – 1.26	Barth-Jensen et al. 2020 (**Paper I**)
Spawning strategy	Sac-spawner	Sac-spawner with possible early release of egg sacs	Broadcast-spawner	Norrbin 1991, Kiørboe & Sabatini 1994, Koski et al. 2014
Trophic Regime	Omnivore	Omnivore-detritivore	Omnivore	Norrbin 1991, González & Smetacek 1994, Yamaguchi et al. 2002, Maar et al. 2006, Castellani et al. 2008
Feeding strategy	Active ambush	Cruise, settling on sinking marine snow	Filter	Svensen & Kiørboe 2000, Yamaguchi et al. 2002, Koski et al. 2007
Preferred pelagic layer and environment	Surface and subsurface, coastal, and oceanic	Surface and subsurface, coastal	Subsurface and mesopelagic, coastal	Ashjian et al. 2003, Zamora-Terol et al. 2014, Arendt et al. 2016, Svensen et al. 2018, Koszteyn et al. 1991

* The total length is reported here instead of the prosome length.

Compared to other small copepods, the population dynamics and reproductive rates of *O. similis* are relatively well-studied in high-latitude environments (Nielsen et al. 2002, Lischka & Hagen 2005, Dvoretsky & Dvoretsky 2009b). *O. similis* reproduces year-round, with two egg production peaks in the spring and autumn. Therefore, high-latitude *O. similis* populations contain all copepodid stages year-round, with a higher proportion of younger stages right after the egg production peaks. Comparatively, *M. norvegica* and *Microcalanus* spp. are poorly studied in Arctic and sub-Arctic environments (but see Ashjian et al. 2003, Lischka & Hagen 2016, Svensen et al. 2018). *M. norvegica* reproduces during spring and summer, which is easily ascertained by the presence of egg-carrying females (Svensen et al. 2018, Koski et al. 2021). As for the genus *Microcalanus*, the first impediment to a proper study is the difficulty of species identification of the sibling species composing the group: *M. pusillus* and *M. pygmaeus* (Norrbin 1991, Ashjian et al. 2003, Walkusz et al. 2009, WoRMS Editorial Board 2022). *M. pygmaeus* is assumed to prefer oceanic environment, while *M. pusillus* prefers coastal areas (Koszteyn et al. 1991). The main reproductive periods of *Microcalanus* spp. seem to be in summer and late winter, but continuous reproduction seems likely (Norrbin 1991, Lischka & Hagen 2016). The reproductive rates and parameters (i.e., egg hatching rate, development time, clutch size, and hatching success) of *M. norvegica* and *Microcalanus* spp. are unknown at low temperatures. Uye et al. (2002) studied *M. norvegica* in a temperate habitat (17 to 27°C) and found that the egg hatching rate of *M. norvegica* increased with increasing temperatures.

2 Objectives

Main objective:

To describe the population dynamics and the secondary production of *Oithona similis*, *Microsetella norvegica*, and *Microcalanus pusillus* in high-latitude ecosystems.

Secondary objectives:

1. Determine temperature-dependent responses of the egg hatching rates, egg hatching success, and egg production or clutch size of *O. similis*, *M. norvegica*, and *M. pusillus* at low temperatures (**Paper I**).
2. Describe the seasonal age structures and overwintering strategies of *O. similis*, *M. norvegica*, and *M. pusillus* populations (**Paper II and III**).
3. Estimate the daily seasonal and annual production rates of *O. similis*, *M. norvegica*, and *M. pusillus* applying two independent methods (**Paper III**).
4. Compare biomass, phenology, and production rates of *O. similis*, *M. norvegica*, and *M. pusillus* with those of the large copepods *Calanus finmarchicus* and *Metridia longa* (**Paper II and III**).

3 Methods

The egg hatching rates of *O. similis*, *M. norvegica* and *Microcalanus* spp. were investigated at low temperatures (**Paper I**) and included the genetic identification of the *Microcalanus* specimens used. The egg production of *Microcalanus* spp. and the seasonality of the clutch sizes of each species were observed (**Paper I and III**). The seasonal biomass and population dynamics of small copepods were described in three north-Norwegian fjords (**Paper III**), and winter biomass and population structures were described in Svalbard fjords, the Barents Sea, and the shelf north of Svalbard (**Paper II**). The temperature-dependent hatching rate coupled with the seasonal dynamics of each species permitted the estimation of the copepod secondary production (**Paper III**). The comparisons with larger copepod species were drawn in **Paper II and III**.

3.1 Areas of study

The study area is located in the Atlantic-influenced inflow shelf of the Arctic Ocean and the north-Norwegian coastal area and spans over a wide latitudinal range (69°N to 81°N), which includes the western Barents Sea and Svalbard fjords as well as mainland fjords that are open towards the Barents Sea and exchange water with the Norwegian Coastal Current (Svendsen 1995, Mankettikkara 2013, Wassmann et al. 2020, Figure 3). The ecosystems studied have low water temperatures and share an extreme seasonal fluctuation in irradiation, which governs an intense and relatively short primary production period (Eilertsen & Frantzen 2007). A more detailed overview of the different study locations is presented in the respective papers (**Paper I, II, and III**).

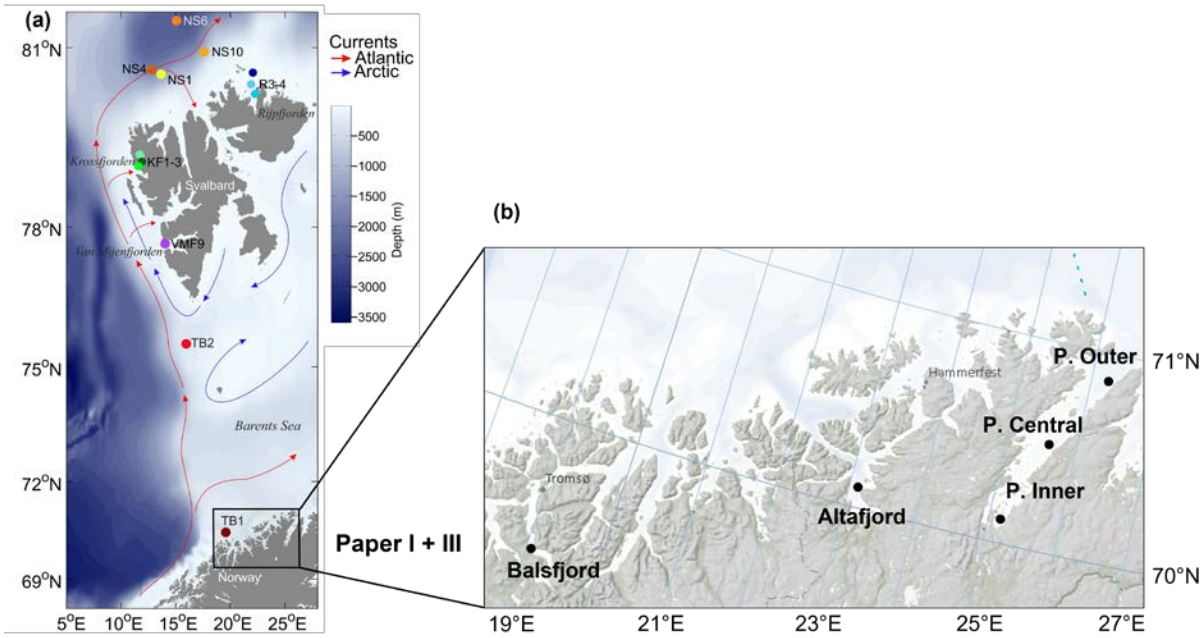

*Figure 3. Map of the sampling area covered in this thesis. (a) Stations sampled in **Paper II**. Bathymetry and currents are given for reference. Modified from **Paper II**. (b) Stations sampled in **Papers I and III**. For the Porsangerfjord stations, Porsangerfjord was abbreviated P. for convenience. Base map made at the Norwegian Polar Institute Barentsportal (https://geokart.npolar.no/Html5Viewer/index.html?viewer=Barentsportal).*

The Barents Sea and adjacent fjords are located in the Atlantic-influenced inflow shelf of the Arctic Ocean (Wassmann et al. 2020). This region is characterized by the advection of warm and saline waters of Atlantic origins (red arrows in Figure 3a), which also advects sub-arctic and boreal biota into the region. The Arctic and sub-Arctic shelves and coastal area are highly productive and support various fisheries (Falk-Petersen et al. 1990, Frantzen 2007, Węsławski et al. 2009, Thomas 2021). The Barents Sea is a region of high interest for the study of the effect of temperature rise in the Arctic, as it might be strongly affected by the warming of the water masses (Alexander et al. 2018). Therefore, the study of the present population dynamics and secondary production can work as a future reference for modelling the changes in the region, and the study of the temperature-dependent egg hatching rate may help model future changes to the production of small copepods in this region.

3.2 Field sampling

Field sampling was used to obtain the abundances and clutch sizes of *O. similis*, *M. norvegica* and *Microcalanus* spp., and to observe the seasonal age structure and dynamics of the copepod populations. Experimental specimens were also collected during the field sampling.

The field sampling was conducted onboard R/V Hyas (**Paper I and III**), R/V Johann Ruud (**Paper III**), and R/V Helmer Hanssen (**Paper II**) and comprised hydrological sampling, water sampling, and zooplankton sampling. A variety of tools and procedures were used due to the diverse onboard facilities and procedures on the different research vessels, which sometimes restricted the use of specific tools or chemicals onboard. Detailed descriptions of field sampling are available in the respective papers, but the main procedures used during this thesis are summarized here. This chapter explains the use of different sampling as well as the choice of gear to reach my thesis' goals.

Hydrography

Temperature, salinity, and fluorescence are necessary environmental parameters to understand and assess the population dynamics and biological rates of copepods. These hydrographical data were collected at every sampling occasion with a conductivity, temperature, and depth profiler (CTD, **Paper I, II, and III**). Supplementing hydrographical profiles from Balsfjord, Altafjord and Porsangerfjord were available from the Havmiljødata dataset (monitoring program running from 1928 to 2018, https://dataverse.no/dataverse/nmdc, **Paper III**).

Chl *a*, POC and PON, and nutrients

Discrete water samples were collected to provide background data on the food available for copepods, which were the chlorophyll *a* (Chl *a*) and particulate organic carbon (POC), and nitrogen (PON) concentrations. A vertical profile was made by sampling water at different depths, and the filtration was done onboard when feasible or back at UiT (**Paper I, II, and III**). For each depth, total Chl *a* was sampled in triplicates, and for some studies, one replicate for Chl *a* ≥ 10 µm (**Paper III**), and three pseudo-replicates for POC and PON (**Paper II and III**) were also taken. The procedures to obtain these environmental values are described in the respective papers.

In addition to the Chl *a*, POC, and PON, the concentration of nutrients (nitrate + nitrite, phosphate, and silicate) was investigated in Balsfjord between August 2015 and August 2016. The

methodological details are in **Paper III**. The changes in nutrient concentrations helped define the seasons in the fjords (**Paper III**).

Zooplankton

The choice of sampling method was crucial in obtaining trusted abundances and proportions of the different copepodid stages of *O. similis*, *M. norvegica*, and *M. pusillus*. The capture efficiency of a net (*CE*, %) is a function of the copepod width to mesh size ratio (*R*):

Equation 1 $$CE = \frac{1}{1+ e^{-8.9 \times (R-1)}}$$ *(Nichols & Thompson 1991)*

Net meshes ≥ 180 µm are commonly used for zooplankton sampling (Gallienne & Robins 2001). These mesh sizes are unsuitable for small copepods as well as nauplii and young copepodids of the larger species because their slender bodies can easily pass through the meshes leading to their underestimation (Table 3, Dugas & Koslow 1984, Pasternak et al. 2000, Turner 2004). For example, a 64-µm mesh net would capture a young copepodid stage III (CIII) *M. norvegica*, but less than 2% would be retained with a mesh ≥ 180µm (Table 3). This sampling flaw leads to a general underrepresentation of small copepod communities and the underestimation of their abundances and biomasses (Turner 2004).

Bottle- and net-sampling (64- or 90-µm mesh) were used in this study for quantitative sampling of the young stages of small copepods. The bottle-sampling of copepods was followed by a filtration of the water on a 20-µm sieve for collection of the smaller zooplankton fraction. The identification of the copepod species and stage is described in **Paper I, II, and III**. For sampling the experimental specimens (**Paper I**), a non-filtering cod end was equipped on the WP-2 nets (64- or 90-µm mesh) to ensure gentle filtration, thereby avoiding damage to the copepods. On deck, the content of the cod end was placed in 20 L of surface seawater and transported to the laboratory within 2 h. Copepod samples were stored in an 8°C cold room, where the identification and handling of the copepods was conducted prior to incubation for experiments. The protocol for the experimental handling of the copepods is described in **Paper I**.

Table 3 – Capture efficiency (%) of 240-, 180- and 64-µm mesh sizes on varied species and life stages of copepods, calculated from Equation 1 (Nichols & Thompson 1991).

Species	Stage	Size (µm)	Width (µm)	Capture efficiency (%)			Measurement reference
				240 µm	180 µm	64 µm	
Microcalanus pusillus	Female	521	248	57	97	100	This study
Oithona similis	Female	440	169	7	37	100	This study
Microsetella norvegica	Female	516	132	2	9	100	This study
Microsetella norvegica	Copepodid III	375	96	0	2	99	Diaz and Evans (1983)
Pseudocalanus spp.	Nauplius I	157	87	0	1	96	Siefert (1998), Nichols and Thompson (1991)
O. similis	Nauplius I	100	59	0	0	33	This study
Calanus spp.	Nauplius I	190-240	110	1	3	100	Nichols and Thompson (1991)

3.3 Biomass conversion

The field abundances of each stage (ind. m^{-3}) were converted to biomass using published length-to-carbon relationship for each species and developmental stage (individual carbon weight, µg C ind^{-1}). Egg carbon content was calculated based on volumes (**Paper I and III**). For **Paper II**, nauplii, copepodid, and adult biomass were taken from the published biomass in Svensen et al. (2019). The stage-specific biomass for each copepod in **Paper III** is converted from length-to-carbon relationship, using the average length measured on 30 to 60 copepodids of each stage (CI-CIII, CIV-CV, males, and females).

3.4 DNA identification of Microcalanus

The species identification of *Microcalanus* was conducted both morphologically and genetically. *Microcalanus pusillus* and *M. pygmaeus* are morphologically similar and hard to differentiate visually (Box 2). Visual identification relies on differences in the terminal spines on the second and fourth exopods, which are serrated for *M. pusillus* and smooth for *M. pygmaeus* (Koszteyn et al. 1991). Additionally, the antennule to prosome length ratio is longer for *M. pygmaeus* than for *M. pusillus* (Koszteyn et al. 1991). We performed morphological identification on 58 individuals from Balsfjord using the antennule-to-prosome length ratio. Genetic analysis was thereafter carried out on the same individuals (**Paper I**). DNA was extracted from individual females, followed by the amplification of the Leray fragment of the mitochondrial cytochrome c oxidase subunit I (COI). The sequencing and the bioinformatic cleaning steps to obtain usable sequences are described in **Paper I**. The most abundant sequence obtained from each specimen was compared to sequences from the barcode reference database BOLD for *M. pusillus* and *M. pygmaeus*.

3.5 Estimating secondary production

History overview and different methods to estimate secondary production

Early concepts of production can be found already in 1919 (Kimmerer 1987), emerging from the need to assess the population yield of species of human interest (e.g., harvest of fish population). The production of a population describes the rate of biomass accumulation (Calow 2009), regardless of the fate of the produced biomass (Kimmerer 1987). Production is mainly used to quantify the energy flow within a food web, evaluating how much a population can be harvested for human use (Runge & Roff 2000, Calow 2009, Dolbeth et al. 2012).

Zooplankton species often have a complex life cycle, which includes several developmental stages. For example, copepods have 13 stages (Diaz & Evans 1983), euphausiids can have 19 stages but the number can vary inter- and intra-species and geographical location (Brinton et al. 2013, Qualls 2019), and many species of benthos have a pelagic phase and are therefore temporally part of the zooplankton (Michelsen et al. 2017). Secondary production refers to the production of the group of species feeding on the primary producers, i.e., the zooplankton.

Production (*P*) can be quantified by measuring the increase in biomass over time, given by:

Equation 2 $$P = \sum B_i \times g_i$$

With B_i and g_i the biomass and weight-specific growth rate of stage *i* (Edmondson & Winberg 1971). It includes the juvenile production, i.e., the increase in biomass from each stage to another, and the adult production, which is estimated as egg production (Runge & Roff 2000). Each life stages have its own growth rate, and growth rates can vary seasonally with temperature and food availability (Lonsdale & Levinton 1986, Uye & Sano 1998, Richardson & Verheye 1999, Uye et al. 2002, Bunker & Hirst 2004).

Ideally, the measurement of the growth rate for a species would include the frequent sampling of all the species' developmental stages throughout the year and ensuring to follow the same population over time. This is an arduous task due to the logistical constraints and cost of sampling, the movement of water carrying the zooplankton, and the time required for such a study, as some zooplankton generation times can vary from weeks to months (Hirst et al. 2005). Therefore, different approaches to simplify the estimation of growth rates have developed over time, and the main methods for estimating growth rates are reviewed in Table 4. There are three general types of methods, grouped as field-based observations, experimentally obtained values, or empirical modelling of previously acquired rates aiming to find a more general rule to growth. Each method is based on a set of assumptions and/or limitations, which will affect the results obtained (Table 4). Ignoring these conditions can severely under- or over-estimate growth and production (Runge & Roff 2000). In conclusion, the history of estimating the growth rate in zooplankton shows that no technique is perfect. Any method can be used as long as its drawbacks are known so that the results can be put into perspective.

Out of the several methods available for estimating secondary production, we chose two independent methods commonly applied for copepods (e.g., Castellani 2001, Halsband-Lenk et al. 2001, Madsen et al. 2008, Dvoretsky & Dvoretsky 2009b, Moon & Oh 2021): the weight-specific egg production rate method and the temperature-dependent model of Huntley and Lopez (1992).

Table 4. Comprehensive list of estimation methods for growth, focused on methods for copepods though some are used for other zooplankton groups. The estimation methods are divided into experimental, field-based, or empirical model, with their main assumptions and limitations provided. The table is modified from Runge and Roff (2000), with additional references from works either using or commenting on each method.

Type	Method	Assumption(s) (A) and Limitation(s)(L)	References
Experimental	Physiological models (e.g., based on assimilation and respiration)	L1) Physiological rates are complicated to obtain. L2) Large intra-specific variations with laboratory-reared results.	Huntley & Boyd 1984, Uye et al. 1986
Experimental	Weight-specific egg production rate	A1) Female growth rate equals egg production rate. A2) All developmental stages have the same growth rate as females. L1) Production is limited to the egg-laying period.	Runge & Roff 2000, Hirst & Bunker 2003
Experimental	Direct growth rate measurement (e.g., moult rate, modified moult rate, artificial cohort method)	A1) Growth is exponential during incubations. A2) Uniform age distribution within the incubated stage. L1) Stage duration must be relatively short (≤ 1.2 days) to avoid large errors in the estimated rates.	Runge & Roff 2000, Hirst et al. 2005, Hirst et al. 2014, Kimmerer et al. 2007
Experimental	Hormones and growth factor (e.g., ecdysteroid levels, proliferating cell nuclear antigen)	L1) Can only give a "labelling" rate that can be used as an "indice or correlate of growth or developmental rate".	Runge & Roff 2000, Sastri 2007, Moore et al. 1994, Gomez et al. 2001
Experimental	Biochemical and enzyme activity (e.g., chitobiase, DNA polymerase, aminoacyl-tRNA)	L1) If the size variations are large in a community, the enzyme activities will likely be a crude approximation. L2) Intra-specific variation and seasonal variations are hard to take in account.	Runge & Roff 2000, Sastri 2007, Hirst 2017
Experimental	Radiochemical (e.g., uptake, ingestion or injection of the radioisotope or stable isotope of amino-acids or dissolved organic matter)	L1) Only species that can be cultivated can be used due to lengthy incubations. L2) The radio tagging makes wastes difficult to process.	Runge & Roff 2000, Sastri 2007

Table 4. Continued.

Type	Method	Assumptions (A) and Limitation(s)(L)	References
Field-based	Demographic information (from fixed samples) or cohort analysis	A1) The population sampled is the same over time. L1) Does not work in advective systems, or with indistinct cohort structures or large laps between samplings.	Herman & Heip 1985, Kimmerer 1987
Modelling	Models based on single or multiple variables model (e.g., temperature, individual body weight or food concentration)	A1) The assumptions depend on the model, but always exists to simplify the number of variables used. A2) When used for entire communities, the growth rates transcend species within groups of species clustered together following the model's assumptions, meaning that individual species will react similarly to the same environmental stimulus within each species cluster.	Hunter & Lopez 1992, Hirst & Bunker 2003

The weight-specific egg production rate method

We estimated the production of *O. similis*, *M. norvegica*, and *M. pusillus* using the weight-specific egg production rate method (Table 4). The female weight-specific egg production rate (*SEP*, d^{-1}) is applied as the growth rate for the entire population of biomass *B* (mg C m^{-3}, Berggreen et al. 1988). Following Equation 2 (p.10), the production (*P*, mg C m^{-3} d^{-1}) of the population (including all developmental stages) can be described as:

Equation 3 $$P = B \times SEP$$

The weight-specific egg production rate is calculated as:

Equation 4 $$SEP = HR \times \frac{E}{F} \times \frac{Wegg}{Wfemale}$$ (Nielsen et al. 2002)

Or *Equation 5* $$SEP = HR \times \frac{Begg}{Bfemale}$$

Where *E* and *F* are the abundances of eggs (eggs m^{-3}) and females (ind. m^{-3}), respectively; *HR* is the temperature-dependent egg hatching rate (d^{-1}); W_{egg} and W_{female} are the individual egg and female carbon content (µg C), respectively; and B_{egg} and B_{female} are the total egg and female biomasses (mg C m^{-3}), respectively.

The seasonal abundance (*F*) and biomass (B_{female}) of female and the total population biomass (*B*) were obtained from the field samples (Chapter 3.2). The next paragraphs explain how we obtained the egg hatching rates (*HR*) and the egg abundance (*E*) needed in Equations 3, 4, and 5. A methodological discussion follows to explain the main potential bias of our experimental setup.

Egg hatching rates

The detailed experimental designs for determining egg hatching rates are described in **Paper I**, but a summary is presented here. 10 to 60 female copepods were incubated at *in situ* temperatures between 1.3°C and 13.2°C for *O. similis* (6 incubations), 3.0°C and 13.2°C for *M. norvegica* (10 incubations), and 3.0°C and 9.8°C (6 incubations) for *M. pusillus*. Each female was incubated individually without temperature acclimation in wells with filtered seawater (Nielsen et al. 2002, Halvorsen 2015). The experimental design differed for the egg-carrying copepods and the broadcast-spawning copepod.

For the sac-spawners, clutch size, defined as the total number of eggs carried in the egg sac(s) of a female (Figure 2), was obtained for each female prior to the incubations. Hatching of eggs was checked every 8 to 24 hours (depending on temperature, see **Paper I**). A hatching event for the entire clutch was defined as the time when at least one freely swimming nauplius was observed in the well. The cumulative hatching events of the sac-spawners were plotted against the incubation time: the egg hatching rate (*HR*, d^{-1}) was defined as the slope of the linear regression between the cumulative hatching events and the incubation time.

For the broadcast spawner, the eggs produced in each well (the clutch) were counted after a 24-hours incubation. The average clutch size was calculated by averaging the number of eggs in the wells where

females did produce, while egg production (eggs female^{-1} d^{-1}) was estimated as the total number of eggs produced in 24 h divided by the number of females (so it included the non-producing females). The clutches were followed thereafter every 8 h for 6 days to get the hatching time of the clutches. The mean development time (d) refers to the time between egg production and egg hatching and was calculated as the mean of all hatching events in all wells incubated at the same temperature. Hatching events for the broadcast-spawner *M. pusillus* were rather synchronous in a single incubation, as clutches were all produced within 24 h. Therefore, the estimation of the egg hatching rate (*HR*) was not determined by linear regression, but as the reciprocal of the mean development time, for all hatching events within a single incubation.

All the temperature-specific egg hatching rates were then plotted against the temperature to model the temperature-dependency of the egg hatching rate of each species, in the form of $HR = aT + b$ (with T, the temperature, and a and b, the species-specific constants, **Paper I**). The hatching rate of each species was therefore expressed as a temperature-dependent equation. These equations could be used to calculate the hatching rate of each species (needed in Equation 4 and 5) at the average *in situ* water temperature over the upper 100 m (**Paper III**). The published temperature-dependent equation for the hatching rate of *O. similis* was used at temperatures ≤ 1°C, because our equation for O. similis gave negative egg hatching rates (Nielsen et al. 2002):

Equation 6

$$HR = 4.2176 + 1.7545 \times T \quad \text{(Nielsen et al. 2002)}$$

Egg hatching success

The egg hatching success was determined by following the incubating clutches after the first nauplii appeared (similar for all species). In the first experiments, the clutches were monitored until all eggs hatched, and a few days went without an additional egg hatching from the clutches. We observed that the remaining eggs that did not hatch changed color during the experimental time. Discoloration of the eggs was interpreted as a sign of degradation (Burkart & Kleppel 1998, Drillet et al. 2011). Therefore, discolored eggs were assumed to be unviable in the following experiments, and the clutches were followed until all viable eggs had hatched.

Seasonal egg production rates

Clutch sizes vary with season (Drif et al. 2010). Estimating the *in situ* egg abundance (*E*, egg m^{-3}) relies on these clutch sizes. The clutch size of broadcast-spawners is estimated as the number of eggs laid in 24 hours, i.e., the daily egg production rate (Halsband & Hirche 2001). For *M. pusillus*, the *in situ* abundance of eggs (*E*, egg m^{-3}) was estimated as the abundance of females multiplied by the average daily egg production rate, which was obtained from the incubations and 4.8 eggs female^{-1} d^{-1} regardless of the season (**Figure 5 of Paper I**). The mean daily egg production rate of *M. pusillus* was assumed to be null from October to December, following the proposed seasonal cycle in egg production of *M. pusillus* by Norrbin (1991). For the sac-spawners, the seasonal abundance of eggs (*E*) was found by multiplying the abundance of egg sacs (i.e., the sum of egg sacs either attached to a female or detached) by the average number of eggs in an egg sac. The seasonal variation of eggs in an egg sac was determined by dissecting some egg sacs from the fixed samples from Balsfjord in 2015-2016. Eggs were counted after perforating each egg sac (*O. similis*: n = 1-5, *M. norvegica*: n = 15-30) using a fine needle and averaged per sampling date. The average from the closest calendar day was used in the production calculations.

Methodological considerations to the use of the weight-specific egg production rate method

The experimental design is essential to the validity of the results obtained. Here, some of the possible sources of influence are discussed for the design of the weight-specific egg production rate experiments. Devreker et al. (2012) stressed the need to include the latency time (*LT*, d) in the calculation of the egg production rates of sac-spawners, as it will affect their secondary production estimates. The latency time is defined as the time between the hatching event of one clutch and the extrusion of the next clutch (Devreker et al. 2012). Taking the latency time into Equation 4, the equation for the production of sac-spawners would be:

Equation 7

$$SEP = (HR + \frac{1}{LT}) \times \frac{Begg}{Bfemale}$$

M. norvegica is particularly challenging to maintain in the laboratory, as the species is fragile and does not keep well in culture. The egg hatching experiments were already a complicated matter, but we would have had to design a longer experiment with food included to enable the production of the next clutch. Such a design was not feasible as it would have increase female mortality. Instead, we privileged the experimental design by Nielsen et al. (2002) that minimized the handling time. Published latency times for *M. norvegica* is 0.39 d and was independent of temperature (Uye et al. 2002). For *O. similis*, the latency time is 0.5 d (Ward & Hirst 2007), which was assumed to be independent of the temperature as it is for *Oithona davisae* (Uye & Sano 1995). The productions calculated, including the latency time, were on average 2 ± 1% and 4 ± 1% lower than the productions calculated without considering the latency time for *M. norvegica* and *O. similis*, respectively. The addition of the latency time was of little relevance for this study because the hatching rates far exceeded the latency time at cold temperatures. Omitting the latency time seems acceptable at low temperatures but should be included in experiments at higher temperatures.

The incubation of females without food may influence egg production. We are not aware of studies analyzing the effect of starvation on the hatching time of already produced eggs, although a low food concentration can influence females to produce a higher proportion of eggs with delayed hatching (Drillet et al. 2011). The experimental design used here relies on previous experiments done on *O. similis* in filtered water (Nielsen et al. 2002), as well as the possibility of phytoplankton adversely influencing the hatching rates and success of the produced eggs (Ianora et al. 2003). *C. finmarchicus* showed a large difference in female egg production between fed and unfed experiments (Pasternak et al. 2013). However, the females in their experiment were reared and acclimatized before the experiment, which means that females at the time of egg production had experienced and adapted to low environmental food concentrations. In the sampling design, the incubated females were collected with egg sacs, meaning that the eggs were produced *in situ* food, and the lack of food in the incubation wells should have no impact on the egg hatching. For broadcast-spawners, an incubation time of 24 h is a standard procedure (Halsband & Hirche 2001, Head et al. 2013), and egg production can be reduced after 24 h (Drif et al. 2010). The lack of food in the incubation wells was not expected to delay egg hatching because most previous studies on egg hatching rates have also used filtered seawater (e.g., Andersen & Nielsen 1997, Nielsen et al. 2002, Evjemo et al. 2008, Henriksen et al. 2012, Halvorsen 2015). Therefore, the experimental design used in our study has likely not impacted egg production and reflected field values.

The temperature-dependent model

The main characteristic of the temperature-dependent model of Huntley and Lopez (1992) is that species-specific reproductive behaviors are ignored to simplify the growth rate of copepods as a function of the environmental temperature. Huntley and Lopez (1992) observed that 90% of the variance in growth rate could be explained by temperature and hypothesized that natural populations of copepods are rarely food-limited, and, therefore, their growth rate is likely mainly dependent on temperature.

Here, the weight-specific growth rate (g, d^{-1}) is given as:

Equation 8 $$g = 0.0445 \times e^{0.111 \times T}$$ *(Huntley & Lopez 1992)*

where T is the temperature averaged over the top 100 m.

The production was calculated by multiplying the weight-specific growth rate by the total biomass (mg C m^{-3}) of each species (Equation 2).

4 Results and Discussion

4.1 Temperature-dependency of the reproductive rates of small copepods

Temperature is an environmental stressor for poikilothermic ectotherms such as copepods because it impacts their physiological performance or fitness (Kroeker & Sanford 2022). Hence, the metabolic rates of copepods are temperature-dependent, including the growth rate, the egg hatching rate, and the development rate (Uye & Sano 1995). The limited number of studies available on metabolic rates of small copepod species at low temperatures hinders understanding the population dynamics of these abundant organisms. In **Paper I**, the reproduction rates at low temperatures of three cosmopolitan copepod species (*O. similis*, *M. norvegica*, and *M. pusillus)* were compared. The egg hatching rate of the egg-carrying cycloid *O. similis* increased linearly from 0.05-0.06 d^{-1} at 1.3°C to 0.29 d^{-1} at 13.2°C (**Paper I**). The reproduction of *O. similis* seems highly effective at low temperatures, with egg hatching success ≥ 75% regardless of the temperature (**Paper I**). The egg hatching rate of *M. pusillus* increased from 0.23 d^{-1} at 3.0°C to 0.61 d^{-1} at 9.8°C, but its hatching success was low (≤ 25% in all incubations, **Paper I**). The egg hatching rates of *M. norvegica* increased linearly from 0.02 d^{-1} at 3.0°C to a maximum of 0.14 d^{-1} at 7.0°C (**Paper I**). From 7.9°C to 13.2°C, the egg hatching rates were slightly lower (between 0.08 and 0.11 d^{-1}). Coincidentally, the highest egg hatching successes (40 - 80%) of *M. norvegica* were reached between 5°C and 8°C, but ≤ 25% below 5°C and above 8°C (**Paper I**).

For copepods in general, growth rates and egg hatching rates are highest within the species-specific optimal temperature range but may even out or decrease outside of it (Lonsdale & Levinton 1986, Uye & Sano 1995, Holste et al. 2009, Pasternak et al. 2013, Ershova et al. 2016). For eurythermal species, such as *O. similis*, *O. davisae*, and *M. norvegica*, the egg hatching rate increases linearly over a large temperature range, meaning that the species has a broad adaptability to temperatures (Uye & Sano

1995, Nielsen et al. 2002, Uye et al. 2002). The egg hatching rates of *O. similis* found in this study are comparable to that of other Arctic populations, confirming that *O. similis* has a wide thermal plasticity and thrive even at low temperatures (Nielsen et al. 2002). The comparison of our results to the study by Nielsen et al. (2002) is possible because only one genetic lineage of *O. similis* is found in the Arctic Ocean within the newly defined *O. similis* species complex (Box 2, Cornils et al. 2017). The wide thermal adaptability of the Arctic lineage of *O. similis* coupled with a high egg hatching success may partly explain the success of *O. similis* in Arctic ecosystems as one of the most abundant small copepods (Ashjian et al. 2003, Dvoretskii 2007, Dvoretsky & Dvoretsky 2009a).

Compared to the egg-carrying cyclopoid copepods, free-spawning calanoid copepods are known for their faster egg development rates (Kiørboe & Sabatini 1994). For free spawning copepods, fast egg development rates likely compensate for the lack of parental care and, therefore, a high mortality rate of eggs freely released in the surrounding waters. To the best of my knowledge, **Paper I** is the first to present egg hatching rates for the free-spawning calanoid *M. pusillus*. The egg hatching rate of *M. pusillus* was faster than that of *O. similis* and egg-carrying harpacticoid *M. norvegica* at any temperature. Therefore, *M. pusillus* had the shortest egg development of the three species, which was 4 days for *M. pusillus* compared to 15 days for *O. similis* and 25 days for *M. norvegica* at 3°C (**Paper I**). The egg development time of *M. pusillus* at 3°C was similar to that of the large Arctic *C. glacialis* (4 days) and faster than the egg development time of other small calanoid copepods such as *Pseudocalanus minutus* (7 days) and *Acartia clausi* (8 days, McLaren 1966). Our study confirms that small broadcast-spawning copepods have faster hatching rates than similarly sized egg-carrying cyclopoid copepods, in accordance with Kiørboe and Sabatini (1994). However, our study also includes the egg-carrying harpacticoid *M. norvegica* in the comparison. Therefore, the spawning strategy may be more important in determining the speed of the egg development than the taxonomical order at similar sizes, though further study on harpacticoid would be needed to assess this supposition. The high egg hatching rates of *M. pusillus* could suggest a successful reproduction at low temperatures, but this view seemed contradicted by the low hatching success. Low egg hatching successes are occasionally observed but are uncommon for calanoid eggs (Miralto et al. 1998, Tang et al. 1998, Yamaguchi et al. 2010, Devreker et al. 2012). The hatching success design used in **Paper I** is commonly used for calanoid copepods and should not cause low hatching success (Andersen & Nielsen 1997, Drillet et al. 2008). Various factors independent of temperature could affect hatching success, including successful mating and fertilization, phytoplankton composition and release of extracellular substances, and food composition (Ambler 1985, Jónasdóttir et al. 2005, Li et al. 2009, Mironova & Pasternak 2017). The cause of the low egg hatching success might be diverse and cannot be assessed from the results of **Paper I**. However, the wide and abundant distribution of *M. pusillus* indicates a successful establishment of the species in sub-Arctic and Arctic ecosystems (**Paper II and III**, Barthel et al. 1995, Arendt et al. 2013, Arendt et al. 2016). As high mortality is expected from predation on broadcast-spawner eggs, *in situ* egg hatching success might be expected to be occasionally high to ensure the recruitment of enough offspring that will reach adulthood (Kiørboe & Sabatini 1994).

The egg hatching rates of *M. norvegica* have been studied in only one other study. In the temperate population of the Inland Sea of Japan, Uye et al. (2002) found a linear increase of the egg hatching rates between 12°C and 27°C, indicating the species is eurythermal. Based on this, we expected a linear correlation between temperature and egg hatching rates in our incubations. Instead, the two key

reproductive parameters of *M. norvegica* in Balsfjord appear temperature optimized for a narrow but locally relevant temperature range, which contradicts the large thermal adaptation of the population studied by Uye et al. (2002). *M. norvegica* is described as eurythermal, with a geographical distribution extending from the Southern hemisphere to Arctic ecosystems in both the Atlantic and Pacific Oceans (Hirakawa 1974, Uye et al. 2002, Antacli et al. 2014, Barth-Jensen et al. 2020). Such a wide distribution range may have led to local adaptations, as seen in other copepod species (Lonsdale & Levinton 1986, Drillet et al. 2008, Hong & Shurin 2015). Another explanation might lie in the DNA of *M. norvegica*. While the genetics of *M. norvegica* populations worldwide have not yet been compared, DNA barcode sequences in the BOLD repository (accessed on 28 March 2019) showed a considerable divergence between sequences from specimens collected in Norway, Canada, and the USA (pers. comm. Paul D. N. Hebert, Figure 4). It is, therefore, possible that *M. norvegica* is a cryptic species complex. Further studies are encouraged to include genetic analysis of *M. norvegica* to elucidate the cause of the differences between geographically distant populations.

Global warming steadily increases the temperature of the water column. This temperature increase will impact the three copepod populations differentially because of their different thermal preferences (Balazy et al. 2018, Balazy et al. 2021, Pasternak et al. 2013). Within global warming projections, the RCP8.5 high-end scenario for greenhouse gases emissions represents a baseline “no-policy” scenario, where nothing is done to curb those emissions. This scenario is in the range of possible outcomes by 2100 but is unlikely due to recent technological improvements and changes in governmental and company policies (Mohr et al. 2015, Ritchie & Dowlatabadi 2017). Even though this scenario is unlikely to happen, it can be interesting to explore how the egg hatching rates may change, considering the most extreme scenario applied to two different high-latitude ecosystems. Based on RCP8.5 high-end scenario, Alexander et al. (2018) predict an increase of sea surface temperatures of 3.2°C in the Arctic by 2100. Following the prediction of Alexander et al. (2018), the present study considers simplistic scenarios of changes in the egg hatching rates of populations of *O. similis*, *M. norvegica*, and *M. pusillus* in two ecosystems with different average surface temperatures: 1) central and eastern Barents Sea, and 2) Balsfjord.

Scenario 1 in the Barents Sea: Average summer surface temperature is 3°C in the central and eastern Barents Sea (Dvoretsky & Dvoretsky 2009c). An increase from 3°C to 6.2°C would imply a 4.5-fold increase in the summer egg hatching rate of *M. norvegica* compared to the present, while those of *O. similis* and *M. pusillus* would double (Figure 5). All three Arctic populations may benefit from the temperature increase by having a shorter development time, though *M. norvegica* might be more advantaged.

Scenario 2 in Balsfjord: The average summer surface temperature is 8°C in Balsfjord (Eilertsen & Skarðhamar 2006). An increase from 8°C to 11.2°C would cause the future egg hatching rate of *M. norvegica* to be slightly lower than the present egg hatching rate in summer (Figure 5). At the same time, both *O. similis* and *M. pusillus* would have increased their summer egg hatching rate by 1.5-fold. In this scenario, only the egg hatching rates of *O. similis* and *M. pusillus* would increase, while that of *M. norvegica* would stay comparable to the present.

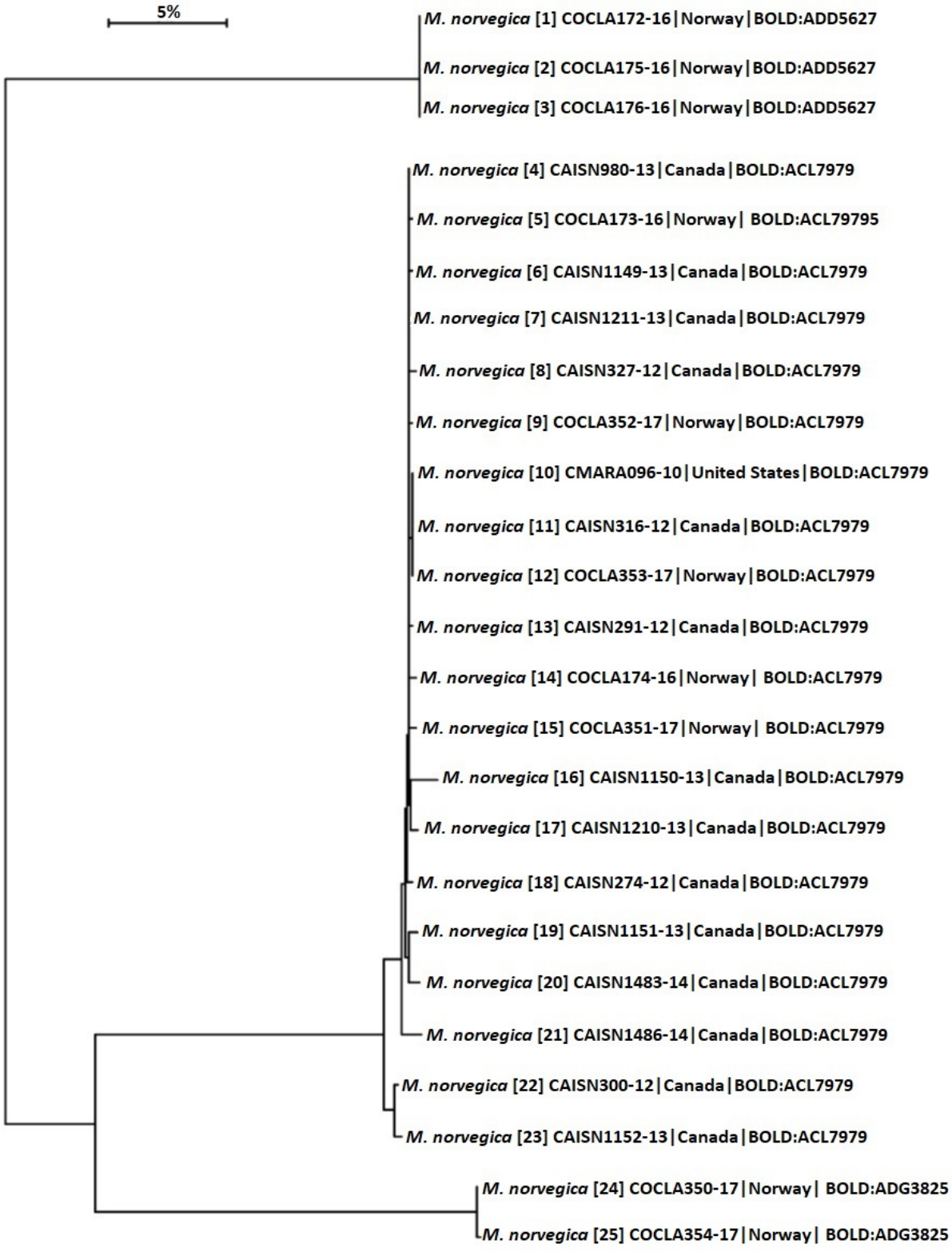

Figure 4. Preliminary tree of DNA barcode sequences for M. norvegica *in the BOLD repository (accessed on 28 March 2019) from specimens collected in Norway, Canada, and the USA. Figure made by Paul D. N. Hebert; text modified by Coralie Barth-Jensen.*

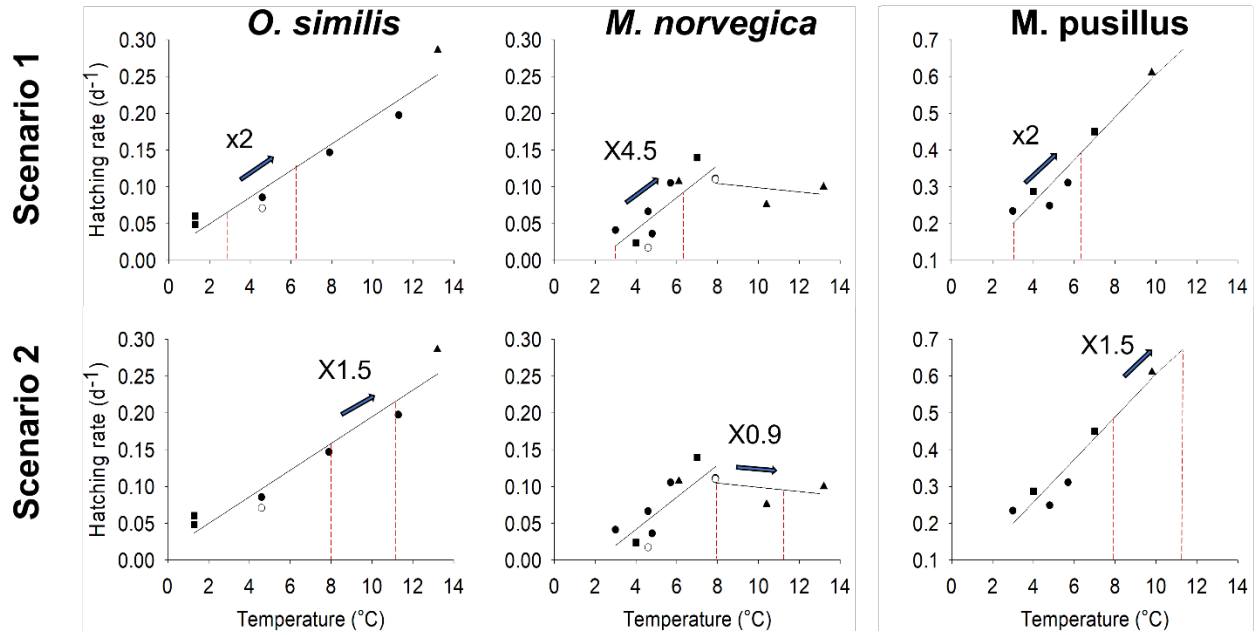

Figure 5. Projected increase of the egg hatching rates of O. similis, M. norvegica *and* M. pusillus *from the present surface temperatures to a potential increase of 3.2°C by 2100 (Alexander et al. 2018). The dashed vertical lines mark the temperature interval of each scenario. The effect of the potential temperature increase effect on the egg hatching rate is shown as a multiplicate of the egg hatching at present temperature. The references to present summer surface temperatures are taken from Dvoretsky and Dvoretsky (2009c) for the Barents Sea and Eilertsen and Skarðhamar (2006) for Balsfjord.*

Higher egg hatching rates might lead to changes in the naupliar recruitment of *O. similis*, *M. norvegica*, and *M. pusillus*, thereby impacting their abundances and population dynamics (Allan 1976, Tang et al. 1998). The uneven temperature response of the egg hatching rates shown in both scenarios might cause a shift in their recruitment and proportional abundances within the small copepod community. In scenario 1, the larger temperature response of *M. norvegica* hatching rate might result in its greater naupliar recruitment compared to that of *O. similis* and *M. pusillus*. These changes might lead to a higher proportion in the numerical abundance of *M. norvegica* in the small copepod community compared to the present. In scenario 2, the summer recruitment of nauplii might increase for *O. similis* and *M. pusillus*, while that of *M. norvegica* might slightly decrease compared to the present. In this case, the abundances of *O. similis* and *M. pusillus* would grow faster than the abundance of *M. norvegica*, shifting the proportion in the numerical abundance of *O. similis* and *M. pusillus.* However, population dynamics are also influenced by food availability, natural mortality, and predation pressure (Allan 1976, Tang et al. 1998, Hirst & Kiørboe 2002). These factors are also subject to change with global environmental changes: natural mortality is temperature-dependent, while phytoplankton and predator assemblages are already ongoing shifts caused by, e.g., the borealization of Arctic ecosystems (Dvoretsky & Dvoretsky 2011, Polyakov et al. 2020, Csapó et al. 2021, Mańko et al. 2022). The study of the reproductive rates can only describe parts of the population dynamics of small copepod species. Both scenarios 1 and 2 are too simple to capture the complexity of real future scenarios but give a perspective on how temperature change may affect the copepod community. Studies on other metabolic rates will be needed to gain better understanding of the phenology of small copepod species and the impact of environmental changes.

4.2 Phenology of copepods in high latitude ecosystems

Phenology refers to the study of the timing of recurring biological events in relation to seasonal environmental cycles (Calow 2009). Studying the phenology of copepods encompasses the study of their population dynamics, including the timing of reproduction, age structure, and overwintering strategies of the different populations (Beaugrand & Kirby 2018, Winder & Varpe 2020). Here, the phenology of *O. similis*, *M. norvegica*, and *M. pusillus* was studied in the sub-arctic Balsfjord, Altafjord, and Porsangerfjord, and compared to the phenology of large copepod species in Balsfjord (**Paper III**). A complementary study of overwintering strategies was made in Arctic fjords and surrounding oceanic stations (**Paper II**). Results on overwintering presented here summarize the findings of **Paper II and III**, because the overwintering strategies were similar in the Arctic and sub-Arctic ecosystems and can be compared and discussed together.

The species-specific patterns revealed different dynamics between the high-latitude populations of three studied small copepod species, such as distinct reproduction periods, presence of nauplii, and peak abundance of young copepodids (CI-CIII, Figure 6). The year-round study of the sub-Arctic fjords showed that all copepodid stages of *O. similis* were present in all seasons, which was confirmed in the polar night study of Arctic ecosystems (**Paper II and III**). The dominant *O. similis* stages during winter were older copepodids CIV-CV and shifted towards adults in late winter. Young copepodids CI-CIII were seen year-round and peaked twice during summer and fall (**Paper II and III**, Figure 6). Egg-carrying *O. similis* females were continuously present, as were small-sized cyclopoid nauplii (**Paper I, II, and III**, Figure 6). Clutch sizes of *O. similis* were small before the spring bloom (8 ± 3 eggs in March), peaked during spring bloom and summer (up to 23 ± 9 eggs), and decreased again during the autumn (6 eggs, **Paper I and III**). Like *O. similis*, *M. pusillus* populations were composed of all copepodid stages year-round. The abundance of *M. pusillus* CI-CIII was highest in late winter or before the spring bloom in Balsfjord, Altafjord, and Porsangerfjord, and represented ≤ 9% of the populations (**Paper III**, Figure 6). This finding contrasted with the Arctic populations, which were made of ≥ 50% young copepodids in January (**Paper II**). In the sub-Arctic fjords, the proportion of young *M. pusillus* copepodids decreased during early spring while the proportion of older copepodids simultaneously increased (**Paper III**). This shift from young to older copepodid was accompanied by increasing abundances of *M. pusillus* adults from spring to winter. The clutch size of *M. pusillus* was highest in May (9 ± 3 eggs) and August (12 ± 8 eggs, **Paper I**). The winter egg production of *M. pusillus* was not studied, but a large proportion of the winter nauplii communities were small-sized calanoid nauplii, which meant that *M. pusillus* might have been reproducing during winter (**Paper II**, Figure 6). In contrast to *O. similis* and *M. pusillus*, *M. norvegica* only carried egg sacs between April and August, indicative of a time-limited reproduction (**Paper I, II, and III**, Figure 6). The average clutch size of *M. norvegica* varied between 9 ± 3 and 12 ± 3 eggs and peaked in May and June (**Paper I and III**). This peak was followed by subsequent increases in CI-CIII and CIV-CV in summer and adults in fall (**Paper III**, Figure 6). *M. norvegica* overwintered mainly as adults, with very few non-adult specimens present in the water column (**Paper II and III**). The age structure of these three small copepods (i.e., the number of egg production peaks and of peaks in young copepodids abundance) suggests that two *O. similis* generations are produced annually while only one is produced for *M. pusillus* and *M. norvegica* (**Paper III,** Figure 6).

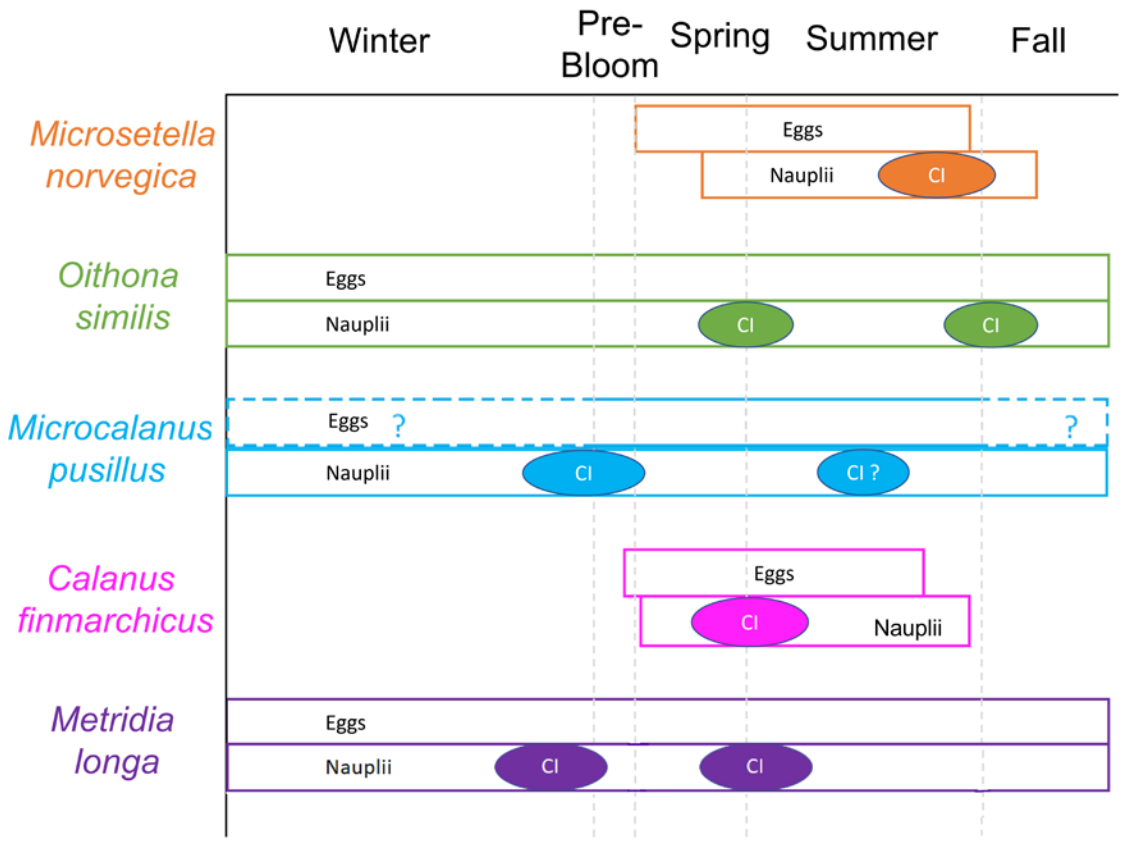

*Figure 6. Timing of reproduction and nauplii presence in the water column for M. norvegica, O. similis, M. pusillus, C. finmarchicus and M. longa according to **Paper I, II and III**, and previous work in sub-Arctic and Arctic ecosystems (Tande & Grønvik 1983, Norrbin 1991, Lischka & Hagen 2005, Lischka & Hagen 2016). The peak(s) of CI abundance is marked for each species. The "?" denote insecurities in the timeline of M. pusillus, as egg production was not studied during late fall and winter (**Paper I**) but suggested by Norrbin (1991), and the summer CI peak was not observed in **Paper III** but described by Lischka and Hagen (2016).*

The large copepods *C. finmarchicus* and *M. longa* also showed different phenology in Balsfjord, including distinct overwintering strategies. The overwintering stages of *C. finmarchicus* comprised mainly older copepodids and a few adults (**Paper II and III**). From March to May, the abundance of females increased, followed by the appearance of young *C. finmarchicus* copepodids mainly between April and June (**Paper III**, Figure 6). In contrast to *C. finmarchicus*, *M. longa* had all copepodid stages present year-round (**Paper II and III**). The abundance of *M. longa* CI-CIII increased during the spring, followed by an increase in older copepodids in the summer (**Paper III**, Figure 6). Adults of *M. longa* were the dominant overwintering stage in Balsfjord and the Arctic stations, with a higher proportion of CI-CIII found in Arctic stations than in Balsfjord (**Paper II and III**). The population structures of *C. finmarchicus* and *M. longa* suggest that one main generation is produced annually for each species. However, the recruitment of young copepodids occurs year-round for *M. longa* and likely blurs the signal of a possible second generation in Balsfjord (**Paper III**).

In summary, the strategies developed by small and large copepods to strive in highly pulsed ecosystems are varied (Figure 6). The small and large copepods have distinct phenology with various reproductive periods, overwintering strategies, and peak recruitment periods for young copepodids. These life history strategies can be separated into two general types of species with a "time-limited reproduction" or a "continuous reproduction", as described by Ashjian et al. (2003).

Time-limited reproduction: Species with a time-limited reproduction rely on a relatively short but intensive reproductive period when food concentration is high, facilitating the successful recruitment of offspring. The length of the reproductive period can range from a couple of months for *C. finmarchicus* to half a year for *M. norvegica* (Figure 6, Diel & Tande 1992), **Paper III**). These different reproduction lengths are likely connected to the species' feeding strategies, as both species are income breeders (i.e., fuel reproduction from direct food intake, Varpe & Ejsmond 2018). *M. norvegica* feeds on sinking aggregates or marine snow, while *C. finmarchicus* feeds primarily on suspended diatoms (Koski et al. 2005, Castellani et al. 2008, Koski et al. 2021). Therefore, *C. finmarchicus* reproduction peaks during the spring bloom when the food supply is highest, while *M. norvegica* can take advantage of a longer reproduction period (Koski 2007, Svensen et al. 2018). The reproductive period is followed by the recruitment period of the young copepodids and their development into overwintering stages, which become the most abundant stages at the beginning of autumn (Figure 6, **Paper III**). The successful establishment of species with time-limited reproduction within an ecosystem is partly determined by their ability to secure enough food to grow from nauplii to overwintering stages during the reproductive period. The partitioning of preferential food sources between species with time-limited reproductive strategies probably facilitates their simultaneous survival within the same ecosystem by lowering the inter-specific competition for preferred food. For the species with time-limited reproduction, successful overwintering has a high survival of overwintering individuals at the end of winter that can ensure the production of a new generation. The different species overwinter either as immature older copepodids or non-reproducing adults (**Paper II and III**). The overwintering stages may be an indicator of the type of life strategy used by the species. Overwintering as older copepodids is seen in either income-breeding or capital-breeding large copepods, such as *C. finmarchicus*, *C. glacialis* and *C. hyperboreus* (Ashjian et al. 2003, Falk-Petersen et al. 2009, **Paper II and III**). These large copepods arrest their growth during winter to hibernate at depth, which is possible due to their large lipid reserves (Falk-Petersen et al. 2009). The molting of older copepodids into the adult only occurs close to the start of reproduction and is accompanied by the maturation of gonads (Tande 1982, Kosobokova 1999, Ashjian et al. 2003). Delaying molting into adults may increase survival from visual predators present in the water column even at low ambient light, as these predators can prey more easily on larger adults than the smaller copepodids (Cohen et al. 2015, **Paper II**). Overwintering as non-reproducing adults, also called “reproducing-resting stage”, is common in small income breeders such as *M. norvegica*, *Acartia longiremis* and *Coullana canadensis* that stay winter active (Norrbin et al. 1990, Lonsdale et al. 1993, Ashjian et al. 2003, **Paper III**). Feeding during winter is vital for small copepods as their body volume cannot store large energy reserves that last all winter (Norrbin 1991). The body volume of adults is larger than copepodids, and is, therefore, advantageous for storing a larger quantity of lipids before winter, providing a greater buffer to fend off possible starvation. Females *M. norvegica* loose up to 53% of their carbon weight during winter (Svensen et al. 2018, **Paper I**). This large body weight loss indicates that the female metabolic requirement is probably not met. Therefore, using part of the energy income during winter to produce eggs is likely impossible, as suggests the absence of egg sacs on *M. norvegica* after fall (Uye et al. 2002, Svensen et al. 2018, **Paper II and III**). The advantage of having a larger body volume can, however, increase the probability of detection by visual predators. Therefore, small copepods relying on a time-limited reproduction may overwinter as adults as a trade-off between the possibility of being preyed upon and the possibility of starving.

Continuous reproduction: Species with continuous reproduction are characterized by the year-round presence of all copepodid stages, including younger copepodids and egg sacs for egg-carrying species.

Such population dynamics were observed in income breeders such as the small copepods *O. similis*, *M. pusillus*, and *Pseudocalanus* spp. and the large copepod *M. longa* (**Paper I, II, and III**). The mixed age structures suggest continuous reproduction and recruitment, although they are not constant during the year (Figure 6, **Paper I and III**). The spring peak of *M. longa* CI-CIII (**Paper III**) seems to originate from a high spring egg production in Balsfjord (Grønvik 1980, Tande & Grønvik 1983). Therefore, spring and summer is likely the most crucial season for the development of the main *M. longa* generation, although a fall egg production peak might also happen (Lischka & Hagen 2016). For *O. similis*, the spring peak in CI-CIII abundance likely comes from an early spring egg production, while the fall CI-CIII peak originates from eggs laid during summer (**Paper III**), as described in Svalbard (Lischka & Hagen 2005). The isochronal development of nauplii suggests that, similarly to eggs, lower winter temperature in the Arctic environments likely causes a longer development time of copepodids compared to sub-Arctic environments (Sabatini & Kiørboe 1994), **Paper I**). A longer development of nauplii and copepodids could explain the higher proportion of *O. similis* CI-CIII in the Arctic populations in late winter compared to the *O. similis* sub-Arctic populations (**Paper II and III**). The population dynamics of *O. similis* at high latitudes show that all seasons are essential for the development of two generations annually. The populations of *M. pusillus* in the three sub-Arctic fjords showed one main late winter CI-CIII peak, also seen in our Arctic study (**Paper II and III**). A Svalbard fjord population recruited two generations in June-July and February-March (Lischka & Hagen 2016). Our sub-Arctic fjord study may have overlooked a possible second summer peak in CI-CIII (**Paper III**), as no cruise was conducted between end of June and end of August. The larger clutch size laid by *M. pusillus* in May and August (**Paper I**) might explain the two CI peaks (Lischka & Hagen 2016): the summer peak of CI could come from eggs laid in May while the late-winter peak of CI may originate from eggs laid during the fall. It seems that *M. pusillus* and *O. similis* have a similar strategy in high-latitude ecosystems, with one generation recruited in summer and a second generation in winter. Winter is, therefore, a strategic season for some of the continuously reproducing species, which may be partly explained by a reduced winter predation pressure on small copepods. Large copepods, such *M. longa*, *C. finmarchicus*, and *C. glacialis*, though predominantly herbivorous, can prey on copepods eggs and nauplii, including their own (Sell et al. 2001, Basedow & Tande 2006, Cleary et al. 2017). Winter has a marked reduction in activity or hibernation of part of the predator populations, including large copepods and other large zooplankton (Hirche 1996, Daase et al. 2013, Grigor et al. 2014). The decreased predation during winter may lead to a decreased mortality rate of the most vulnerable stages of small copepods, i.e., their eggs and nauplii, even during a period of low food concentration.

The large variation of small copepod phenology shows that caution needs to be applied in grouping small copepods together for ecological studies, as similar-sized species can have heterogeneous population dynamics and reproductive strategies. This poses a challenge for modelling by increasing the complexity of defining small copepods.

4.3 Biomass of small copepods in the Arctic

The general undersampling of small copepods in zooplankton studies is still relatively common in high-latitude ecosystems, although this problem has been pointed out for decades (Gallienne & Robins 2001, Turner 2004, Svensen et al. 2018). An underestimation of small copepods abundance and biomass originates from the common use of nets with mesh sizes ≥ 180 µm for zooplankton studies

focusing on larger copepods (e.g., Hirche & Kosobokova 2011, Kosobokova & Hirche 2016, Daase et al. 2018, Skjoldal et al. 2021). Quantitative sampling of small copepods can be done by using 64 µm-mesh nets or 20-L Go-Flo bottle sampling, as done in this study (Nichols & Thompson 1991, Svensen et al. 2018). The targeted sampling of small copepods uncovered high abundances of small copepods in Arctic and sub-Arctic environments and further established that small copepods can have high biomasses in surface waters (e.g., Svensen et al. 2011, Arendt et al. 2013, Svensen et al. 2019, Coguiec et al. 2021, **Paper III**). In January, small copepods represented ≥ 50% of the total zooplankton community abundance in the Arctic fjords and offshore stations (**Paper II**). Total copepod biomass was dominated by large copepods (≥ 1 mg C m^{-3}), but small copepods biomass (mainly *Pseudocalanus* spp., *Microcalanus* spp., and *O. similis*) still made up ≤ 21% of the total copepod biomass (≤ 1 mg C m^{-3}, **Paper II**). Among the small copepods, the biomass of *O. similis* and *M. pusillus* (≤ 0.5 mg C m^{-3} and ≤ 0.4 mg C m^{-3}, respectively) was always higher than the biomass of *M. norvegica* (≤ 0.03 mg C m^{-3}, **Paper II**). In the sub-Arctic Balsfjord, the total winter biomass of *C. finmarchicus* and *M. longa* was ≤ 10 mg C m^{-3}, which was higher than the summed biomasses of *O. similis, M. norvegica* and *M pusillus* in 3 out of 5 samplings (≤ 6 mg C m^{-3}, **Paper III**). However, the higher total biomass of these three small copepods was found in 8 out of the 14 sampling dates covering all seasons in Balsfjord compared to the biomass of *C. finmarchicus* and *M. longa* (**Paper III**). *M. norvegica* dominated the biomass year-round (≤ 24 mg C m^{-3}), while *O. similis* (≤ 2 mg C m^{-3}) and *M. pusillus* (≤ 0.5 mg C m^{-3}) had lower biomasses (**Paper III**). The maximum population biomasses of *M. norvegica* and *O. similis* were, however, halved in 2016-2017 compared to 2015-2016 in Balsfjord (**Paper III**). The maximum biomass of *M. norvegica* was also higher than the maximum biomass of *C. finmarchicus* (18 mg C m^{-3}) and *M. longa* (0.7 mg C m^{-3}, **Paper III**). Of the investigated fjords, Balsfjord had the highest cumulated biomass of the three small copepod species (≤ 27 mg C m^{-3} in autumn, **Paper III**). The population size in terms of biomass was, in general, lower in Altafjord and Porsangerfjord than in Balsfjord in 2016-2017. The dominance of *M. norvegica* compared to *O. similis* was also present in Altafjord and Porsangerfjord, with the highest biomass of *M. norvegica* in Porsangerfjord Inner (≤ 8 mg C m^{-3}). The biomass of *M. pusillus* was always low in all fjords irrespective of the season (≤ 0.6 mg C m^{-3}, **Paper III**).

These results confirm that small copepods are important contributors to copepod and total zooplankton biomasses year-round in high latitude ecosystems and support the growing awareness of the need for studies focusing on small copepods (Pasternak et al. 2000, Turner 2004, Madsen et al. 2008, Svensen et al. 2019). The study of small copepods in the Barents Sea and Svalbard during the polar night (**Paper II**) only offers a time-limited snapshot of Arctic environments, but findings clearly showed higher biomasses of *O. similis* and *M. pusillus* than of *M. norvegica*. Similarly, other marine Arctic ecosystems seem to have higher abundances or biomasses *O. similis* and *M. pusillus* than *M. norvegica* when sampled with ≤ 64-µm nets (Pedersen et al. 2005, Hirche & Kosobokova 2011, Arendt et al. 2016, Trudnowska et al. 2020a, Trudnowska et al. 2020b). In comparison to these Arctic ecosystems, the higher biomass of *M. norvegica* than of *O. similis* and *M pusillus* was observed in the three investigated sub-Arctic fjords (**Paper III**) and in other sub-Arctic fjords investigated with nets with ≤ 90-µm meshes (Barthel et al. 1995, Halliday et al. 2001, Hjorth & Dahllöf 2008, Arendt et al. 2013). The dominance of *M. norvegica* in sub-Arctic environments may be facilitated by warmer surface waters during its reproductive season. For example, waters above 50 m have temperatures ≥ 5°C in Balsfjord and Porsangerfjord between March and October (Eilertsen & Frantzen 2007, Svensen et al. 2018). Additionally, *M. norvegica* migrates to the surface during the same period (Pasternak et al. 2000, Halliday et al. 2001, Svensen et al. 2018). Therefore, *M. norvegica* could profit from the

higher egg hatching success and faster egg hatching rates at temperatures < 5°C (**Paper I**) to increase its reproductive success, likely affecting the overall recruitment of the species in sub-Arctic fjords. In contrast to sub-Arctic fjords, the surface waters of Arctic fjords rarely exceed 5°C year-round (Svendsen et al. 2002, Lischka & Hagen 2005, Leu et al. 2011, Arendt et al. 2016). The egg hatching rates and egg hatching success of *O. similis* and *M. pusillus* are higher than *M. norvegica* at temperatures < 5°C (**Paper I**). This higher affinity to low temperatures would give *O. similis* and *M. pusillus* a thermal advantage over *M. norvegica*, and the reproduction and recruitment of *M. norvegica* is likely more challenging than in sub-Arctic ecosystems. Therefore, high biomasses of *O. similis* and *M. pusillus* in Arctic copepod communities may originate from their affinity with lower temperatures than *M. norvegica*, which increases their competitiveness in the colder Arctic ecosystems.

The future increase in water temperature may lead to a change in the community composition of small copepods (Scenarios 1 and 2 in Chapter 4.1), thereby potentially altering the present observations of species dominance in the Arctic or sub-Arctic. Such changes could affect the ecosystems in more ways than a dominance shift with the small copepod community. Small copepods have various feeding strategies (Table 2) and can have strong but various impacts on prey populations (Roura et al. 2018). For example, *O. similis* nauplii can graze 0.1 to 82% of the standing stock of phytoplankton biomass < 10 μm, while *M. norvegica* has a higher ingestion rate of algal aggregates than appendicularian houses (Svensen et al. 2011, Koski & Lombard 2022). The fate of the phytoplankton bloom and the functioning of the microbial loop could be altered by large changes in small copepod populations, thereby affecting the carbon flux in the upper water column. Several reports urge for more studies on the metabolism and physiology of small copepods, because this lacking knowledge hampers the present understanding and future modelling of the processes happening in the surface waters (Turner 2015, Roura et al. 2018, Mayor et al. 2020).

4.4 Production of small copepods in high-latitude ecosystems

The production of small copepods is likely underestimated in high-latitude ecosystems because it requires an accurate estimate of abundance (Equation 2, p. 10). Therefore, **Paper III** assesses the daily seasonal, annual, and interannual production of small copepods (*O. similis*, *M. norvegica*, and *M. pusillus*) based on quantitative abundance sampling of small copepods. Two different methods were used to estimate production in three fjords (Balsfjord, Altafjord, and Porsangerfjord) in different seasons: the weight-specific egg production rate (SEPR) and the temperature-dependent model of Huntley and Lopez (1992) (H&L).

The production rates of the three small copepods in Balsfjord revealed a large seasonal variation. The total daily SEPR productions[*] of *O. similis*, *M. norvegica*, and *M. pusillus* combined varied between seasons from 0.03 to 12.5 mg C m^{-2} d^{-1}, while the combined H&L productions ranged from 2.3 to 199.6 mg C m^{-2} d^{-1} (Table 5, **Paper III**). H&L production rates for *O. similis* and *M. norvegica* were highest in the summer with daily production estimates of 10.0 mg C m^{-2} d^{-1} and 189.6 mg C m^{-2} d^{-1},

[*] Note that the daily (mg C m^{-2} d^{-1}) and annual production rates (g C m^{-2} yr^{-1}) are given in different units in this chapter than in **Paper III** to simplify the comparison with other studies in Table 5. Conversions from m^{-3} to m^{-2} were done by integrating the production rates over 100 m.

respectively (Table 6, **Paper III**). In contrast, *M. pusillus* had a maximum daily production of 2.7 mg C m^{-2} d^{-1} in the fall (Table 6, **Paper III**). SEPR production estimates were consistently lower than H&L production estimates, but the methods agree upon the most productive season for all species (Table 6, **Paper III**). Large discrepancies between the two methods were found for *M. norvegica* during fall and winter, where no SEPR production occurred, but daily H&L production was estimated between 11 and 62.0 mg C m^{-2} d^{-1} (**Paper III**). Due to their continuous reproduction, *O. similis* and *M. pusillus* were the only productive copepods during fall and winter according to the SEPR model (**Paper III**). The annual SEPR production for 2015-2016 was estimated to 2.0 g C m^{-2} yr^{-1}, while the H&L production estimate was 32.2 g C m^{-2} yr^{-1} for the three small copepod species combined in Balsfjord (Table 5). Interannual variation was also large: annual SEPR production was 0.3 g C m^{-2} yr^{-1}, while annual H&L production was 10.1 g C m^{-2} yr^{-1} in 2016-2017, lessening the productions 3-7 times compared to 2015-2016 (**Paper III**). *M. norvegica* contributed 61 to 92% of total production in 2015-2016 (both methods) and in 2016-2017 (H&L). However, *M. pusillus* contributed 75% of total production in 2016-2017 using the SEPR (**Paper III**), suggesting possible interannual shifts in species-specific contributions to production.

The seasonal and species-specific discrepancies were also noted between the SEPR productions and the H&L productions in Altafjord and Porsangerfjord. The total daily production of the three small copepods was ≤ 1.3 mg C m^{-2} d^{-1}, comparable to the total daily production in Balsfjord in 2016-2017 (**Paper III**). *M. pusillus* had the highest SEPR productions, while *M. norvegica* and *O. similis* had the highest H&L productions. The total annual production of the three small copepod species was 0.3-1.3 g C m^{-2} yr^{-1} in Altafjord, and 0.2-5.2 g C m^{-2} yr^{-1} Porsangerfjord (Table 5, **Paper III**). It should be noted that the lack of sampling during spring 2016-2017 likely resulted in the underestimation of *M. norvegica* and *O. similis* contribution to the annual production of the fjords, as both species were most productive during summer in Balsfjord (Table 6, **Paper III**). *M. pusillus* contributed ≥ 63% to the annual SEPR productions, while *O. similis* (≤ 47%) and *M. norvegica* (≤ 67%) dominated the annual H&L productions in Altafjord and Porsangerfjord (**Paper III**).

The comparison of the two methods revealed considerable discrepancies in the estimation of daily and annual production and the relative contribution of each species to total production. The annual H&L productions were 5 to 32 times higher than the SEPR productions among all fjords (**Paper III**). Other high-latitude studies have reported small copepod annual productions of 0.1 – 1.7 g C m^{-2} yr^{-1} and daily productions of 0.6 – 15.5 mg C m^{-2} d^{-1} (Table 5), which are comparable to our SEPR productions (**Paper III**). The large differences between the methods were due to the disagreement between the seasonal production of each species: the SEPR productions followed the seasonality of reproduction of each species (e.g., no production for *M. norvegica* during winter), while the H&L productions followed the biomass trends of the different populations. The consistently high daily H&L productions (**Paper III**, Table 6) suggest that all H&L productions are overestimated. Conflicting results are found in the literature when comparing H&L productions to production estimates using other methods: H&L estimates were high in temperate ecosystems, while H&L estimates were similar to other model estimates in an Arctic fjord (Dahmen 1997a, Nielsen & Andersen 2002, Madsen et al. 2008). In Huntley & Lopez's model (1992), the extremely low temperatures (-1.6 to 3.4°C) result in low growth rates, which likely explains agreement with the SEPR estimates. It seems that Huntley & Lopez's model might be better suited for estimating copepod production in Arctic ecosystems as the extremely low temperatures would hinder the overestimation of production rates.

On the other end, SEPR production estimates of small copepods might be too conservative: our SEPR estimates are low compared to estimates from other methods, also reported in other high-latitude ecosystems (0.1-0.2 g C m^{-2} yr^{-1}Table 5, Dahmen 1997b, Nielsen & Andersen 2002, Madsen et al. 2008). Estimating production using the SEPR method entails the use of the female egg production rate as a proxy for the whole population growth rate (Table 4). Juvenile growth rates may, however, be higher than the female egg production rate, leading to the underestimation of population production (Leandro et al. 2014). For example, the weight-specific juvenile growth rate of *O. similis* is 20% body weight d^{-1}, while weight-specific female egg production is only 10% body weight d^{-1} (Sabatini & Kiørboe 1994, SEP_{OV} in **Paper I**). The halving growth rate between juveniles and females cannot account for the 10-fold difference observed in this study between methods. Different studies showed that the juvenile growth rates could be both higher and lower than the weight-specific egg production rate of females depending on environmental conditions such as food concentrations (Klein Breteler et al. 1982, Leiknes et al. 2016). Leiknes et al. (2016) discourage using the SEPR method or temperature-dependent models alone when estimating copepod secondary production because the assumptions and limitations in these approaches may engender large errors. The present findings illustrate how the use of a single method increases the risks of providing an inaccurate production rate because of model bias. Instead, Leiknes et al. (2016) suggested to combine the use of SEPR approach for females and the somatic growth rate for juvenile copepods. This approach may be possible for the better-studied copepods, but juvenile growth rates and female egg production rates are unknown for most small copepod species, and even more so at low temperatures, rendering this solution unachievable at present. For now, the study of small copepods production should provide a range of production estimates using different methods until their egg production rates and juvenile growth rates are better known.

Comparing the production of small copepods to that of large copepods can help understand the importance of small copepods for the food web and carbon cycling in high-latitude ecosystems. In Balsfjord, the large copepods *C. finmarchicus* and *M. longa* had equal or lower H&L productions than the small copepods *O. similis* and *M. norvegica* throughout the year (**Paper III**). The large copepods had a combined daily H&L production of ≤ 90 mg C m^{-2} d^{-1}, which amounted to an annual H&L production of 18 g C m^{-2} yr^{-1} (**Paper III**). *C. finmarchicus* contributed 96% of the annual production. The maximum H&L production of large copepods was observed in the fall, while it was minimal during the pre-bloom. Although the SEPR production of large copepods was not studied here, SEPR production estimates would likely be highest during the spring bloom when the abundance of eggs and small developmental stages peaked (Diel & Tande 1992, Koski 2007). The annual production of *C. finmarchicus* and *C. glacialis* was estimated to 1.8 and 3.4 g C m^{-2} yr^{-1} in the Barents Sea, which is much lower than our findings (Table 5, Slagstad et al. 2011). High daily productions of 500 mg C m^{-2} d^{-1} have been observed for *Calanus* spp. during the spring bloom (Madsen et al. 2001). Therefore, large copepods can be extremely productive, but only episodically over a short productive period. The previously estimated maximum daily production of *O. similis* was also low compared to our findings, with values between 0.6 and 1.9 mg C m^{-2} d^{-1} (Dahmen 1997b, Ward & Hirst 2007). Our study of the copepod production in Balsfjord suggests that small copepod production can rival (or/and (even) exceed) that of large copepods. Balsfjord is known for its high abundance of small copepods e.g., *M. norvegica*, limiting the generalizability of this finding (Svensen et al. 2018). Previous studies have sampled the biomass of small mesozooplankton using adequate sampling gear and pointed out that the production of small-sized zooplankton can sometimes exceed that of larger zooplankton (Basedow et al. 2014, de Melo Júnior et al. 2021). These studies, and ours, highlight the need to assess small

copepods production properly. The high biomass of small copepods, combined with their long or continuous reproduction, suggests that their overall contribution to production in high-latitude ecosystems has been underestimated in the past.

Proper estimates of small copepod production are essential for understanding the food web efficiency. A 10% carbon transfer between two trophic levels is considered an efficient trophic transfer in the food chain. (Dahmen 1997a, Węsławski et al. 2009). It means that the secondary production rate could equal 10% of the primary production rate in highly productive ecosystems. In Balsfjord, the annual primary production is estimated to be 120 g C m^{-2} yr^{-1} (Tande 1991). According to the H&L productions, the small copepod production equaled 8% to 27% of the primary production. When the production of the 5 species studied were combined, copepod production totaled 23% to 42% of the primary production. Carbon transfer between trophic levels of this magnitude is unrealistic and illustrates the above-mentioned overestimation of the temperature-dependent method. In contrast, the SEPR production estimates only give 0.3% to 2% of carbon transfer between primary production and copepods. These rates may be more realistic, as they represent the total production of only three small copepod species, with a high biomass in these fjords. Even the low estimate of carbon transfer indicates the importance of small copepods to the productivity and carbon cycling of high-latitude ecosystems. Future climate change is predicted to affect the secondary production of the large copepods *C. glacialis* and *C. finmarchicus* in the Arctic differently, partly because of their different physiological responses to temperature (Slagstad et al. 2011, Pasternak et al. 2013). The secondary production of the different small copepod species will also likely be affected unevenly by future temperature changes, following the physiological temperature responses of each species (scenarios presented in Chapter 4.1), thereby affecting the carbon flow in high-latitude food webs.

*Table 5. Literature review of annual and daily production of small copepods and Calanus spp. in Arctic and sub-Arctic ecosystems. The reported daily productions are seasonal rates and do not come from the simple division of an annual rate by 365 days. The bold numbers are from **Paper III**. Max. refers to the maximum value reported. Notes: ([a]) Production reported is the sum of the productions of M. longa with C. finmarchicus; ([b]) Daily production given in mg C m^{-3} d^{-1} and converted to mg C m^{-2} d^{-1} by integrating the value over 100 m, to simplify comparison with the Balsfjord population.*

	Small copepods	*Calanus* spp.	Estimation method(s)	Note on small copepod species	Reference
Annual production (g C m^{-2} yr^{-1})	**0.3 - 2.0**	-	Weight-specific egg production rate	Sum of *O. similis*, *M. norvegica* and *M. pusillus*	**Paper III**
	1.3 - 32.2	**18[a]**	Huntley and Lopez 1994 model	Sum of *O. similis*, *M. norvegica* and *M. pusillus*	**Paper III**
	0.2 - 1.7	5.4 - 12.7	Weight-specific egg production rate, Huntley and Lopez 1994 model, Hirst and Bunker 2003 model	All small copepods	Madsen et al. 2001, 2008
	-	1.8-3.4	Estimated from authors' own model		Slagstad et al. 2011
	0.1		Calculated from Edmondson & Winberg (1971)	Only *O. similis*	Dahmen 1997
Daily production (mg C m^{-2} d^{-1})	**0.03 - 12.5**	**-**	Weight-specific egg production rate	Sum of *O. similis*, *M. norvegica* and *M. pusillus*	**Paper III**
	2.3 - 199.6	**8.1 - 89.9[a]**	Huntley and Lopez 1994 model	Sum of *O. similis*, *M. norvegica* and *M. pusillus*	**Paper III**
	max. 7.7 - 15.5	max. 500[b]	Weight-specific egg production rate, Huntley and Lopez 1994 model	All small copepods	Madsen et al. 2008
	max. 0.6	-	Weight-specific egg production rate	Only *O. similis*	Ward and Hirst 2007
	max. 1.9	-	From Edmondson & Winberg 1971	Only *O. similis*	Dahmen 1997b

*Table 6. Maximal seasonal production (mg C m^{-2} d^{-1}) in Balsfjord of the five copepods O. similis, M. norvegica, M. pusillus, C. finmarchicus and M. longa, estimated using the weight-specific egg production rate or the temperature model of Huntley and Lopez (1992). The data presented are taken from **Paper III**.*

	Weight-specific egg production rate (mg C m^{-2} d^{-1})	Temperature model (mg C m^{-2} d^{-1})	Season
Oithona similis	3.7	10.0	Summer
Microsetella norvegica	8.8	189.6	Summer
Microcalanus pusillus	1.0	2.7	Winter
Calanus finmarchicus	-	88.0	Fall
Metridia longa	-	3.1	Summer

5 Concluding remarks

This thesis aimed to add to the limited knowledge on the phenology and production of small copepods in high-latitude ecosystems, particularly of *O. similis*, *M. norvegica*, and *M. pusillus*. The key findings of this thesis are:

1. The temperature dependency of the egg hatching rate is species-specific and differs widely between *O. similis*, *M. norvegica*, and *M. pusillus*. The egg hatching successes were markedly different between these species and was not affected by changes in temperatures, except for *M. norvegica*. The high-latitude populations of *M. norvegica* seem to have a narrow thermal plasticity compared to *O. similis* and *M. pusillus*.
2. The observed phenology of the three studied small copepods can partly be explained by the species-specific thermal plasticity and life-history strategies. The success of *M. norvegica* in high-latitude ecosystems probably relies on its seasonal vertical migration targeting warmer surface waters combined with its preferential feeding on food sources less used by other species. In contrast, *O. similis* and *M. pusillus* may be successful in high-latitude ecosystems due to their affinity to low temperatures and potential ability to produce two generations per year.
3. It is necessary to improve the standard copepod sampling routine in high-latitude ecosystems to include the use of appropriate sampling gear targeting small copepods. The quantitative sampling of small copepods with ≤ 64-µm mesh size revealed high abundances and biomasses that can rival that of large copepods.
4. The total production of *O. similis*, *M. norvegica*, and *M. pusillus* were equal to or higher than that of the large copepods *C. finmarchicus* and *M. longa*. Therefore, small copepods are important to the food web and carbon cycling of high-latitude ecosystems.

The study of the egg hatching rate and secondary production of three small copepod species results in finding three unique strategies, with potentially large variation between the species-specific temperature response of metabolic rates and the phenological diversity of small copepods. Therefore, the study of the myriad of other small copepod species might lead to an increasing complexity within the small copepod community, which will be hard to model. However, the existence of different strategies cautions against the use of one species to model other similar-sized species. Other metabolic rates, such as juvenile growth rates, ingestion rates, respiration rates, and excretion rates, are also unknown for many species. Knowing more about the metabolism of small copepod species will help advance our understanding of the food web, the carbon pump, and the biogeochemical cycling of high-latitude ecosystems. Therefore, studies on the metabolic rates of small copepod species should be a priority.

Temperature has a significant impact on the population dynamics and production of small copepods, although other factors, such as food availability, mortality, and predation, are also important. In a warming Arctic, the different thermal plasticity of small copepods may partly drive shifts in their interspecific competition and affect population recruitment, biomass, and production. These shifts may, in turn, impact the functioning of high-latitude ecosystems at larger scales. It is imperative to study individual small copepod species to understand the present and predict the future functioning of high-latitude ecosystems.

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Paper I

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ORIGINAL ARTICLE

Temperature-dependent egg production and egg hatching rates of small egg-carrying and broadcast-spawning copepods *Oithona similis*, *Microsetella norvegica* and *Microcalanus pusillus*

CORALIE BARTH-JENSEN[1,*], MARJA KOSKI[2], ØYSTEIN VARPE[3,4], PETER GLAD[1], OWEN S. WANGENSTEEN[1], KIM PRÆBEL[1] AND CAMILLA SVENSEN[1]

[1]FACULTY OF BIOSCIENCES, FISHERIES AND ECONOMICS, UIT THE ARCTIC UNIVERSITY OF NORWAY, TROMSØ, NORWAY, [2]NATIONAL INSTITUTE FOR AQUATIC RESOURCES, TECHNICAL UNIVERSITY OF DENMARK, LYNGBY, DENMARK, [3] NORWEGIAN INSTITUTE FOR NATURE RESEARCH, BERGEN, NORWAY AND [4]DEPARTMENT OF BIOLOGICAL SCIENCES, UNIVERSITY OF BERGEN, BERGEN, NORWAY

*CORRESPONDING AUTHOR: coralie.barth-jensen@uit.no

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Reproductive rates of copepods are temperature-dependent, but poorly known for small copepods at low temperatures, hindering the predictions of population dynamics and secondary production in high-latitude ecosystems. We investigated egg hatching rates, hatching success and egg production of the small copepods *Oithona similis* and *Microsetella norvegica* (sac spawners) and *Microcalanus pusillus* (broadcast spawner) between March and August. Incubations were performed at ecologically relevant temperatures between 1.3 and 13.2°C, and egg production rates were calculated. All egg hatching rates were positively correlated to temperature, although with large species-specific differences. At the lowest temperatures, *M. pusillus* eggs hatched within 4 days, whereas the eggs from sac spawners took 3–8 weeks to hatch. The egg hatching success was ≤25% for *M. pusillus*, >75% for *O. similis* and variable for *M. norvegica*. The maximum weight-specific egg production rate (μg C μg^{-1} C d^{-1}) of *M. pusillus* was higher (0.22) than *O. similis* (0.12) and *M. norvegica* (0.06). *M. norvegica* reproduction peaked at 6–8°C, the prevailing *in situ* temperatures during

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its reproductive period. The difference in reproductive rates indicates species-specific thermal plasticity for the three copepods, which could have implications for present and future population dynamics of the species in arctic fjords.

KEYWORDS: female carbon content; hatching success; low temperature; seasonality; weight-specific egg production rate

INTRODUCTION

Small copepods, such as the cosmopolitan *Oithona* spp., are numerically abundant (Ormańczyk *et al.*, 2017; Poulsen and Kiorboe, 2006; Schnack-Schiel, 2001; Zamora-Terol *et al.*, 2013), and can seasonally dominate copepod biomass at high latitudes (Arendt *et al.*, 2013; Svensen *et al.*, 2011). They are an important food source for early larval stages of fish and carnivorous zooplankton, and can serve as an alternative or complementary carbon source for older larval stages (Castellani *et al.*, 2007; Grønkjær *et al.*, 2018; Turner, 2004). Some small copepod species are important for biogeochemical cycles (Koski *et al.*, 2017; Turner, 2004), including the biological carbon pump, both through their diet (e.g. feeding on suspended particles and microzooplankton) and their sloppy feeding behavior (Shoemaker *et al.*, 2019; Svensen and Vernet, 2016). Most small copepod species are active year round (Madsen *et al.*, 2008; Zamora-Terol *et al.*, 2014) while the large copepod species such as *Calanus* spp. hibernate in winter (Conover, 1988).

A body size of <2 mm defines small copepod species (Roura *et al.*, 2018), but these species are not functionally uniform (Litchman *et al.*, 2013). There is large variability in their feeding behavior (Drits and Semenova, 1984; Nishibe *et al.*, 2010), reproductive strategies (Kiørboe and Sabatini, 1994) and seasonal population dynamics (Arendt *et al.*, 2013; Ashjian *et al.*, 2003; Madsen *et al.*, 2008). At temperate and high latitudes, small copepods have been suggested to increase in abundance relative to larger ones due to climate-induced changes in salinity (Mäkinen *et al.*, 2017) and temperature (Beaugrand *et al.*, 2002; Coyle *et al.*, 2008; Eisner *et al.*, 2014). For example, small copepods tend to have increased production in warmer and more stable surface waters (Coyle *et al.*, 2008; Mäkinen *et al.*, 2017).

Measurements of growth (Uye *et al.*, 2002) or egg production (Zamora-Terol *et al.*, 2014) are commonly used to understand population dynamics and to estimate secondary production of copepods. These measurements are species-specific and time-consuming to obtain (Avila *et al.*, 2012), and limited knowledge is available on small copepods growth and reproductive rates (Madsen *et al.*, 2008; Norrbin, 1991; Turner, 2004). For the understudied species, rates from similar-sized or taxonomically close species are often used (e.g. Madsen *et al.*, 2008; Middelbo *et al.*, 2019; Nielsen and Andersen, 2002). However, the same environmental forcing may have different effects on different species, even when they belong to the same genus (Eisner *et al.*, 2014; Ershova *et al.*, 2016; Ershova *et al.*, 2017; Jónasdóttir, 1989). Estimation of copepod secondary production based on average rates of model species rather than the dominant (but perhaps understudied) ones may therefore result in erroneous estimates.

A species response to increasing temperature is an important facet of environmental ecophysiology, with phenotypic plasticity being the capacity of organisms to modify their morphology, physiology or life history under environmental influence (Booth *et al.*, 2018; Calow, 2009; Ortega-Mayagoitia *et al.*, 2018). Thermal plasticity is attributed to temperature-induced modifications and can result in local adaptation in copepods (Drillet *et al.*, 2008; Lonsdale and Levinton, 1986). Water temperature in the Arctic is predicted to rise over the next decades (Alexander *et al.*, 2018). To assess the present state of the community and a future possible shift from large to small copepod species, more knowledge is needed about the temperature dependence of the vital rates of small copepod species. Temperature-dependent reproductive rates of copepods include the egg hatching rate (Ambler, 1985; Andersen and Nielsen, 1997) and egg production (Bunker and Hirst, 2004; Huntley and Lopez, 1992) whereas the clutch size and hatching success have been described as both temperature-dependent (Devreker *et al.*, 2012; Ershova *et al.*, 2016; Hansen *et al.*, 2010) and temperature-independent (Dvoretsky and Dvoretsky, 2009a; Ershova *et al.*, 2016; Kurbjeweit, 1993; Weydmann *et al.*, 2015). The latency time, i.e. the time between the separation of hatched eggs from the female to the production of a new egg sac (Devreker *et al.*, 2012), seems to be temperature-independent for some small copepod species (Uye *et al.*, 1982; Uye *et al.*, 2002; Uye and Sano, 1995; Ward and Hirst, 2007), but was described as temperature-dependent for other species (Devreker *et al.*, 2012). However, few studies have measured the reproductive rates of small copepods at low temperatures, although a broad range of life history adaptions could be expected in response to the highly seasonal environment of high-latitude seas (Varpe, 2017).

In the present study we investigated three small copepod species: *Oithona similis* (Cyclopoida), *Microsetella*

norvegica (Harpacticoida) and *Microcalanus pusillus* (Calanoida). All three species are abundant in sub-arctic Balsfjord (69°N; northern Norway), have comparable body size (~500 μm), but differ regarding life-history strategies (Benedetti *et al.*, 2016; Brun *et al.*, 2017). Copepods have two main reproductive strategies; broadcast spawners (or free spawners) release a relatively large number of eggs (Kiørboe and Sabatini, 1994), whereas egg-carrying copepods (or sac spawners) produce fewer eggs clustered in one or two egg pouches. Although Kiørboe and Sabatini (1994) compared the reproductive strategies of sac spawners and broadcast spawners, their dataset include few small copepods, mainly from the genus *Oithona* that is the most investigated small copepod (e.g. Mironova and Pasternak, 2017; Nielsen *et al.*, 2002; Sabatini and Kiørboe, 1994; Zamora-Terol *et al.*, 2014). In contrast, the reproduction and population dynamics of the egg-carrying *M. norvegica* (Koski *et al.*, 2014; Mironova and Pasternak, 2017; Svensen *et al.*, 2018; Uye *et al.*, 2002) and broadcast spawner *M. pusillus* have been scarcely investigated (Norrbin, 1991).

We investigated the temperature-dependent responses of reproductive rates in *O. similis*, *M. norvegica* and *M. pusillus*, expecting that egg hatching rates of the three species will increase with temperature within their tolerance range. We also compared the influence of temperature on the egg hatching success and egg production of these ubiquitous species with different reproductive strategies. Genetic tools have revealed that cryptic or pseudocryptic species may be relatively common in marine species, including copepods (Lajus *et al.*, 2015). It is therefore unsure if the historically reported broad tolerance ranges within a certain morphologically identified species can still be trusted for single species (Knowlton, 1993). The *Microcalanus* species identification was therefore resolved through genetic analysis. For *O. similis*, several lineages have been described, but only one was found in the Arctic (Cornils *et al.*, 2017). We can therefore assume that the *O. similis* specimens in the present study belonged to the same species lineage.

MATERIAL AND METHODS

We investigated egg hatching rates, egg development times and hatching success of *O. similis*, *M. norvegica* and *M. pusillus* as a function of temperature, within the range of 1.3–13.2°C. In total, 22 incubations were conducted (Table I). The temporal spread of the incubations covered a wide temperature range so that the copepods response to different temperatures could be studied without needing a prior acclimation period.

Sampling

Copepods were collected in June and August 2017, and in March, May, June and August 2018 (Table I) at Svartnes, Balsfjord, Norway (N: 69° 22.947′; E: 19° 05.414′, depth 180 m). Balsfjord is one of the coldest fjords in Norway (Hopkins *et al.*, 1989), with mean surface temperature ranging from 1.3°C in February to 8.6°C in July and August (Eilertsen and Skarðhamar, 2006). A WP-2 net (64 or 90 μm-mesh, Hydro-Bios, Germany, 0.25 m^2 opening), equipped with a non-filtering cod end, was raised at 0.3–0.4 m s^{-1} from 50 m (2017) or 100 m (2018) to the surface. On deck, the content of the cod end was placed in 20 L of surface seawater, and transported to the laboratory within 2 h. Copepod samples were stored at 8°C for ~8 h during the experimental set-up, and the handling time was minimized for incubations with temperatures that deviated most from 8°C. *In-situ* temperature of the water column was obtained using conductivity, temperature, depth (CTD) profiler (Seabird model 25 Sealogger). Water samples were collected at four depths (5, 20, 50 and 150 m) using 20 L Go-Flo bottles (General Oceanics, Florida, USA). Water samples were stored in acid-washed Nalgene bottles in a dark cooler for 3 h until arrival at the laboratory. For each depth, three 100 mL aliquots were filtered for total chlorophyll *a* (Chl *a*, GF/F filter, 0.7 μm). The filters were extracted in 5 mL methanol for 12–18 h at 4°C in the dark (modified from Strickland and Parsons, 1972). Chl *a* was measured with a fluorometer (10-AU, Turner Designs, California, USA), and concentrations for the three aliquots were averaged for each depth.

Oithona similis and *Microsetella norvegica* egg-hatching incubations

Egg hatching was investigated at temperatures between 1.3°C and 13.2°C for *O. similis*, and at temperatures between 3.0°C and 13.2°C for *M. norvegica*. With the exception of August 2017 and May 2018, incubation temperatures reflected the *in situ* temperature at the time of sampling (Table I). Incubation temperatures were 3.5 and 4.2°C above *in situ* temperatures in May 2018 and August 2017, respectively. These higher temperatures were necessary to cover a 10°C temperature range. All incubations were performed without acclimation of the animals, following the procedure of Nielsen *et al.* (2002).

Uye *et al.* (2002) removed egg sacs manually from females *M. norvegica* and incubated them separately. This procedure is not usual for other egg-carrying copepods, including *O. similis,* where females and eggs are typically incubated together. In our first incubations, we therefore tested whether hatching rates of attached vs. detached egg sacs differed. For both species, we sorted 60 egg-carrying females using a stereomicroscope. The egg sacs

Table I: Overview of the incubations including the start date, in situ minimum and maximum temperatures at the depths from 170 to 0 m, incubation temperature (mean ± SD) and number of females used in each incubation

Start date	Temperature (*in situ*, °C)	Temperature (incubation, °C)	*Oithona similis*	*Microsetella norvegica*	*Microcalanus pusillus*
9.06.2017	4.8–11.4	4.6 ± 0.1	60 (H*[1])	60 (H*[1])	
19.06.2017	5.0–9.8	7.9 ± 0.2	61 (H[1])	57 (H*)	
		11.3 ± 0.1	65 (H)		
15.08.2017	Surface 9.0	10.4 ± 0.1		30 (H)	
		13.2 ± 0.2	30 (H)	30 (H)	
1.03.2018	1.7–2.1	1.3 ± 0.1	10 (H[2])		
12.03.2018	1.2–1.8	1.3 ± 0.1	30 (H[3])		
3.05.2018	2.0–3.5	4.0 ± 0.1		30 (H)	30 (H, EP)
		7.0 ± 0.2		30 (H)	30 (H, EP)
11.06.2018	2.5–7.7	3.0 ± 0.1		30 (H)	30 (H, EP)
		4.8 ± 0.1		30 (H)	29 (H, EP, DNA)
		5.7 ± 0.1		30 (H)	30 (H, EP, DNA)
24.08.2018	6.8–10.2	6.1 ± 0.2		30 (H)	
		9.8 ± 0.1			30 (H, EP)

H, hatching; EP, egg production; DNA, DNA sequencing of the female *Microcalanus* used in the incubation. *both attached and detached egg sacs, (blank) no experiment. Duration was 7 days for all experiments except for: [1]11 days, [2]15 days and [3]18 days.

were detached from 40 females, while 20 females were incubated with their egg sacs attached. Single females with their egg sacs or single egg sacs were individually incubated for 12 days, in order to ensure that all eggs had sufficient time to hatch. Since there were no significant differences in hatching rates between the two methods (Mann–Whitney rank-sum test, $P \geq 0.424$), the egg sacs were not separated from the females in the remaining incubations.

The duration of each incubation at the different temperatures was determined on the basis of the first incubations at 4.6°C, which lasted for 12 days. In these incubations, all viable eggs hatched within 11 days (*O. similis*) or within 4 days (*M. norvegica*). A change of color of the eggs was interpreted as a sign of degradation (Burkart and Kleppel, 1998; Drillet *et al.*, 2011), and discolored eggs were assumed to be unviable. For incubations at higher temperature, we assumed that 7 days would be sufficient as this represented the median duration of egg hatching of both species at 4.6°C. The two incubations at 1.3°C (*O. similis*, Table I) were prolonged to 15 and 18 days, in accordance with published data (Nielsen *et al.*, 2002). For all incubations, females with egg sacs were placed individually into 2.5 mL of 0.2 µm filtered seawater (FSW; Halvorsen, 2015), in 12-well culture plates and incubated in temperature-controlled incubators (Termaks KB8182, Termaks, Norway). The experimental design by Nielsen *et al.* (2002) relies on an even spread of the females through their egg-carrying cycle. We aimed for a minimum of 30 females per incubation, unless the total abundance of females in the sample was <30 (Table I). The water temperature was logged (model Kistock, Kimo, France) every 5 min for the duration of the incubation. We defined the number of eggs carried in the egg sacs of a female as a clutch. Clutch size was obtained for each female at the beginning of incubations by counting the number of eggs carried. Every 24 h (for incubations at 1.3°C) or 8 h (for all other temperatures), the wells were checked for hatching following gentle mixing of the water. Every second day ~50% of the water was replaced with fresh FSW. A hatching event for the entire clutch was defined as the time when at least one freely swimming nauplius was observed in the well. After the hatching event was recorded, the well was monitored to determine the final number of hatching eggs. Newly hatched nauplii were removed. The handling time was <10 min/plate. Wells containing a dead female during the first 24 h of the incubation were excluded from the dataset. During the first 2 days of the incubation, all females were photographed using a camera (Leica DFC450) connected to a stereomicroscope (Leica MZ16, ×84–100 magnification) for measurements of prosome length (for *O. similis*) or total length (for *M. norvegica*). In addition, 50 eggs of each species (×100–110 magnification) were photographed and measured with a precision of ±7 µm.

Microcalanus pusillus egg production and hatching rate

Incubations of *M. pusillus* were conducted in May, June and August 2018. For each incubation, 29 to 30 females were randomly selected from the samples (Table I) and individually incubated for 24 h in 2.5 mL of 0.2 µm-FSW in 12-well culture plates, under similar conditions to

those used for *O. similis* and *M. norvegica*. Overall mortality within the 24-h incubations never exceeds 7%, except for 23% mortality in the 9.8°C incubation. After 24 h, the eggs in each well (the clutch) were counted. The average clutch size for *M. pusillus* excluded the non-producing females. Females were photographed and size measured, before being preserved in pure grade ethanol (96%). The clutches were returned to the incubators and followed for 6 days. Eggs were checked for hatching every 8 h, with a handling time of maximum 10 min per plate. The same definition of a hatching event was used for *M. pusillus* as for the sac spawners. The mean development time (D, d) refers to the time between egg production and egg hatching and was calculated as the mean of all hatching events in all wells incubated at the same temperature.

Species determination of *M. pusillus*

It is uncertain whether one or two *Microcalanus* species are present in Balsfjord: *M. pygmaeus* and/or *M. pusillus* (S. Kwaśniewski, personal communication). The species can be identified on the basis of differences in the terminal spines on the second and fourth exopods, and from differences in the antennule/prosome length ratio (Koszteyn *et al.*, 1991). Use of both methods is challenging on live specimens and species identification could not be conducted prior to the egg incubations. We employed the length ratio method for all specimens after fixation in ethanol, using a stereomicroscope at ×100 magnification. Additionally, 58 females from two incubations (4.8°C and 5.7°C in June 2018) were sequenced to confirm taxonomic identification. DNA was extracted from individual females following a modified version of the HotShot protocol (Meissner *et al.*, 2013; Truett *et al.*, 2000). The Leray fragment of the mitochondrial cytochrome c oxidase subunit I (COI) was amplified using tagged mlCOIintF-XT 5′-GGWACWRGWTGRACWITITAYCCYCC-3′ as forward primer and tagged jgHCO2198 5′-TAIACYTCIGGRTGICCRAARAAYCA-3′ as reverse primer, and the polymerase chain reaction (PCR) was performed with conditions described in Wangensteen *et al.* (2018). Multiplexed libraries for next generation sequencing were obtained using the NEXTflex PCR-free DNA-seq kit (BIOO Scientific, TX, USA) and sequencing was performed on an Illumina MiSeq using a nano-kit V2 2x250 bp (Illumina, CA, USA) following the manufacturer's protocol. The obtained paired-end reads were aligned, demultiplexed, quality-filtered, and dereplicated using a custom pipeline based on OBITools (Boyer *et al.*, 2016), following procedures described in Ershova *et al.* (2019). The most abundant sequence obtained from each individual was compared to available sequences in BOLD (barcode reference database) for *M. pusillus* and sequences of *M. pygmaeus* (T. Falkenhaug, Institute of Marine Research, Norway). The morphological identification of the 58 females was then compared to their genetic identification to check for the robustness of the species identification.

Copepod carbon content

The particulate organic carbon (POC) contents of female *O. similis, M. norvegica* and *M. pusillus* were analyzed for samples collected in August 2016, February, March and April 2017 and June 2018. Between 60 and 300 females (without egg sacs) were sorted under a stereomicroscope (Leica MZ16, ×64–80 magnification), rinsed in 0.2 µm-FSW and placed onto precombusted GF/F filters (450°C, 0.7 µm pore size). The filters were stored frozen at −20°C until analysis. Prior to analysis, the filters were dried (60°C) and thereafter fumed with concentrated HCl (12 mol L^{-1}) to remove inorganic carbon. The filters with the females were analyzed using a CHN Lab Leeman 440 elemental analyzer. Measured values of POC for blanks (filters without copepods) were subtracted from filters containing copepods. Due to the loss of the June carbon measurement, *M. norvegica* carbon weight was approximated as the average between the April and August measurement for this month.

CALCULATIONS AND STATISTICAL ANALYSIS

Five variables were extracted from egg incubations with *M. norvegica* and *O. similis*: hatching rate of eggs, hatching success of clutches, hatching success of eggs in each clutch, total egg hatching success and weight-specific daily egg production.

Egg hatching rate

To obtain the egg hatching rate, the cumulative hatching events of the sac spawners were plotted against the incubation time. The large number of females incubated was assumed to ensure an even spread of the females' egg-carrying cycle (Nielsen *et al.*, 2002), which resulted in a linear increase of hatching events with time. The egg hatching rate (HR, d^{-1}) was defined as the slope of this linear regression between the cumulative hatching events and the incubation time. The regressions were forced through the origin as no females with already hatched clutches were incubated at T_0. Hatching events for the broadcast spawner *M. pusillus* were rather synchronous in a single incubation, as clutches were all produced within 24 h. Therefore, the estimation of the egg hatching

rate was not determined by linear regression, but as the reciprocal of the mean development time (D, d), for all hatching events within a single incubation.

Hatching success

The hatching success of clutches (HS_C, %) for each incubation was estimated as a percentage of clutches with at least one hatching event. The hatching success of eggs in each clutch (HS_E, %) was derived from the same incubation. This was expressed as the percentage of eggs in each clutch that had hatched by the end of the incubation. Total egg hatching success (HS_T, %) was then calculated by multiplying HS_C by HS_E. These variables were calculated in the same way for the three species.

Egg production

For *M. pusillus*, egg production (eggs female^{-1} d^{-1}) was estimated as the total number of eggs produced in 24 h divided by the number of females (including the non-producing females). Population-specific egg production could not be estimated for *O. similis* and *M. norvegica*, as the *in situ* ratio of females with egg sacs to the females without eggs was unknown. However, we estimated the individual carbon-specific egg production of the ovigerous (or reproducing) females (SEP_{OV}, μg C μg^{-1} C d^{-1}) for all three species, assuming that the latency time would be short and not temperature-dependent (Uye *et al.*, 2002; Uye and Sano, 1995). The SEP_{OV} was thus calculated by multiplying the average clutch size by the temperature-specific egg hatching rate obtained from the hatching incubations and the egg to female carbon ratio as:

$$\text{Sac spawners}: SEP_{OV} = CS \times HR \times C_{EGG}/C_{♀} \quad (1)$$

$$\text{Broadcast spawner}: SEP_{OV} = CS \times C_{EGG}/C_{♀} \quad (2)$$

where CS is the average clutch size (# eggs female^{-1}), HR is the estimated hatching rates (d^{-1}), C_{EGG} is the carbon content of an egg (μg C), and $C_{♀}$ is the carbon content of a female (μg C).

Egg hatching rate for the sac spawners was calculated using the surface temperature (depending on the sampling date, Table I). The carbon content of females was measured at different times of the year, and the value closest in time to the incubation was used. Egg carbon content was calculated based on volumes (calculated from diameters), converted to carbon using the conversion 0.14×10^{-6} μg C μm^{-3} for *O. similis* and *M. pusillus* (Kiørboe *et al.*, 1985; Sabatini and Kiørboe, 1994). *M. norvegica* eggs are spherical or ovoid (Uye *et al.*, 2002), and their egg volume was calculated from length and width measurements and converted to carbon using 0.19×10^{-6} μg C μm^{-3} (Uye *et al.*, 2002).

Statistics

Data are presented as means with standard deviation (mean ± SD) when available. The effect of temperature on hatching rate (HR), hatching success of clutches (HS_C), hatching success of eggs within clutches (HS_E), total hatching success (HS_T), and development time (D; *M. pusillus* only) was tested using linear regressions following a Shapiro–Wilk normality test. If the assumption of normality was not met, the correlation between two variables was tested by the nonparametric Mann–Whitney rank-sum test. The differences in egg production of *M. pusillus* between incubation temperatures and sampling times were tested using a Kruskal–Wallis 1-way analysis of variance (ANOVA) on Ranks because the dataset could not be normalized due to a high number of zero values. Differences in clutch sizes between temperatures and sampling times were tested by two separate 1-way ANOVAs. These were followed by Holm-Sidak's *post hoc* test to test for significant differences between groups. All statistical analyses were conducted with SigmaPlot 14.

RESULTS

Environmental background

Trends in temperature and Chl *a* followed a typical seasonal succession for Balsfjord. In March, the water column (0–100 m) was homogeneous, with temperatures of ~2°C (Table I) and Chl *a* concentration below detection limits. By May, the surface temperature had increased to 3.5°C, and a thermocline was developing, with a temperature of 2.0°C at 20 m. Chl *a* peaked at 20 m with 1.2 μg L^{-1}. In June, the water column was stratified with warmer surface waters (~11.4°C in 2017 and 8.0°C in 2018), dropping to 6.5°C (2017) and 5.3°C (2018) at 20 m, and with a Chl *a* peak of 3.4 μg L^{-1} in 2017 and 1.0 μg L^{-1} in 2018 at 10 m. In August, the water column was still stratified, with warm surface temperatures (9.0°C in 2017 and 10.2°C in 2018) decreasing to 6.8°C at 50 m. The maximum Chl *a* concentration was 0.9 μg L^{-1} (20 m depth). Hence, the copepods collected for incubations in early spring (March) had experienced low temperatures and low Chl *a*. The copepods collected in late spring (May) had been subject to slightly warmer temperatures and increasing Chl *a* concentration, and the copepods collected in early and late summer (June and August) had experienced a combination of a relatively warm surface temperature and medium to high Chl *a* concentrations.

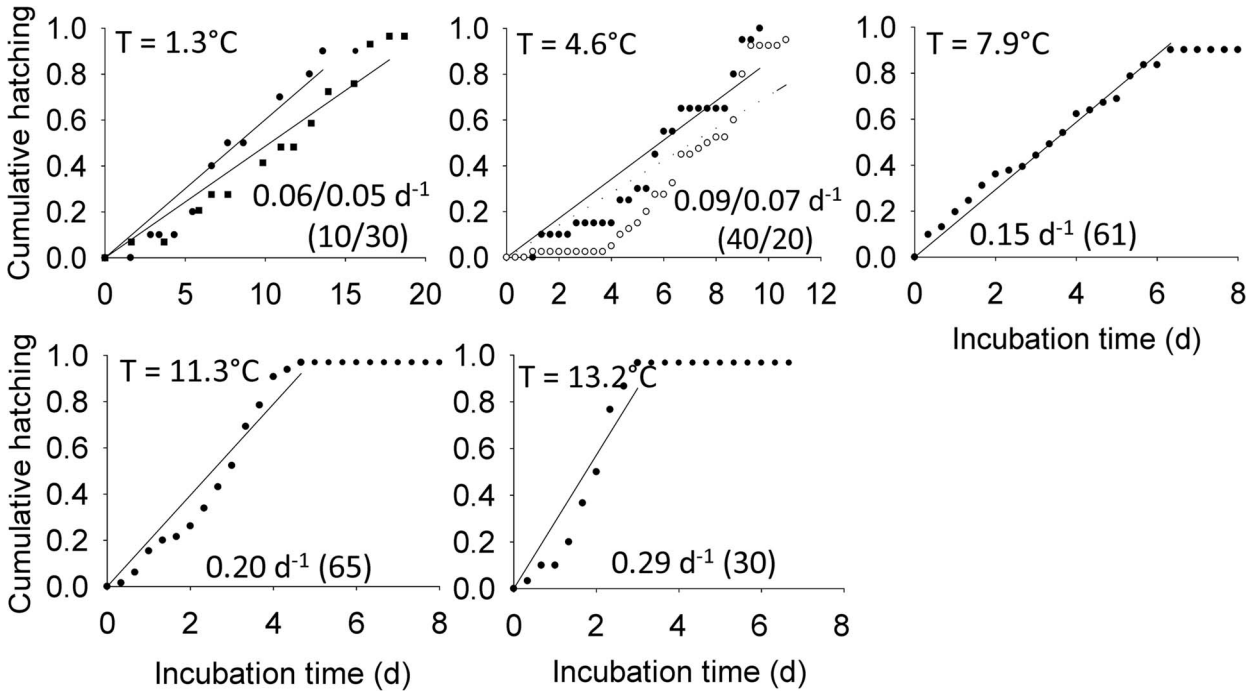

Fig. 1. *Oithona similis*. Cumulative hatching (ratio) as a function of temperature (T) at five different temperatures, with the lines representing a linear model of its increase over time. The hatching rate (slope of linear model, d^{-1}) and number of individuals incubated (n) are given for each incubation. Different symbols indicate replicate experiments. Open circles and dashed lines are used for experiments on egg sacs alone, while black circles and squares and full lines are used for replicates of experiments with egg sacs attached to females. Note the different incubation times (x-axis).

Egg hatching rate and hatching success

The egg hatching rate of *O. similis* increased from 0.05–0.06 d^{-1} at 1.3°C to 0.29 d^{-1} at 13.2°C (Fig. 1), and was correlated to temperature (linear regression, $P < 0.001$; Fig. 2a). The egg hatching rate of *M. norvegica* was lowest at temperatures < 4.8°C (<0.07 d^{-1}; Fig. 3), reached a maximum of 0.14 d^{-1} at 7.0°C but decreased slightly at temperatures ≥ 7.9°C (0.1 d^{-1}, Fig. 2b). *M. norvegica* egg hatching rate was thus positively correlated to temperature within the temperature range 3.0 to 7.9°C ($P = 0.003$). The mean development time of *M. pusillus* eggs decreased from 4.3 ± 0.4 d at 3.0°C to 1.6 ± 0.7 d at 9.8°C, and was linearly correlated to temperature ($P < 0.01$, Fig. 2f). Therefore, *M. pusillus* egg hatching rate, calculated as the reciprocal of the mean development time, increased from 0.23 d^{-1} at 3.0°C to a maximum of 0.61 d^{-1} at 9.8°C (Fig. 2c).

During the 7-days incubations, ≥90% of *O. similis* clutches hatched (HS_C, Table II). Average egg hatching success within clutches (HS_E) was between 79 and 93%, and total egg hatching success (HS_T) varied between 75 and 90% (Fig. 4). *M. norvegica* had a highly variable percentage of clutches that hatched (13–87%; Table II). At low temperatures (<5°C), the average HS_C was low (13–37%), while between 66 and 87% of the clutches hatched at temperatures from 5 to 8°C. HS_C decreased to 33–37% during late summer at temperatures of >10°C. In total, >50% of the eggs in each clutch hatched (HS_E, Table II), except for the 4.0°C incubation (May 2018). The combination of *M. norvegica* HS_C and HS_E resulted in a bell-shaped distribution of the total egg hatching success (HS_T, Fig. 4): the HS_T was ≤25% at the lowest and highest incubation temperatures, but peaked at temperatures between 5 and 8°C. For *M. pusillus*, only 27 to 47% of the clutches hatched (HS_C) during the 6-days incubations, with 28 to 65% hatching success of the eggs within the clutches (HS_E, Table II). Therefore, *M. pusillus* total egg hatching success (HS_T) was ≤25% for all incubations (Fig. 4). None of the variables contributing to egg hatching success (HS_C, HS_E and HS_T) were correlated to incubation temperature for the three copepod species (linear regressions, all $P \geq 0.336$).

Seasonal variations in clutch size, carbon content and specific egg production rate

In our study, *O. similis* females carried eggs from March to late August, whereas *M. norvegica* only started carrying eggs from May onwards. Ovigerous *M. pusillus* females were present throughout the study, and represented 51% ± 9% of the incubated females, independent of temperature (linear regression, $P = 0.883$). Average clutch

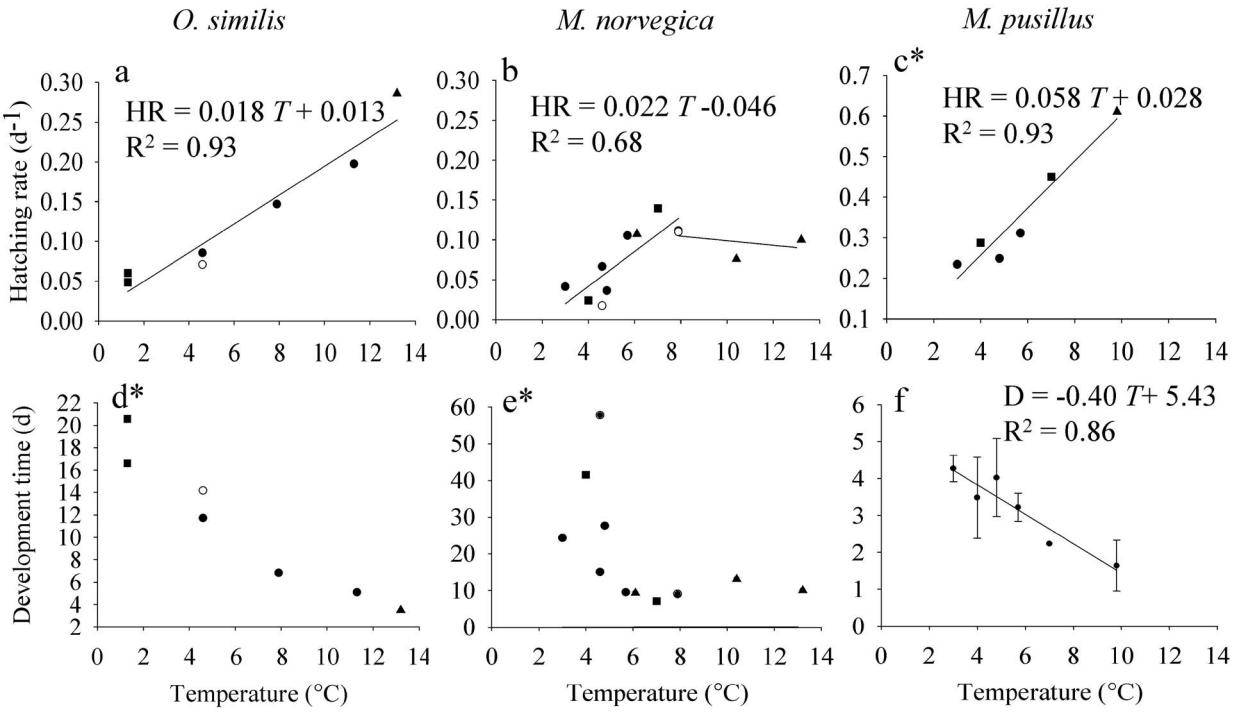

Fig. 2. (**a**–**c**) Egg hatching rates (HR, d^{-1}) and (**d**–**f**) Development time (D, d) of (a + d) *Oithona similis*, (b + e) *Microsetella norvegica* and (c + f) *Microcalanus pusillus* as a function of temperature. * The data were calculated as reciprocals of the experimentally obtained values. The seasons are represented by different symbols: squares for spring, circles for early summer, and triangles for late summer. The lines are the linear regressions made from the pooled data including all seasons, with their equations displayed when a linear model was fitting. Note the difference in the hatching rate scale (*y*-axis) for c. Color coding as in Fig. 1.

sizes of *O. similis* and *M. norvegica* peaked in June (Table III), and differed significantly between months (ANOVA on ranks, $P < 0.001$). *O. similis* had larger clutches (~23 ± 9 eggs $clutch^{-1}$) than *M. norvegica* at all seasons (~12 ± 3 eggs $clutch^{-1}$; Table III). The clutch size of *M. pusillus* varied over time (ANOVA on ranks: $P = 0.003$): the ovigerous females produced fewer eggs in June (6 ± 5 eggs $female^{-1}$) than in May (9 ± 3 eggs $female^{-1}$) and August (12 ± 8 eggs $female^{-1}$, Table III). Higher temperatures increased the numbers of eggs produced by ovigerous females but temperature could only explain a small part of the variation in egg production rate of *M. pusillus* (linear regression: $P = 0.004$, $R^2 = 0.08$).

Female carbon weight was lowest in February and peaked in June for *O. similis* and *M. pusillus*. The carbon content of *O. similis* females ranged from 0.32 to 0.61 μg C $female^{-1}$ and the carbon content of *M. pusillus* females from 0.76 to 1.26 μg C $female^{-1}$ (Table IV). Female *M. norvegica* carbon weight was lower in April (0.32 μg C $female^{-1}$) than in August (0.51 μg C $female^{-1}$; Table IV). The eggs of *O. similis* and *M. norvegica* were of similar size (diameter of 58 ± 3 and 59 ± 4 μm, respectively), equivalent to a calculated carbon content of 14×10^{-3} and 15×10^{-3} μg C egg^{-1}, respectively. *M. pusillus* eggs were larger (diameter of 65 ± 10 μm) than the sac-spawners' eggs, and therefore had a higher carbon content (20×10^{-3} μg C egg^{-1}).

The mean egg production of all incubated *M. pusillus* females (i.e. including non-producing females) was stable irrespective of the season or temperature (Fig. 5), varying from 2.9 to 6.6 eggs $female^{-1}$ d^{-1}. There was no significant linear correlation between the egg production and temperature ($P = 0.059$), nor were there any significant differences between the incubations conducted at different times (ANOVA on ranks: $P = 0.208$). The SEP_{OV} of *M. pusillus* was 0.20 μg C μg^{-1} C d^{-1} in May, 0.09 μg C μg^{-1} C d^{-1} in June and 0.22 μg C μg^{-1} C d^{-1} in August (Table III), and similar to egg production, independent of temperature.

The SEP_{OV} of *O. similis* was lowest in spring at 0.02 μg C μg^{-1} C d^{-1} (Table III), peaked in June at a maximum of 0.12 μg C μg^{-1} C d^{-1}, thereafter decreasing to 0.07 μg C μg^{-1} C d^{-1} in late summer. *O. similis* SEP_{OV} was correlated to surface temperatures (linear regression, $P = 0.004$). For *M. norvegica*, the SEP_{OV} was relatively low and ranged from 0.03 to 0.06 μg C μg^{-1} C d^{-1} (Table III), with the highest values during the summer. In contrast to *O. similis*, the SEP_{OV} of *M. norvegica* was independent of the surface temperatures (linear regressions; $P > 0.05$).

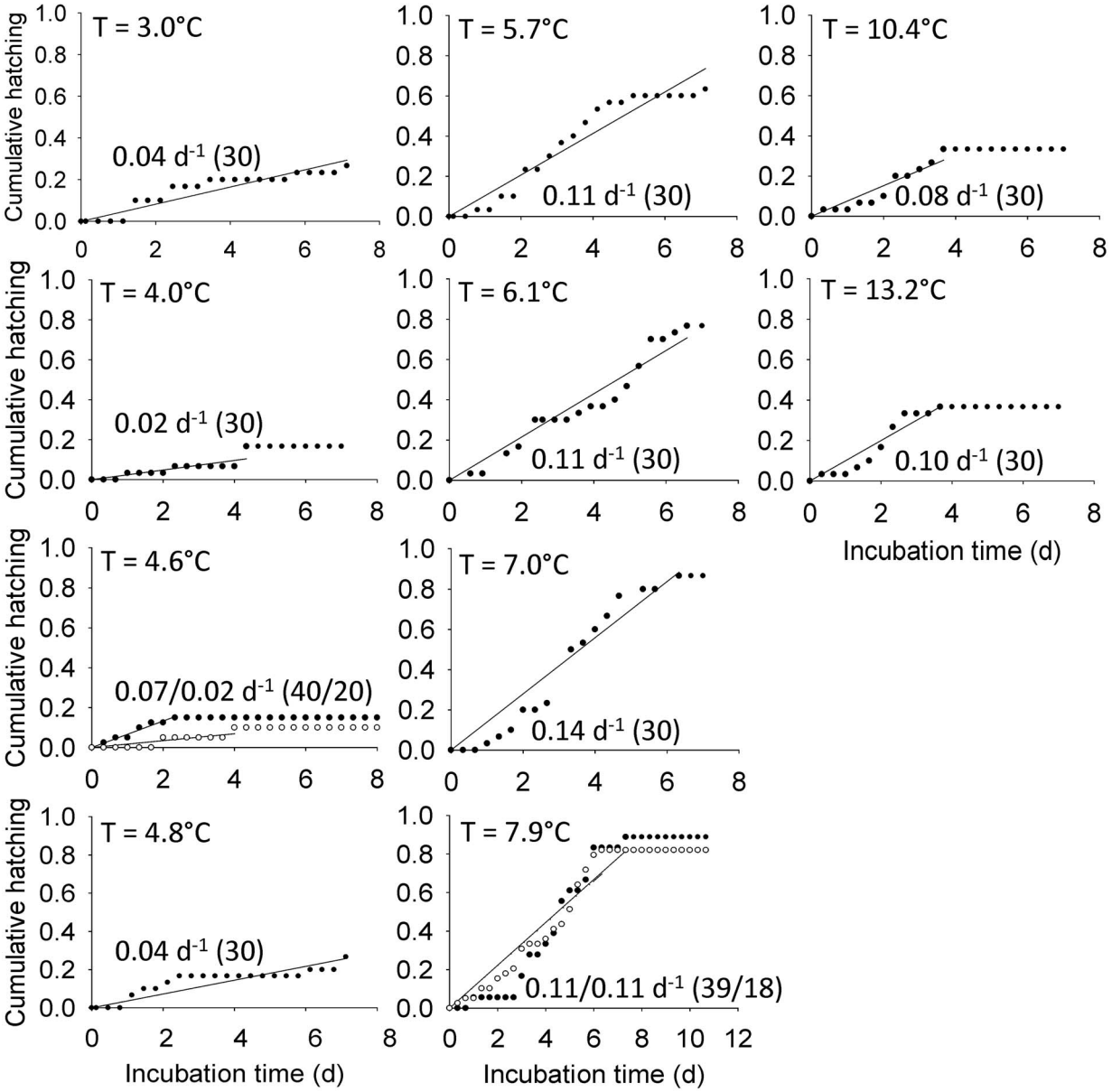

Fig. 3. *Microsetella norvegica*. Cumulative hatching (ratio) as a function of temperature at 10 different temperatures, with the lines representing a linear model of its increase over time. The hatching rate (slope of linear model, d^{-1}) and number of individuals incubated (*n*) are given for each incubation. Different symbols indicate replicate experiments. Open circles and dashed lines are used for experiments on egg sacs alone, while black circles and full lines are used for replicates of experiments with egg sacs attached to females. Note the different incubation times (*x*-axis).

Microcalanus species identification

The genetic identification of the 58 *Microcalanus* females used in the incubations revealed that only *M. pusillus* were present (Table SI). The morphological examination of the specimens matched the genetic species identification as only one morphological type of *Microcalanus* was observed, with short antennae. Therefore, we assume that all *Microcalanus* in our incubations were *M. pusillus*.

Discussion

Egg production, hatching success and egg development time differed between the three species, as did their response to temperature. *O. similis* and *M. pusillus* had increasing egg hatching rates over the full temperature range studied, with a shorter development time but lower hatching success for the broadcast spawner *M. pusillus*. In contrast, *M. norvegica* had maximum egg hatching rate at 8°C, and a decrease thereafter. *M. norvegica* also

Table II: Range and mean (±SD) of hatching success of clutches (HS_C, %; based on the first appearance of a freely swimming nauplius) and egg hatching success within clutches (HS_E, %; mean ± SD) for the three copepod species obtained within all incubations

Species	HS_C		HS_E	
	Range	Mean ± SD	Range	Mean ± SD
Oithona similis	90–97	94 ± 3	79–93	84 ± 5
Microsetella norvegica	13–87	47 ± 28	21–92	66 ± 18
Microcalanus pusillus	27–47	36 ± 7	38–65	49 ± 9

Table III: Mean clutch size (±SD), clutch to female carbon ratio ($C_{clutch}/C_{♀}$, %) and specific egg production rate of ovigerous female (SEP_{OV}, μg C μg^{-1} C d^{-1}) for each experimental date

Species	Date	Clutch size	$C_{clutch}/C_{♀}$	SEP_{OV}
Oithona similis	9.06.2017	20 ± 9	45 ± 20	0.10
	19.06.2017	23 ± 9	51 ± 20	0.10
	15.08.2017	17 ± 7	42 ± 17	0.07
	1.03.2018	8 ± 3	30 ± 11	0.02
	12.03.2018	9 ± 2	39 ± 9	0.02
Microsetella norvegica	9.06.2017	11 ± 2	50 ± 9	0.06
	19.06.2017	10 ± 3	45 ± 14	0.05
	15.08.2017	9 ± 3	33 ± 11	0.03
	3.05.2018	10 ± 1	58 ± 6	0.03
	11.06.2018	12 ± 3	54 ± 14	0.05
	24.08.2018	9 ± 2	33 ± 7	0.03
Microcalanus pusillus	12.03.2018	Spawning observed but not quantified		
	3.05.2018	9 ± 3	20 ± 7	0.20
	11.06.2018	6 ± 5	9 ± 8	0.09
	24.08.2018	12 ± 8	22 ± 15	0.22

Clutch sizes are pooled from all experiments started the same day, and the SEP_{OV} is calculated based on the mean clutch size and surface water temperature

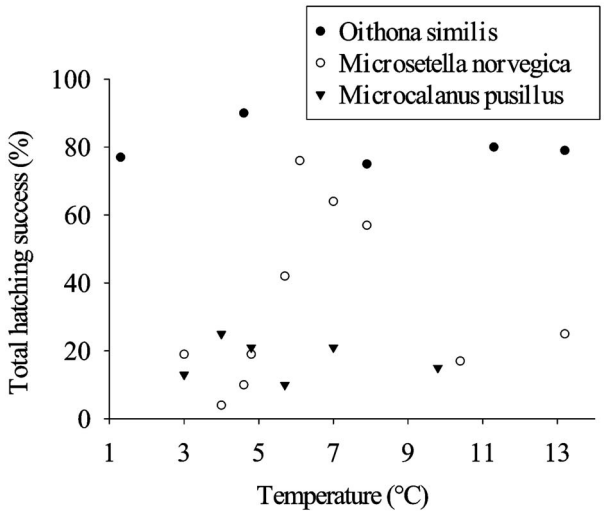

Fig. 4. Total hatching success (percentage) of *Oithona similis*, *Microsetella norvegica* and *Microcalanus pusillus* eggs as a function of temperature.

had the lowest specific egg production at all time-points. It appears that *O. similis* and *M. pusillus* could increase their reproductive output with increasing temperature, whereas *M. norvegica* was most productive between 6 and 8°C. The observed differences could neither be attributed to body size for these similar-sized species, nor to their reproductive strategy (sac spawners versus free spawner). Our study demonstrates that small copepod species show variable responses of egg hatching and productivity to temperature.

Temperature dependence of hatching rates and hatching success

The threefold increase of the egg hatching rate of the broadcast-spawning *M. pusillus*, within the 10°C increase in temperature, is comparable to that of the small calanoid *Pseudocalanus* spp. that tripled its hatching rate between 1 and 7°C (Middelbo *et al.*, 2019). In a previous study, a Q_{10} of 2.45 was found for the egg hatching rate of broadcast spawners (Hirst and Bunker, 2003), which is comparable to our findings. *M. pusillus* is a sub-surface species (Norrbin, 1991), and is mostly found <50 m in Balsfjord where water masses were <6°C during the study. Previously, this species has probably been grouped with *M. pygmaeus* as *Microcalanus*

Table IV: Mean sizes (±SD, μm) and carbon weight of female copepods ($C_{♀}$, μg C) by date

Species	Date	Female size	$C_{♀}$
Oithona similis	23.08.2016	472 ± 48	0.54
	27.02.2017	429 ± 25	0.36
	17.03.2017	490 ± 16	0.32
	7.04.2017	440 ± 36	0.48
	11.06.2018		0.61
Microsetella norvegica	23.08.2016	463 ± 24	0.51
	7.04.2017	471 ± 16	0.32
	11.06.2018	478 ± 22	0.42[a]
Microcalanus pusillus	23.08.2016	494 ± 48	1.05[b]
	27.02.2017	450 ± 21	0.76
	7.04.2017	521 ± 34	0.87
	11.06.2018	539 ± 36	1.26

[a]Due to technical problems, the true carbon value was lost and it is approximated as the average between the female carbon weights of April and August.
[b]The carbon value may be underestimated as the filter contained some stage five copepodites due to the scarcity of females.

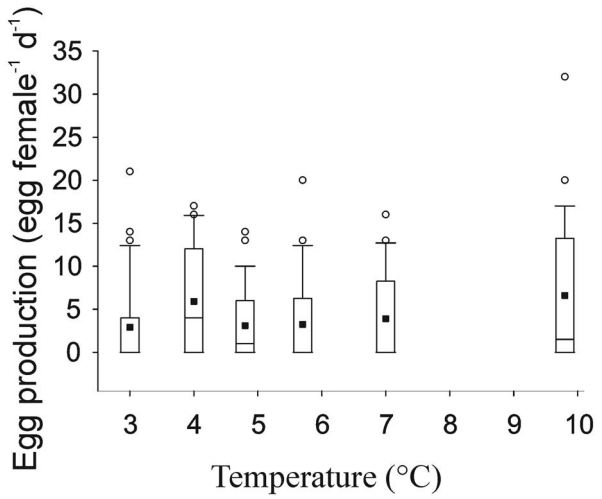

Fig. 5. Egg production of *Microcalanus pusillus* as a function of temperature (°C). The bottom and top of the box are the 25th and 75th percentiles with median indicated by a line inside the box (often not visible because it superposes with the 25th percentile). The whiskers show the 10th and 90th percentiles. The outliers are shown by open circles outside the box. The black squares represent the average egg production for all incubations.

spp. (Hop *et al.*, 2019b; Madsen *et al.*, 2008; Riisgaard *et al.*, 2014; Walkusz *et al.*, 2009), which was observed at temperatures within the range from −2 to 13°C in the Arctic. In our study, the egg hatching rate of *M. pusillus* showed a strong response to increasing temperature, suggesting that its reproductive rate would increase with an increase in temperature. Similar to the typically high egg hatching rates of other broadcast spawners (Hirst and Bunker, 2003; Mauchline, 1998), the non-motile free-floating eggs of *M. pusillus* hatch rapidly, perhaps easing the risk of cannibalism and predation on the eggs (Hirst and Lopez-Urrutia, 2006; Kiørboe and Sabatini, 1994; Weydmann *et al.*, 2015). Higher temperatures could thus increase early-stage survival of *M. pusillus* by ensuring a faster transition from a non-motile to a motile stage.

In contrast to the short egg hatching time of broadcast-spawning copepods, a longer egg development time is characteristic of egg-carrying copepods (Kiørboe and Sabatini, 1994). An egg-carrying strategy usually constrains lifetime fecundity. It may prove disadvantageous in cases of high mortality of egg-bearing females (Ward and Hirst, 2007), but will pay off in environments where predation is high on pelagic eggs (Kiørboe and Sabatini, 1994). An increase in temperature might change the cost–benefit ratio of the egg-carrying strategy if mortality and egg hatching time respond differently to increasing temperature. This could be the case for *M. norvegica* where the maximum egg hatching rate was reached at 7°C with no further increase at higher temperatures, which describes a performance curve. Performance curves, i.e. the curve illustrating the effect of a climatic variable like temperature on a physiological rate, are often bell-shaped (Dam and Baumann, 2018). However, previous studies on copepods have reported a positive linear or power relationship between investigated temperatures and egg development times (e.g. Andersen and Nielsen, 1997, Ianora *et al.*, 2007, Mclaren, 1966, Middelbo *et al.*, 2019, Nielsen *et al.*, 2002, our observations of *O. similis*). The performance curve of *M. norvegica* hatching rate was therefore surprising. However, it is probable that an optimum may be reached for any particular physiological rate, given that the range of the climatic variable (e.g. temperature) is large enough for that species.

It is possible that the bell-shaped temperature response of *M. norvegica* egg hatching rate reflected an adaptation to temperatures that prevail during the reproductive season. The egg hatching rate of copepods reflects development of an egg, as a reciprocal measure of the time spent

between two developmental stages (Huntley and Lopez, 1992). Development and growth can indeed reach a maximum, after which growth may not further increase with increasing temperature or can be negatively affected (Lee *et al.*, 2003; Lonsdale and Levinton, 1986). It is possible that northern harpacticoid populations, including *M. norvegica*, reach their maximum growth and egg hatching rate at lower temperatures than southern populations, as a local adaptation to the prevailing temperatures. In Balsfjord, egg-carrying females *M. norvegica* are found between May and September (Svensen *et al.*, 2018), mostly above 50 m where temperatures are usually between 5 and 8°C (Eilertsen and Skarðhamar, 2006). Therefore, the Balsfjord population may have adapted to the local temperatures. *M. norvegica* and *O. similis* had comparable egg hatching rate only between 6 and 8°C, whereas the egg hatching rate of *O. similis* surpassed that of *M. norvegica* >8°C. Hence, *O. similis* appeared more thermally plastic than *M. norvegica*. The egg hatching rates of *O. similis* were similar to those observed by Nielsen *et al.* (2002).

In the Arctic, numerical dominance of *M. norvegica* seems to be confined to fjords (Arendt *et al.*, 2013; Hjorth and Dahllöf, 2008; Svensen *et al.*, 2018), whereas *O. similis* can be abundant both in fjords (Hop *et al.*, 2019b; Middelbo *et al.*, 2019) and coastal and shelf areas (Dvoretsky and Dvoretsky, 2009a; Dvoretsky and Dvoretsky, 2015; Hop *et al.*, 2019a; Madsen *et al.*, 2008). *M. norvegica* is present from tropical seas with temperatures > 30°C (Chew and Chong, 2016) to polar areas (Arendt *et al.*, 2013; Svensen *et al.*, 2019). In the Inland Sea of Japan, the population of *M. norvegica* did not reach a maximum egg hatching rate within the temperature investigated (Uye *et al.*, 2002), an observation that differs from ours. This suggests that although *M. norvegica* is present in widely different environments, populations may adapt to local conditions. For *M. norvegica* in Balsfjord, this could mean that recruitment of *M. norvegica* may decline if the temperature increases >8°C during the reproductive period, due to their lowered egg hatching rates at higher temperatures. In contrast, *O. similis* and *M. pusillus* may benefit as a higher temperature increased their egg hatching rate. A higher thermal plasticity of *O. similis* and *M. pusillus* suggests a higher recruitment potential than for *M. norvegica* (Allan, 1976; Devreker *et al.*, 2012; Tang *et al.*, 1998) in Balsfjord, although other processes linked to mortality and survival will also be important to shape the recruitment of species.

Other than the thermal plasticity of the egg hatching rate, the recruitment potential of a species is affected by its egg hatching success (Devreker *et al.*, 2012). Hatching success can be influenced by temperature (Hansen *et al.*, 2010), excreted substances from phytoplankton (Ambler, 1985; Ianora *et al.*, 2007), successful mating/fertilization (Mironova and Pasternak, 2017), and food composition (Jónasdóttir *et al.*, 2005). We found no correlation between egg hatching success and temperature or season, but notable differences were observed between species. *O. similis* had a high total egg hatching success compared to *M. norvegica* and *M. pusillus*. Though the egg hatching success of *M. norvegica* was not linearly related to temperature, the highest egg hatching success was found at the optimum temperatures for the egg hatching rate. This agrees with the possibility of a local temperature adaptation of *M. norvegica*.

The low egg hatching success of *M. pusillus* contrasted with the high thermal plasticity of its egg hatching rate. Egg hatching success of calanoid copepod eggs is rarely <60% (e.g. Devreker *et al.*, 2012; Hansen *et al.*, 2010; Tang *et al.*, 1998), although episodically low hatching success (0–30%) has been observed (e.g. Halsband-Lenk *et al.*, 2001; Ianora and Poulet, 1993; Jónasdóttir *et al.*, 2005; Miralto *et al.*, 1998; Yamaguchi *et al.*, 2010). To our knowledge, no previous estimates of egg hatching success exist for *M. pusillus*. In our incubations, most of the *M. pusillus* eggs that did not hatch were discolored or disintegrated, and only ∼4% of the unhatched eggs seemed still viable at the end of the 6 days observation. Therefore, we assume that the incubated *M. pusillus* female produced mainly subitaneous eggs (i.e. eggs hatching without delay), and that the low egg hatching success was representative of the *in situ* conditions. It should be noted that the incubation methods used in our study followed established methods for broadcast-spawning copepods (Drillet *et al.*, 2008; Halvorsen, 2015), and female mortality was low. A low *in situ* hatching success, as observed in our study, would lower the positive effect of a temperature increase on the egg hatching rate and thereby on the recruitment potential of *M. pusillus*.

Seasonality

Egg-producing females were present at least from March to August (*O. similis* and *M. pusillus*) and from May to August (*M. norvegica*) in Balsfjord, which is in accordance with the long reproductive periods described in previous studies (Dvoretsky and Dvoretsky, 2009b; Norrbin, 1991; Svensen *et al.*, 2018). Small copepods do not accumulate large lipid reserves (Arima *et al.*, 2014; Norrbin, 1991), contrasting with larger diapausing, and sometimes capital-breeding, copepods (Conover, 1988; Sainmont *et al.*, 2014; Varpe *et al.*, 2009). Smaller copepod species typically rely on continuous feeding to fuel their reproduction (Norrbin, 1991; Svensen *et al.*, 2019); i.e. income breeding. The three investigated species are omnivorous, grazing on food sources often

available outside the spring-bloom period, such as marine aggregates (Koski *et al.*, 2005; Norrbin, 1991) and microzooplankton (Castellani *et al.*, 2005; Svensen and Kiørboe, 2000).

The egg production rate for ovigerous females (SEP_{OV}) of *M. norvegica* was unusually low for a sac spawner at all seasons (Uye and Sano, 1995). In temperate waters, *M. norvegica* carried 15.8 eggs female^{-1} with an egg hatching rate of 0.67 d^{-1} at 27.8°C (Uye *et al.*, 2002). Based on Equation 1, the weight-specific egg production rate for the egg-bearing females in the Inland Sea of Japan may be as high as 0.34 μg C μg^{-1} C d^{-1}, which demonstrates a high production potential of *M. norvegica* at high temperature. The difference in egg production rates between *O. similis* and *M. norvegica* in Balsfjord may reflect diverse reproductive investments. Even if the two species carry eggs, the time spent carrying eggs may differ. Female *M. norvegica* are suggested to have a hybrid egg-carrying strategy, where they release their egg sac before the eggs have hatched (Koski *et al.*, 2014). In that case, the egg hatching rate may not represent the time interval between two clutches, resulting in a potential underestimation of *M. norvegica* egg production rate.

We observed that *M. pusillus* had a SEP_{OV} ~3.1 times higher than *O. similis*, and ~7.3 times higher SEP_{OV} than *M. norvegica*. Broadcast spawners have on average a 2.5 times higher weight-specific egg production rate than sac spawners, to compensate for high egg mortality (Kiørboe and Sabatini, 1995). However, we found that the difference in SEP_{OV} between species varied with seasons. Adverse environmental conditions may cause physiological stress, which could lower the egg production of copepods (Uye and Sano, 1995). *M. pusillus* egg production peaked in May and August and the sac spawners had a peak SEP_{OV} in June. The differences between months were significant but not related to surface temperature (except for *O. similis*). The SEP_{OV} is influenced by the egg hatching rate, clutch size and female body weight (Equation 1 and 2). Egg hatching rates investigated at similar temperatures but different months showed no significant differences. Therefore, the seasonal variation observed likely resulted from the changes in the clutch size and the female body weight (i.e. female condition). Food availability and quality varies between March and August in Balsfjord (Eilertsen *et al.*, 1981), which can affect clutch size (Ambler, 1985; Castellani *et al.*, 2007; Halsband and Hirche, 2001) and carbon weight of copepods (Auel and Hagen, 2005, this study). The seasonal pattern in the weight-specific egg production rate of the three copepod species is likely the result of seasonal variation in abiotic and biotic factors that influence clutch size and female weight along with the temperature-dependency of the egg hatching rate.

CONCLUSION

In this study, we provide egg hatching rate and egg hatching success data for three small and abundant copepod species. The egg hatching rates of all three species responded to increasing temperatures but their thermal plasticity differed. Our study therefore highlights species-specific temperature dependencies also within the abundant group of small copepods. Supporting previous observations, we confirmed that small sub-arctic broadcast spawners have faster egg development than co-occurring sac spawners and that their weight-specific egg production rate is higher. Moreover, we found that the weight-specific egg production of ovigerous females varies seasonally, presumably influenced by the seasonal changes in the clutch size and carbon content of the female of the three species. This study therefore also highlights the importance of documenting vital rates at different seasons. In the future, oceans will have conditions combining new ranges of temperature, salinity, pH, oxygen and primary production (IPCC, 2019), including changes in the seasonality of these variables. According to our findings, the consequences of these new conditions will differ across species and potentially impact their phenology and relative biomass. Such alterations may in turn interact with the predator–prey interactions or the cycling of organic matter in the pelagic realm, both of which have implications for the energy flux and carbon turnover.

SUPPLEMENTARY DATA

Supplementary data can be found at *Journal of Plankton Research* online.

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Paper II

Barth-Jensen, C., Daase, M., Ormańczyk, M. R., Varpe, Ø., Kwaśniewski, S., & Svensen, C. (2022).

High abundances of small copepods early developmental stages and nauplii strengthen the perception of a non-dormant Arctic winter.

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ORIGINAL PAPER

High abundances of small copepods early developmental stages and nauplii strengthen the perception of a non-dormant Arctic winter

Coralie Barth-Jensen[1] · Malin Daase[1] · M. R. Ormańczyk[2] · Øystein Varpe[3,4] · Sławomir Kwaśniewski[2] · Camilla Svensen[1]

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Abstract

The traditional view is that the Arctic polar night is a quiescent period for marine life, but recent reports of high levels of feeding and reproduction in both pelagic and benthic taxa have challenged this. We examined the zooplankton community present in Svalbard fjords, coastal waters, and the shelf break north of Svalbard, during the polar night. We focused on the population structure of abundant copepods (*Calanus finmarchicus*, *Calanus glacialis*, *Metridia longa*, *Oithona similis*, *Pseudocalanus* spp., *Microcalanus* spp., and *Microsetella norvegica*) sampled using 64-µm mesh nets. Numerically, copepod nauplii (≥ 50%) and the young developmental stages of small copepods (< 2 mm prosome length as adult) dominated the samples. Three main patterns were identified: (1) large *Calanus* spp. were predominantly older copepodids CIV–CV, while (2) the small harpacticoid *M. norvegica* were adults. (3) For other species, all copepodid stages were present. Older copepodids and adults dominated populations of *O. similis*, *Pseudocalanus* spp. and *M. longa*. In *Microcalanus* spp., high proportion of young copepodids CI–CIII indicated active winter recruitment. We discuss the notion of winter as a developing and reproductive period for small copepods in light of observed age structures, presence of nauplii, and previous knowledge about the species. Lower predation risks during winter may, in part, explain why this season could be beneficial as a period for development. Winter may be a key season for development of small, omnivorous copepods in the Arctic, whereas large copepods such as *Calanus* spp. seems to be reliant on spring and summer for reproduction and development.

Keywords Polar night · Copepod stage structure · Population composition · Svalbard · Fjords · Overwintering strategies

Introduction

Polar environments are characterized by extremes in light conditions, ranging from periods of midnight sun (polar day) to periods when the sun does not rise above the horizon (polar night). The duration of the polar night varies with latitude (Cohen et al. 2020). Zooplankton species have adapted to this period of low light intensities and low food concentrations by developing strategies reducing their metabolic expenditure (see Berge et al. 2020 and references within). In the Arctic, omnivorous copepod species, such as the small cyclopoid *Oithona similis*, remain active during winter although activity may be reduced compared to other seasons (Berge et al. 2020), and feeding continues often accompanied with a change in prey spectrum (Grønvik and Hopkins 1984; Norrbin 1991; Dvoretsky and Dvoretsky 2009a, 2015a). Primarily herbivorous zooplankton such as *Calanus* spp., undertake extensive vertical seasonal migrations, decrease their metabolism while in deep water during winter and survive on accumulated energy reserves (Conover 1988; Atkinson 1998; Varpe 2012). Relatively large and mainly herbivorous copepods of the genus *Calanus* hold a key position in the energy transfer from primary producers to higher trophic levels in the Arctic ecosystem (Søreide et al. 2008). Their low activity during winter may have given rise to the view that the Arctic winter is a season of dormancy (Berge et al. 2015a, 2020). However, recent

✉ Coralie Barth-Jensen
coralie.barth-jensen@uit.no

1 Faculty of Biosciences, Fisheries and Economics, UiT The Arctic University of Norway, 9037 Tromsø, Norway

2 Institute of Oceanology, Polish Academy of Sciences, Sopot, Poland

3 Norwegian Institute for Nature Research, 5006 Bergen, Norway

4 Department of Biological Sciences, University of Bergen, 5020 Bergen, Norway

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observations of high biological activities, such as feeding, growth, and reproduction, during the polar night (Berge et al. 2009, 2015a; Kraft et al. 2013; Båtnes et al. 2015; Vader et al. 2015; Webster et al. 2015) are challenging this traditional view that the polar night is a period of dormancy (Hirche and Kosobokova 2011; Darnis et al. 2012; Berge et al. 2015b).

There are far fewer studies of ecological processes in zooplankton during the polar night than at other times of the year (but see, e.g., Hirche and Kosobokova 2011; Kosobokova and Hirche 2016; Daase et al. 2018; Berge et al. 2020). Studies of zooplankton communities during the Arctic polar night have usually been carried out using acoustic instruments (e.g., Berge et al. 2009; Darnis et al. 2017) or nets with mesh size ≥ 180 µm (e.g., Hirche and Kosobokova 2011; Daase et al. 2014, 2018; Webster et al. 2015; Kosobokova and Hirche 2016). These gears detect large zooplankton, but small-sized taxa and young small life stages are underrepresented or go undetected (Nichols and Thompson 1991; Nielsen and Andersen 2002; Svensen et al. 2019). As a result, knowledge about the small species and life-stage compositions of zooplankton communities in the Arctic during winter is limited (but see Ussing 1938; Digby 1954; Lischka and Hagen 2005, 2016; Arendt et al. 2013; Grenvald et al. 2016).

Small copepod taxa (≤ 2 mm adult prosome length, Roura et al. 2018) and copepod nauplii are widely distributed throughout the Arctic and often numerically dominant in fjords (Madsen et al. 2008; Arendt et al. 2013; Ormańczyk et al. 2017), shallow seas and deeper basins (Apollonio 2013; Dvoretsky and Dvoretsky 2014, 2015b; Balazy et al. 2018). Small copepods, mainly omnivores, are often described as being winter-active, because they feed (Castellani et al. 2007) and reproduce during this period (Lischka and Hagen 2005, 2016). Reproduction is generally lower during winter than during periods of high food availability because most small copepods are income breeders; i.e.they depend on an exogenous food supply to fuel reproduction (Varpe et al. 2009). Their feeding on marine snow and microzooplankton (Svensen and Kiørboe 2000; Calbet and Saiz 2005; Koski et al. 2007) impacts carbon flux; small copepods may be a major contributor to the retention of carbon in surface waters (Svensen et al. 2018; Mayor et al. 2020), and they are probably an important food source for heterotrophic predators in surface waters during winter (Falkenhaug 1991; Saito and Kiørboe 2001; Arendt et al. 2013; Grigor et al. 2014). Therefore, small copepods may have a key role in the Arctic marine ecosystem during winter, and information about their population dynamics could increase our understanding about their ecological role in pelagic waters in the Arctic polar night.

Here, we describe the structure of the mesozooplankton community in the western Barents Sea and Svalbard waters (70° to 81°N) during the polar night (January), focusing on the abundant small copepod taxa (*O. similis*, *Pseudocalanus* spp., *Microcalanus* spp., and *Microsetella norvegica*), the large copepod taxa (*Metridia longa*, *Calanus finmarchicus*, and *Calanus glacialis*), and the most abundant meroplankton. We hypothesize that the population structure of each of these seven taxa will reflect their reproductive strategy: high abundance of young copepodid stages (CI) in January would indicate winter recruitment and likely reproduction of these species, whereas a predominance of older copepodids (IV to adult) would indicate the lack of thereof. This study aims to broaden our knowledge about the life-history of small copepod species in the Arctic.

Materials and methods

Study area

Sampling was conducted onboard R/V Helmer Hanssen during the Polar Night cruise 2017 (PNC17), 6th to 17th January 2017 in the waters of the western Barents Sea and Svalbard archipelago. The area is influenced by the West Spitsbergen Current (WSC), a continuation of the North Atlantic Current that transports Atlantic waters across the western entrance of the Barents Sea and along the western coast of Svalbard (Cottier et al. 2005). The WSC branches North of Svalbard with one branch transporting Atlantic water eastwards along the northern shelf of Svalbard toward the Arctic Ocean, and the other transporting water westward, toward Fram Strait and east coast of Greenland. Sampling was conducted at six oceanic stations and seven stations in three fjords over an 11° latitudinal range (Fig. 1a, Table 1).

Two oceanic stations (TB1 and TB2) were located in the western Barents Sea (Fig. 1a), within the main path of the Atlantic water flow (Cottier et al. 2005). The other four oceanic stations were located on the shelf (NS1, NS4, and NS10) and off-shelf (NS6) north of Svalbard. NS4 and NS6 were deep stations (> 1000 m), whereas NS1 and NS10 were shallower, 208 m and 343 m respectively (Table 1). Bellsund, at the opening of Van Mijenfjorden (station VMF9), and Krossfjorden (stations KF1, KF2, and KF3) were located on the west coast of Svalbard and were affected by the inflow of Atlantic water from the WSC as well as colder Arctic water from the Coastal Current (Cottier et al. 2005). Rijpfjorden (stations R3, R3b, and R4) was located on the northern coast of Nordaustlandet and was mainly influenced by Arctic water, but could seasonally experience an inflow of Atlantic water (Wallace et al. 2010).

Water sampling and analyses

Environmental salinity, temperature, and fluorescence data were collected using a ship-board conductivity,

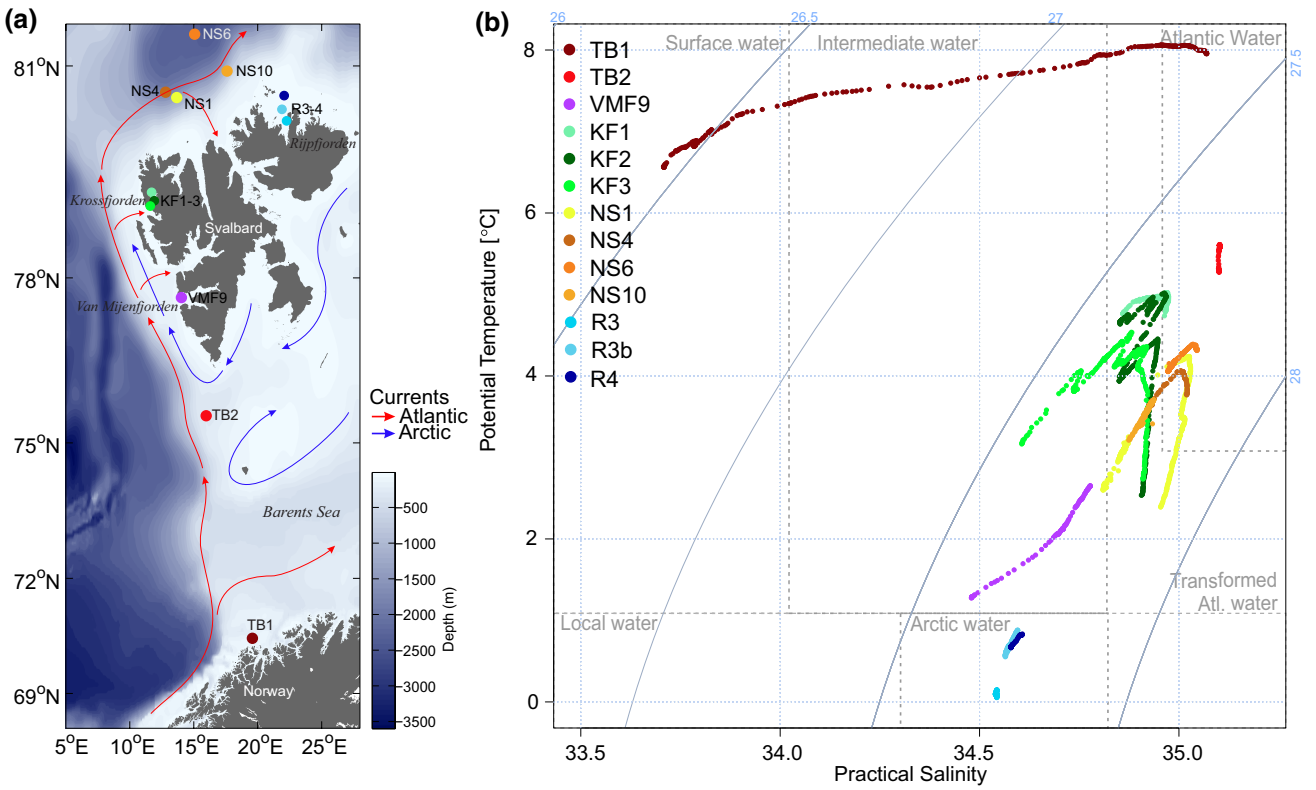

Fig. 1 **a** Map of the study area with sampling station positions and names. Bathymetry and main ocean currents are given for reference. **b** Plot of the temperature and salinity in the water column (down to 138–400 m, see Table 1 for station depths) at each of the 13 stations. Light gray lines show isopycnals. The different water mass boundaries are defined by rectangles, following Cottier et al. (2005), and the blue lines represent pycnoclines

temperature and depth profiler (SBE911plus, SeaBird Electronics). Water samples were collected at depths of 5, 15, 50, 100, 200, and 300 m using 8-L Niskin bottles on a CTD rosette. No water sampling was performed at VMF9 and NS4. The water from each depth was divided into 3 aliquots of 500 mL filtered through GF/F filters (0.7 µm) for total chlorophyll *a* (Chl *a*), and 3 aliquots of 500 mL filtered through pre-combusted GF/F filters for particulate organic carbon (POC). Filters were then stored at − 20 °C until analysis. For Chl *a* extraction, the filters were placed in 5 mL methanol and extracted overnight at 4 °C in darkness (modified from Strickland and Parsons 1972). Chl *a* fluorescence was then analyzed in a fluorometer (10-AU, Turner Designs, California, USA). Prior to analysis, the POC filters were dried and fumed with concentrated HCl to remove inorganic carbon. Filters were analyzed using a CHN Lab Leeman 440 elemental analyzer. Measured values of POC for blanks (unused pre-combusted GF/F filters) were subtracted from those with filtered samples.

Zooplankton sampling and identification

Zooplankton was sampled using vertically stratified net hauls with a multiple opening/closing net (MultiNet type Midi, Hydro-Bios, Germany, mouth opening 0.25 m^2, 64-µm mesh size, towing speed 0.4 m s^{-1}). The four depth strata sampled were 3–50 m, 50–100 m, 100–200 m, and 200–400 m, or to 10 m above the bottom at stations shallower than 400 m. A 64-µm mesh WP-2 net (Hydro-Bios, Germany, opening 0.25 m^2) was used for the 0–50 m sampling at station TB2 due to a tear in the MultiNet net bag. A technical error resulted in only the upper 100 m being sampled at station KF1. We focus on comparing the zooplankton community in the surface layer from 0 to 100 m and the deeper layer from 100 m to bottom (at 138–372 m) or 400 m, and assume that copepods present in the upper 100 m are not in diapause.

Immediately after collection the samples were fixed in hexamethylenetetramine-buffered formaldehyde in seawater solution at 4% final concentration. The samples were later analyzed under a stereomicroscope (Olympus SZX7).

Table 1 Location, bottom depth and sampling date and time of the 13 stations sampled in January 2017 in the western Barents Sea and near Svalbard, with station mean temperature (± *SD*, $n = 99$) of the upper 100 m (°C), and average concentrations in the top 400 m (or to the bottom if the station is shallower) of total Chl *a* (μg m^{-3}) and POC (mg m^{-3})

Station	Location	Latitude (°N)	Longitude (°E)	Sampling date and time (UTC)	Depth (m)	Temperature (°C)	Chl *a* (μg m^{-3})	Total Chl *a* (mg m^{-2})	POC (mg m^{-3})	POC (g m^{-2})
TB1	Offshore	70.507	19.612	2017.01.04 20:07	318	6.8 ± 0.2	7.2	2.3	53.9	17.1
NS6	Shelf	81.356	14.984	2017.01.12 03:30	2269	3.1 ± 0.3	4.0	1.6	47.7	19.1
TB2	Offshore	75.571	16.078	2017.01.06 13:36	325	5.6 ± 0.0	5.2	1.7	32.5	10.6
NS1	Shelf	80.605	13.673	2017.01.11 09:49	208	3.7 ± 0.1	4.7	1.0	57.6	12.0
NS4	Shelf	80.643	12.927	2017.01.11 19:16	1010	4.1 ± 0.0	–	–	–	–
NS10	Shelf	80.932	17.611	2017.01.14 02:20	343	3.5 ± 0.1	6.1	2.1	40.3	13.8
VMF9	Bellsund	77.690	14.096	2017.01.07 17:16	138	2.0 ± 0.4	–	–	–	–
R3	Rijpfjorden	80.305	22.256	2017.01.14 17:25	280	0.1 ± 0.0	8.6	2.4	33.9	9.5
R3B	Rijpfjorden	80.455	21.870	2017.01.14 22:47	288	0.6 ± 0.0	9.2	2.7	27.5	7.9
R4	Rijpfjorden	80.630	22.069	2017.01.15 00:46	164	0.7 ± 0.0	7.7	1.3	19.1	3.1
KF1	Krossfjorden	79.292	11.631	2017.01.09 22:49	213	4.9 ± 0.1	7.4	1.6	66.1	14.1
KF2	Krossfjorden	79.195	11.760	2017.01.10 08:56	372	4.7 ± 0.1	7.1	2.7	49.7	18.5
KF3	Krossfjorden	79.115	11.596	2017.01.10 16:11	342	3.9 ± 0.3	7.3	2.5	68.0	23.3

Organisms with total length > 5 mm were sorted from the sample, identified and counted. Then aliquots were taken with a 2-mL pipette with the tip cut at 5-mm diameter to allow collection of mesozooplankton. The number of aliquots and subsamples analyzed was chosen so that at least 300 individuals were counted in each sample. The remainder of the sample was screened for rare species. Specimens were identified to the lowest taxonomic level possible and classified as holoplankton or meroplankton.

For copepods, a detailed analysis of copepodid stage composition was performed for *Calanus* spp., *O. similis*, *M. norvegica*, *Pseudocalanus* spp., *M. longa*, and *Microcalanus* spp. The CI to CIII stages were not differentiated for *Microcalanus* spp. at station TB1, and for *O. similis* and *M. norvegica* at all stations. Younger stages (CI to CIII) classified as *Microcalanus* spp. probably included young copepodids of *Paracalanus* spp., *Clausocalanus* spp., and *Ctenocalanus* spp. (particularly at the stations TB1 and TB2 in the western Barents Sea), because it is difficult to distinguish these species via visual identification. The CI to CIII stages of *M. longa* and *M. lucens* were not differentiated, and were designated *M. longa*. The three *Calanus* species were differentiated on the basis of size (Kwasniewski et al. 2003); this involves some uncertainty because prosome lengths of species of the genus can overlap (Gabrielsen et al. 2012; Choquet et al. 2018). Copepod nauplii were determined to order (Calanoida, Cyclopoida, and Harpacticoida). Copepod species were differentiated as either "small copepods" (prosome length < 2 mm, Roura et al. 2018) or "large copepods" (prosome length ≥ 2 mm; Online Resource 1) according to female body size.

Ovigerous females of *Oithona similis*

Prosome length and clutch size of egg-carrying *O. similis* were measured at stations KF2 and R3 to assess reproductive status. The number of egg-carrying females of other species was too low to allow assessment. Copepods were collected using a WP-2 net (90-μm mesh, non-filtering cod-end) towed from 100 m to the surface. Three net hauls were taken and the samples were transferred to a 20-L bucket filled with surface seawater. The samples were screened for egg-carrying *O. similis* females under a stereomicroscope in a cold room (+2 °C). The prosome length of females was measured ($n = 59$), and the number of egg sacs and the total number of eggs per female (i.e., the clutch size) were counted by dissecting the egg sacs with a fine needle. Due to rough sea, only approximately half of the sample was screened and the presence of ovigerous females was therefore only qualitatively assessed.

Data analysis

To compare zooplankton communities between stations, a non-metric cluster analysis was performed with complete linkage and chi-square distances for Bray–Curtis similarities calculated for depth integrated species abundances (ind. m^{-2}). The calculations of the Bray–Curtis dissimilarity index did not consider the demographic structure of a given species (abundance of copepodid stages), but only the total number of the species at the station. No data transformation was carried out because the aim was to focus on the most common species in the community comparison. Correspondence analysis (CA) was carried out to clarify which species drove the variability in community structure. Integrated abundances (ind. m^{-2}) of individual species were calculated for each station. The data set was simplified to the 9 most common copepod species, "other copepods", and other taxonomic groups (i.e., chaetognaths, appendicularians, ctenophores, hydrozoans, pteropods, euphausiids, other crustaceans, and meroplankton). Calanoida, Cyclopoida, and Harpacticoida nauplii were included separately. The cluster analysis and CA used the R version 1.3.959 package vegan version 2.5-6 (Oksanen et al. 2019).

Integrated total Chl *a* (mg Chl *a* m^{-2}) and POC (g C m^{-2}) were calculated for the upper 400 m (or less depending on station depth), assuming the depths at which the samples were collected represented the midpoint of each sampling interval. The total biomass (mg C m^{-2}) of the most common species of copepods was calculated by summing stage-specific biomasses for a species. Stage-specific biomasses were estimated by multiplying the stage-specific integrated abundance (ind. m^{-2}) by the individual stage-specific carbon weights of copepodids (µg C ind^{-1}), as published by Svensen et al. (2019). As most of the nauplii were in the size range of *O. similis* nauplii, the carbon weight of *O. similis* nauplii was applied to all nauplii, irrespective of taxonomic order. This may have led to some inaccuracy in nauplii biomass estimations.

Following recommendations from Greenacre (2016), means were reported with the dispersion interval, i.e., the estimated 0.025 and 0.975 quantiles which encompass 95% of the observations, and the number of observations (*n*) in parenthesis. The only exception was for surface temperature (0–100 m) and the clutch size of *O. similis*, which were given as means ± standard deviation (*SD*).

Results

Hydrography and environmental conditions

Atlantic Water ($T > 3$ °C, $S > 34.65$) dominated the southern stations TB1 and TB2 (Fig. 1b). At TB2, the water column was homogeneous, but a halocline was present at TB1 between 100 and 150 m (Fig. 1b). Waters of Atlantic origin (Transformed Atlantic Water ($1 < T < 3$ °C, $S > 34.65$) and Atlantic Water) prevailed in the upper 400 m at the stations north of Svalbard (NS1, NS4, NS6, and NS10).

Krossfjorden (KF1, KF2, and KF3) and Bellsund (VMF9) were characterized by Intermediate Water and Transformed Atlantic Water (Fig. 1b). Water masses were warmer in Krossfjorden (between 3 and 5 °C) than in Bellsund (2 °C, Fig. 1b; Table 1). Rijpforden (R3, R3b, and R4) was the only location with Arctic Water ($T \leq 1$ °C, $34.3 \leq S \leq 34.8$).

All offshore and fjord stations were ice free, with low concentrations of Chl *a* (≤ 9 µg m^{-3}) and POC (≤ 68 mg m^{-3}, Table 1).

Zooplankton community composition

A total of 75 taxa and taxonomic groups were identified (Barth-Jensen et al. 2022). Copepods dominated the zooplankton community both in terms of abundance and biomass. Within the copepod community, copepod nauplii dominated numerically (30 to 3253 ind. m^{-3} per water layer, Fig. 2a, c), but they contributed little in terms of biomass (3 to 123 µg C m^{-3}, Table 2). Cyclopoid nauplii were abundant while harpacticoid nauplii were rare (Fig. 2b, d). The calanoid nauplii were mostly small, but a few large ones (~ 470 µm) were present. The copepod community was numerically dominated by small copepods (18 to 1724 ind. m^{-3}, Fig. 2a, c), with biomass amounting to 19 to 1089 µg C m^{-3} (Table 2). Eighteen small copepod taxa were present, with *O. similis* (6 to 1155 ind. m^{-3}, mean = 17% of the zooplankton community, dispersion interval = [8, 26]%, $n = 13$) and *Microcalanus* spp. (7 to 370 ind. m^{-3}, mean = 12% of the zooplankton community, dispersion interval = [7, 18]%, $n = 13$, Fig. 3) being the most abundant. In contrast, the 14 large copepod taxa identified were present in relatively low abundances (between 3 and 83 ind. m^{-3}, Fig. 2a, c), which accounted in average for only 3% of the total zooplankton abundance across stations (dispersion interval = [1, 8]%, $n = 13$, Fig. 2b, d). The three most abundant large copepod species were *C. finmarchicus* (3 to 61 ind. m^{-3}), *C. glacialis* (0 to 24 ind. m^{-3}), and *M. longa* (0 to 13 ind. m^{-3}, Fig. 3), and they also dominated in terms of biomass (≥ 1038 µg C m^{-3}, Table 2). However, the use of a 64-µm mesh net may underestimate the abundance of large copepods.

Other zooplankton were rare, with the abundance of non-copepod holoplankton ranging from 2 to 719 ind. m^{-3} and meroplankton from 0.3 to 96 ind. m^{-3} (Fig. 2a, c). The pteropods *Clione limacina* and *Limacina* spp. were common (Fig. 4a), with a particularly high abundance of *Limacina* veliger at TB1 (up to 668 ind. m^{-3}, most likely *Limacina retroversa*) where they contributed 28% to the zooplankton community in terms of abundance (Fig. 2b).

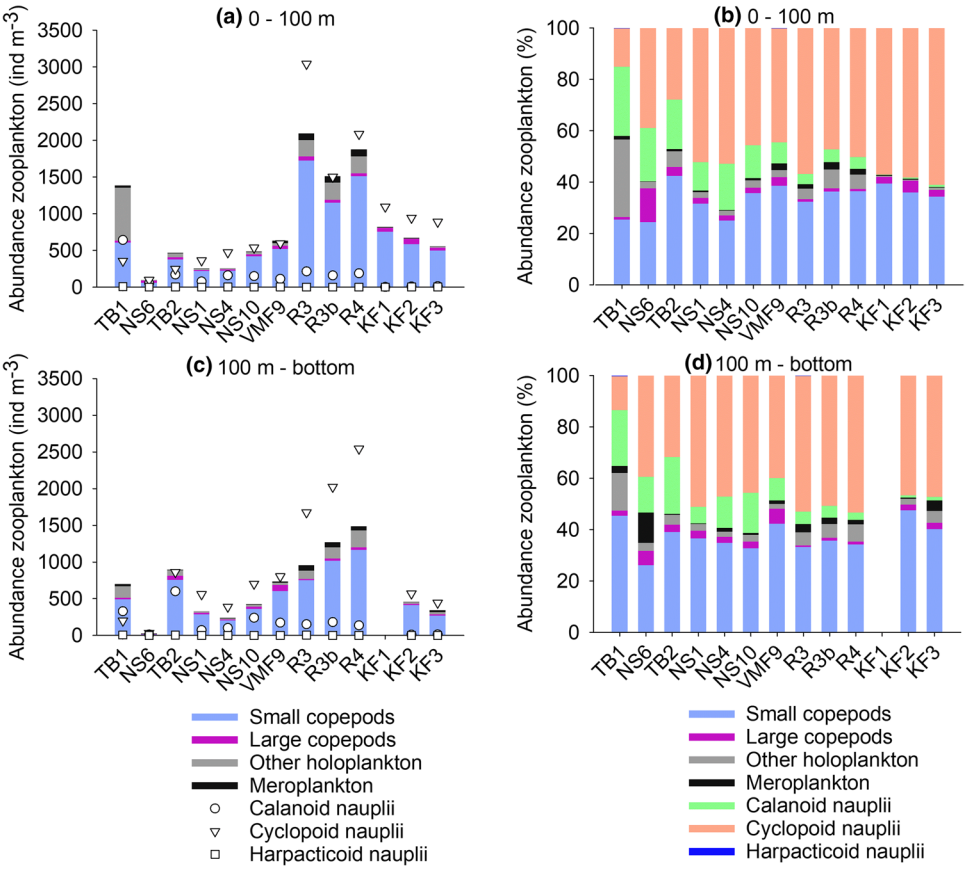

Fig. 2 **a**, **c** Cumulated abundance (ind. m^{-3}) and **b**, **d** relative abundance of the zooplankton community in the study area in January 2017. Depth intervals sampled: 0 to 100 m (**a**, **b**), and 100 m to bottom (max. 400 m) (**c**, **d**). Only upper 100 m sampled at KF1. Copepod nauplii abundance is plotted independently of the large and small copepod groups, and is marked by open triangles

Table 2 Integrated biomass (µg C m^{-3}) of the most abundant copepods in the zooplankton community.

Species	TB1	NS6	TB2	NS1	NS4	NS10	VMF9	R3	R3b	R4	KF1	KF2	KF3
Calanus finmarchicus	362	376	897	253	471	580	356	218	455	252	338	661	404
Calanus glacialis	126	32	828	66	45	344	347	323	504	561	246	990	459
Metridia longa	49	8	77	18	65	81	54	52	37	28	22	71	56
Sum of large copepods	536	415	1802	337	581	1005	757	592	997	842	607	1722	919
Pseudocalanus spp.	25	0	10	2	3	4	38	49	50	31	5	68	43
Microcalanus spp.	42	6	97	14	31	56	29	47	65	55	17	59	38
Microsetella norvegica	8	0	2	0	0	1	1	3	4	2	0	2	1
Oithona similis	42	2	35	9	14	25	9	66	100	68	28	41	32
Sum of small copepods	116	8	144	25	48	85	77	165	219	156	50	171	114
Copepod nauplii	10	1	15	5	10	14	5	19	25	18	6	11	9

The sums of large and small copepods take into account only present species.

For meroplankton, polychaete larvae were common mostly in fjords ($\leq 16 \times 10^3$ ind. m^{-2}), and bivalve veliger were observed at all stations ($\leq 7 \times 10^3$ ind. m^{-2}, Fig. 4b).

Stations that had similar temperature and salinity (T–S) profiles (Fig. 1b) had highest similarity in zooplankton community composition (Fig. 5a). Two main cluster groups were identified, based on mesozooplankton species abundance, one consisting of fjord stations, and the other of offshore stations. Two stations, TB1 and NS6 were not part of either of the groups (Fig. 5). TB1 differed from all other stations primarily due to an unusually high abundance of *Limacina* veliger and the highest abundance of the warmer water copepods *Paracalanus* spp., *Clausocalanus* spp., and *Ctenocalanus* spp. (Fig. 5b; Barth-Jensen et al. 2022). Moreover, TB1 was the only station where the abundance of calanoid nauplii was higher than that of cyclopoid nauplii, representing 63% of the total nauplii abundance (Fig. 3). NS6 was characterized by a low total zooplankton abundance (Fig. 2a,

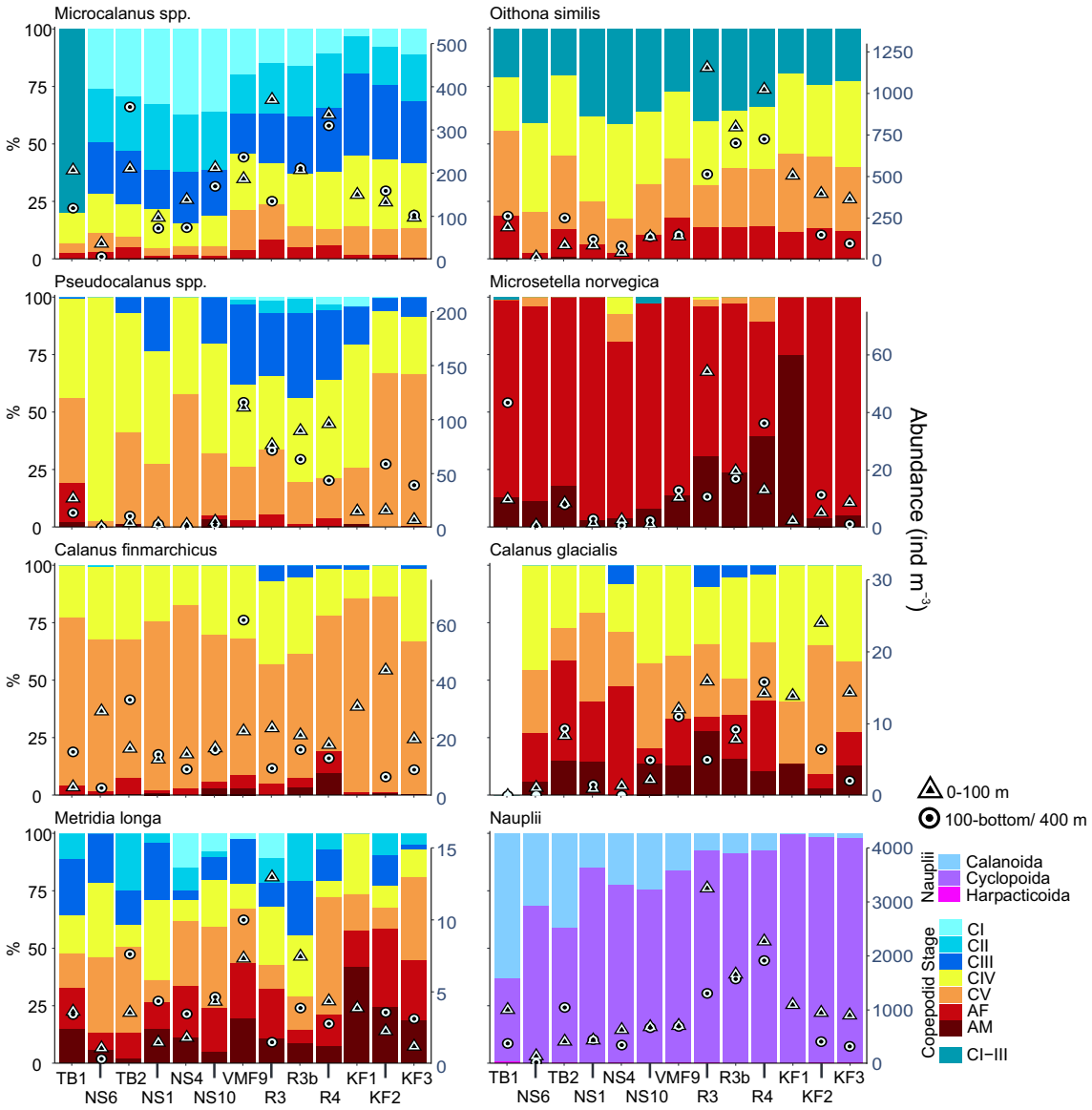

Fig. 3 Stage-specific composition (color bars, relative abundance, left axis) and total abundance of copepodids CI to adults (ind. m^{-3}, right axis) above 100 m (dotted line) or below 100 m (black line) of seven abundant copepod taxa and copepod nauplii (Calanoida, Cyclopoida, Harpacticoida) in the study area in January 2017. Note different scales on the right y-axis

c), but zooplankton composition was similar to that of the other offshore stations (Fig. 5b).

The zooplankton communities at offshore stations were characterized by high proportions of calanoid nauplii (mean = 33% of the total nauplii community, dispersion interval = [16, 60]%, $n = 7$, Fig. 3), Oncaeidae (mostly *Triconia borealis*), and *Microcalanus* spp. (Fig. 5b), but abundances were usually lower than in fjords (Fig. 3). Community compositions at the shelf stations north of Svalbard (NS1, NS4, NS10) were more similar to each other than to the community at TB2, which had higher abundances of large copepods (*C. finmarchicus*, *C. glacialis*, *M. longa*) and *Microcalanus* spp. (Fig. 3).

In contrast to the offshore stations, zooplankton communities in the fjords were characterized by relatively high abundances of *O. similis*, *Pseudocalanus* spp. and cyclopoid nauplii (mean = 94% of the total nauplii population, dispersion interval = [85, 100]%, $n = 7$, Figs. 3 and 5b). Within the fjord cluster, stations from the same fjord showed high similarity in zooplankton community composition. Krossfjorden had the highest proportions of cyclopoid nauplii recorded in the study (Figs. 3 and 5b). Rijpfjorden was characterized by high abundances of *O. similis*, *M. norvegica*, *Pseudocalanus* spp., and nauplii (Fig. 3). The zooplankton community in Bellsund was generally similar to that of the other fjord stations (Fig. 5a), with a generally high abundance of small

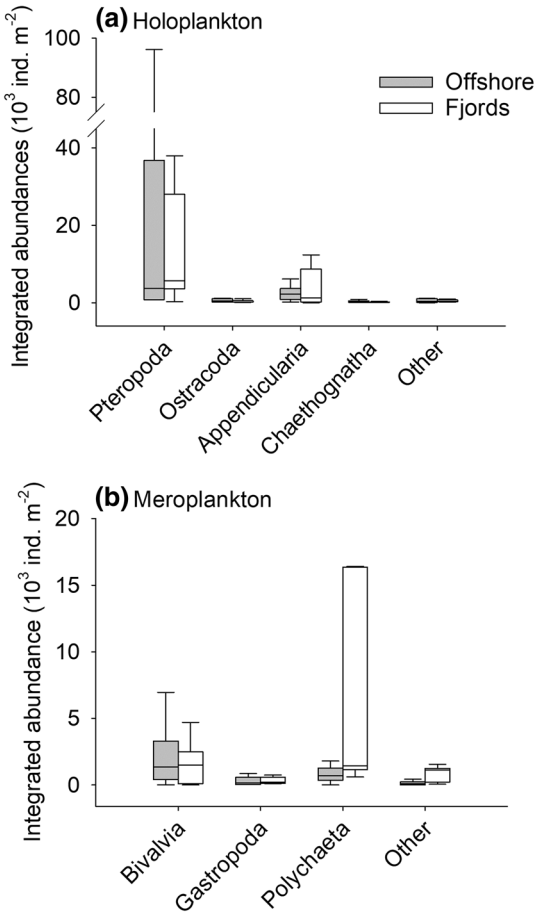

Fig. 4 Boxplot of the integrated abundance (ind. m^{-2}) of **a** non-copepod holoplankton taxa and **b** meroplankton at offshore stations in the Barens Sea and near Svalbard (n = 6) and in Svalbard fjords (n = 7) in January 2017. The top and bottom boundaries of the box indicate the 25th and 75th percentile, and the black line within the box shows the median. Whiskers indicate the 10th and 90th percentiles

copepods, but the proportion of calanoid nauplii was comparable to that of offshore stations (Fig. 3).

Population structure of the most abundant small and large copepod species

Small copepods were usually more abundant in the upper 100 m than deeper, irrespective of the sampling station (Fig. 3), with no specific differences in the depth distribution of each species between stations. *Microcalanus* spp. populations were dominated by young copepodids (CI to CIII), although in higher proportions offshore (mean = 78%, dispersion interval = [72, 84]%, $n = 6$) than at fjord stations (mean = 58%, dispersion interval = [54, 63]%, $n = 7$, Fig. 3). Males were scarce, resulting in a high female:male ratio (maximum of 236).

Oithona similis populations were characterized by the presence of all developmental stages, with younger copepodids CI to CIII making up more than a quarter of a population (Fig. 3). Female abundance varied widely between stations (0.2 to 158 ind. m^{-3}) and males were rare (0 to 6 ind. m^{-3}), resulting in a high female:male ratio (mean = 41, dispersion interval = [10, 94], $n = 7$). The mean prosome length of *O. similis* females was 444 µm (dispersion interval = [364, 563]µm, $n = 59$). Ovigerous females were present in very low numbers, and had an average clutch size of 5 eggs ($SD = 2$ eggs, $n = 12$). Only four females carried 2 egg sacs. One female carried an egg sac that showed signs of recent hatching: a torn sac with eggs at an advanced stage of development (nauplii nearly formed).

For *Pseudocalanus*, copepodids CIV and CV were the most common developmental stages (Fig. 3), and young copepodids CI and CII were only found in the fjords (Fig. 3). Males were rare and only a few *Pseudocalanus* spp. females with egg sacs were observed by chance in the live samples. The mean female:male ratio was 1.8 (dispersion interval = [0.0, 7.4], $n = 7$).

Populations of *M. norvegica* were almost entirely adults, with only a few copepodids CI-CV being recorded (Fig. 3). The female:male ratio was in average 10.6 (dispersion interval = [0.6, 30.1], $n = 13$), with a higher contribution of females at offshore stations (mean = 86%, dispersion interval = [77, 96]%, $n = 6$) than in the fjords (mean = 70%, dispersion interval = [29, 96]%, $n = 7$, Fig. 3). Abundances of *M. norvegica* males were sometimes high locally (maximum 5.7 ind. m^{-3} at station TB1), and they contributed in average 27% to populations in the fjords (dispersion interval = [4, 70]%, $n = 7$).

The depth distribution of *C. finmarchicus* differed between southern and northern locations. *C. finmarchicus* was mostly located below 100 m at southern Barents Sea stations (TB1, TB2) and in Bellsund (VMF9), while in Krossfjorden, Rijpfjorden and at the shelf stations north of Svalbard, *C. finmarchicus* was most abundant in the upper 100 m (Fig. 3). There was no such pattern in the depth distributions of *C. glacialis* and *M. longa* (Fig. 3). Older copepodids CIV and CV were the most commonly encountered stage of both *C. finmarchicus* and *C. glacialis*. For *C. glacialis*, adult females (mean = 20%, dispersion interval = [2, 46]%, $n = 12$) and males (mean = 12%, dispersion interval = [1, 25]%, $n = 12$) were also common (Fig. 3). The female:male ratio was relatively balanced for *C. glacialis* (mean = 1.6, dispersion interval = [0.1, 3.4], $n = 11$), but higher female abundance in *C. finmarchicus* gave a mean ratio of 2.9 (dispersion interval = [0.2, 12.7], $n = 8$). Younger *Calanus* spp. copepodids CIII were observed in low numbers, mostly in the fjords, and CI and CII were usually absent (Fig. 3). For *M. longa*, older copepodids CIV and CV and adults dominated the populations, but younger copepodids CI–CIII were also present (mean = 25%, dispersion interval = [2%, 43%], $n = 13$; Fig. 3). Adult male and female *M. longa* had similar

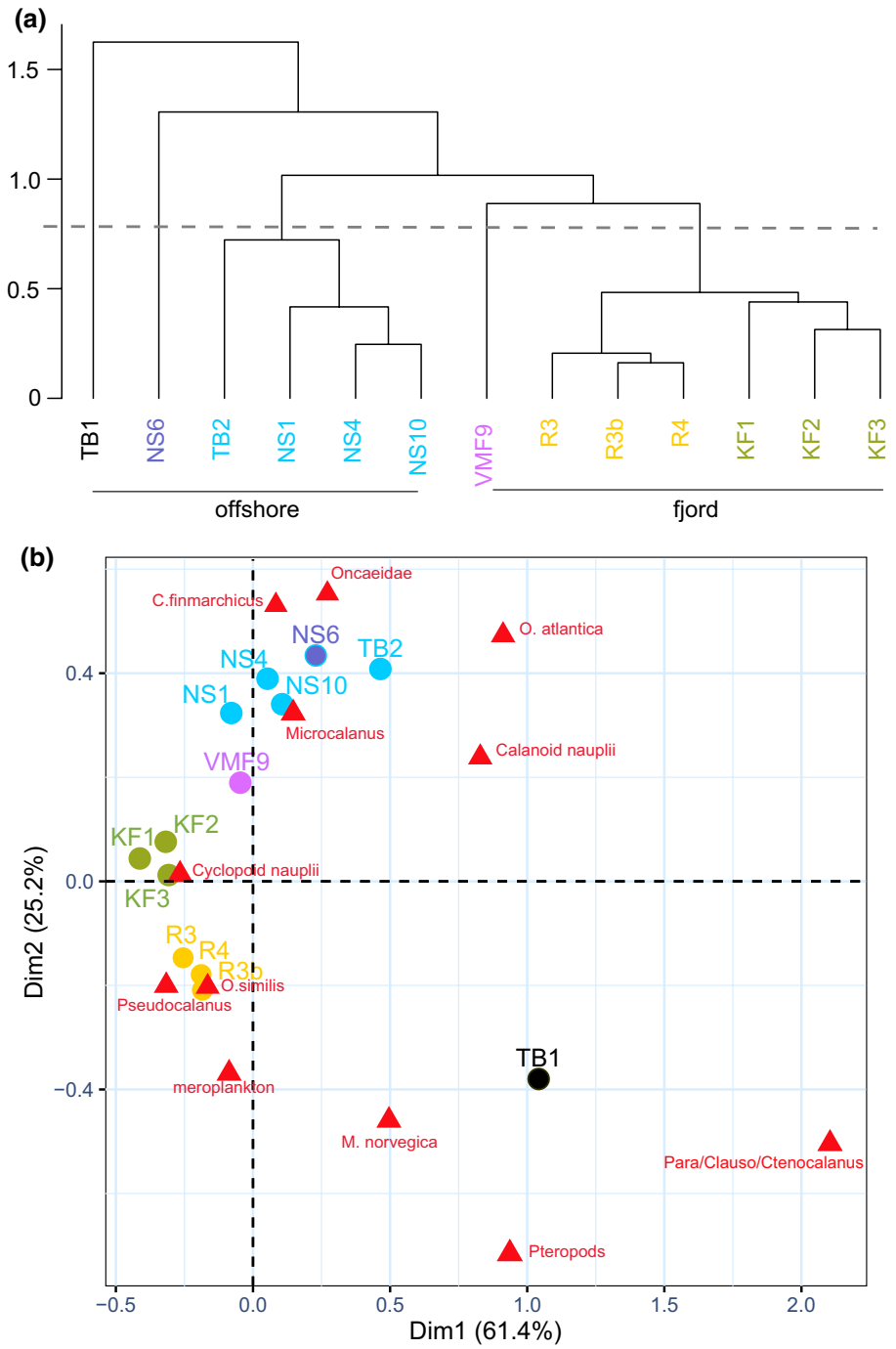

Fig. 5 **a** Cluster dendrogram (based on chi-square distances) and **b** Biplot of correspondence analysis based on the integrated abundance (ind. m^{-2}) of all species at each of the 13 stations in and near Svalbard sampled in January (circles in **b**). Only the 12 taxonomic groups (red triangles) that contributed most to the variance are shown in **b**. The color coding refers to the clustering of stations

abundances, resulting in a female:male ratio of 1.8 (dispersion interval = [0.5, 5.0], $n = 8$).

Discussion

Small taxa (i.e., small copepods, copepod nauplii, and meroplankton) constitute a large part of the mesozooplankton present in the Barents Sea and Svalbard fjords during the polar night of the Arctic winter, as is also the case during other seasons (Basedow et al. 2018; Svensen et al. 2019). Based on copepodid stage composition, we identified three main population structures among the seven dominant copepod species present: (1) populations dominated by near mature stages, specifically copepodid stages CIV and CV (*Calanus* spp.), (2) populations dominated by adults (*M. norvegica*), and (3) populations with all copepodid stages present (*M. longa*, *Pseudocalanus* spp., *Microcalanus* spp., and *O. similis*). In the latter case, the relative contributions of the different stages varied from a high proportion of adults (*M. longa*)

to a dominance of young copepodids (CI–III) (*Microcalanus* spp.). The three population structures indicate that different overwintering strategies are adopted by the copepod species.

Three strategies adopted by copepods during winter

Strategy 1: overwintering as late copepodid stages

Calanus finmarchicus and *C. glacialis* are typically dormant at depth during winter, with CIV and CV as the main diapause stages (Niehoff 2000; Falk-Petersen et al. 2009). *Calanus glacialis* initiates molting to adults in winter and mating has been observed during the polar night (Daase et al. 2018), whereas these occur later in *C. finmarchicus*. The female:male ratios observed in our study in these two *Calanus* species confirm these differences.

Calanus spp. are known to remain at depth during winter and then ascend to surface water prior to the spring bloom (Hirche and Kosobokova 2011), but *Calanus* spp. may be present in surface waters in January (Pedersen et al. 1995; Daase et al. 2014, 2018; Basedow et al. 2018; Berge et al. 2020). We observed a similar situation at our northern stations (both shelf stations and fjords), where the majority of the *Calanus* spp. populations resided in surface waters, but not for the southern offshore stations and at Bellsund.

Individual copepods may not initiate diapause if their lipid reserves are insufficient for them to survive the winter (Pedersen et al. 1995; Maps et al. 2011; Hobbs et al. 2020). Concentrations of Chl *a* and POC registered at the stations south or north of Bellsund gave no clear indications that there were differences in food availability. However, estimates of annual primary production are higher for the southern stations than further north (Reigstad et al. 2011). It is therefore possible that pre-winter feeding by copepods at the southern stations was higher than those further north, allowing more of them to enter diapause. Hobbs et al. (2020) suggested that availability of winter prey (i.e., microzooplankton) allows *Calanus* spp. to be flexible in their overwintering strategies. *Calanus* spp. are not strictly herbivorous, also feeding on microzooplankton, copepod eggs, and nauplii (Ohman and Runge 1994; Bonnet et al. 2004; Basedow and Tande 2006). The copepod nauplii biomass observed in our study may represent a valuable food source for *Calanus* spp. during winter, enabling them to fulfill metabolic demands.

Calanus spp. initiate molting at the end of the winter after hibernation (Falk-Pedersen et al. 2009). It is unclear why the non-hibernating copepods do not initiate their molting earlier. One reason could be that although visual predation might be reduced during the polar night, light intensities near the surface may still allow visual predation by some species, such as fish (Cohen et al. 2015; Langbehn and Varpe 2017). Adult *Calanus* spp. are common prey for visual predators because of their large size (Dahl et al. 2003; Falk-Petersen et al. 2009). *Calanus* spp. CIV–CV are smaller than adults but are large enough to store lipid reserves so overwintering as CIV–CV might increase chances of survival.

Strategy 2: overwintering as an adult

Microsetella norvegica, a pelagic harpacticoid copepod, was a member of the zooplankton communities ubiquitously recorded in our study. A dearth of young copepodids and dominance of adults in the *M. norvegica* populations suggests that recruitment of copepodids probably does not occur during winter. Previous studies in the Arctic and sub-Arctic have failed to register young copepodids during winter (Arendt et al. 2013; Svensen et al. 2018).

Observational evidence (Uye et al. 2002; Arendt et al. 2013; Svensen et al. 2018) indicates that female *M. norvegica* carry eggs shortly after the start of the spring bloom and last until late summer. Females may not lay eggs during winter, as no egg clutches have been observed during the winter from temperate to polar environments (Uye et al. 2002; Arendt et al. 2013), and egg hatching rates and egg hatching success are low at low temperatures (Barth-Jensen et al. 2020). Spending the winter as an adult would allow any energy surplus to be used for initiating reproduction in spring. In the case of large species like *C. glacialis*, females can use energy reserves to generate viable eggs, i.e., capital breeding (Daase et al. 2013; Sainmont et al. 2014). The small body volume of *M. norvegica* is not suited for accumulation of large lipid stores. *Microsetella norvegica* associates with particulate matter aggregates throughout the year (Koski et al. 2005), and could feed during winter to meet energy demands. However, decreases in female body carbon and nitrogen from November to their minimum in March (Svensen et al. 2018) indicate a lack of energy accumulation during winter, so it is unlikely that endogenous energy reserves could be used to fuel egg production in early spring. Therefore, *M. norvegica* is likely dependent on the spring bloom to fuel its reproduction.

Strategy 3: mix of age classes during winter

Four species were represented by all copepodid stages in January, but there were differences between the species as to which stages dominated: *Microcalanus* spp. populations consisted mainly of young copepodids (CI–CIII), *O. similis*, and *Pseudocalanus* spp. were mostly present as CIV and CV, and *M. longa* as adults. A high abundance of young copepodids CI–CIII in *Microcalanus* spp. during winter has been previously observed in Kongsfjorden, Svalbard (Lischka and Hagen 2016), and in the Antarctic (Schnack-Schiel and Mizdalski 1994). In comparison to the > 50% of CI–CIII found during the polar night, CI–CIII

represented only up to 50% in the spring and up to 40% in the summer (Lischka and Hagen 2016). As CI was the most common stage, *Microcalanus* spp. populations recruit copepodids during the winter, and it is likely that they are reproducing (Lischka and Hagen 2016). Given the high proportions of young copepodids, winter may be an important season for recruitment of *Microcalanus* spp.

Late spring and early autumn have been identified as the main reproductive periods of *O. similis* and *Pseudocalanus* spp. (Lischka and Hagen 2005, 2016; Dvoretsky and Dvoretsky 2009a), while for *M. longa* the main spawning period is late summer and autumn (Ussing 1938). Similar to Lischka and Hagen (2005, 2016), we observed only a few CI of *O. similis*, *Pseudocalanus* spp., and *M. longa* during winter while CII and CIII were more abundant. This indicates that recruitment of CI is probably low during winter, and that winter is mainly used for growth and development of the young copepodids (Ussing 1938; Lischka and Hagen 2005).

At low temperatures, development from eggs to CI may take months in polar waters: *O. similis* egg development to the time of hatch can take weeks (Barth-Jensen et al. 2020) and the growth of nauplii is isochronal (Sabatini and Kiørboe 1994). Based on equations developed by Eiane and Ohman (2004), we estimate 114 days are needed for development of *O. similis* from egg to CI at 2 °C. Thus, eggs laid in September would likely have reached the CI stage by January and we suggest that the CI–CIII found in January likely come from eggs produced during the previous autumn. Based on the high abundance of CI–CIII in our study, we suggest that egg fitness, defined as the likelihood of an egg producing an individual that contributes to future generations (Varpe et al. 2007) is quite high for eggs produced during the autumn. This suggestion is supported by the abundances of the different stages of *O. similis* in Kongsfjord, Svalbard, as reported by Lischka and Hagen (2005): the early autumn generation was characterized by low nauplii abundance (data not shown) but high abundance of CI–CIII in November (140,000 ind. m^{-2}) and February (16 500 ind. m^{-2}), while the early summer generation was characterized by a high nauplii concentration (31,000 ind. m^{-2}) which developed into a relative low concentration of CI–CIII (24,000 ind. m^{-2}) in July.

Overwintering in the upper water column as copepodids in *Microcalanus* spp., *O. similis*, *Pseudocalanus* spp., and *M. longa* may be a survival strategy to reduce predation pressure. Predators, such as large copepods (Sell et al. 2001; Bonnet et al. 2004), chaetognaths or fish larvae (Falkenhaug 1991; Swalethorp et al. 2014; Mitsuzawa et al. 2017; Grønkjær et al. 2018) that prey on nauplii and small copepodids may be present in surface waters during winter, but at lower abundances than in other seasons (Daase et al. 2013; Grigor et al. 2014, 2017). Therefore, the impact of the predators' feeding activity is likely reduced, leading to lower copepod mortality.

Copepod nauplii and winter production of copepods

Low temperatures and low food availability in winter impact copepods production by lowering their reproductive output, as the clutch size increase with temperature and prey availability (e.g., Dvoretsky and Dvoretsky 2009b; Head et al. 2013; Barth-Jensen et al. 2020). Therefore, the copepods' winter production can be assumed to be low. Nevertheless, the abundances of calanoid and cyclopoid nauplii during winter cannot be neglected (e.g., Digby 1954; Lischka and Hagen 2005; Grenvald et al. 2016; this study), although spring and summer abundances can be thirty times higher (Lischka and Hagen 2016). We did not classify nauplii according to stage, but they were probably a mix of young (i.e., newly hatched from eggs) and later stages resulting from an earlier egg production event. Therefore, the nauplii were probably of those species whose populations also had young copepodids CI–CIII and ovigerous females. According to the different population structures observed here, the species that likely contributed most to the nauplii population are those with a mix of age classes in their populations (i.e., strategy 3). The low abundances of harpacticoid nauplii corroborate that *M. norvegica* likeky do not reproduce during winter. For *Calanus* spp., females can lay eggs prior to the spring bloom (Sainmont et al. 2014), but the low abundance of females makes them unlikely as major contributors to the observed calanoid nauplii pool.

Winter production of *O. similis* and *Pseudocalanus* spp. in the Arctic has been documented (Digby 1954; Lischka and Hagen 2005) and our finding of egg-carrying females of *O. similis* and *Pseudocalanus* spp. in January corroborates this. Winter reproduction in the Arctic is at its minimum, with ≤ 10% of the *O. similis* females bearing eggs, compared to summer and autumn where up to 50% of the females can be ovigerous (Dvoretsky and Dvoretsky 2009a, 2009b; Apollonio 2013). This is probably due to food shortage limiting the reproduction of income breeders such as *O. similis* and *Pseudocalanus* spp. during winter (Varpe et al. 2009). Although a low winter egg production by *O. similis* and *Pseudocalanus* spp. would supply a few newly hatched nauplii to the nauplii pool, it can not explain the high abundance of nauplii observed in our study.

Lischka and Hagen (2005) observed high concentrations of copepod eggs (33,200 m^{-2}) within the size range of *O. similis* eggs, in Kongsfjorden in November. If we assume that 114 days are needed to development from egg to CI at 2 °C (extrapolated from Eiane and Ohman 2004), most nauplii observed in January could have originated from eggs produced in late autumn. Nauplii of *O. similis* are 111 to 279 µm long (Takahashi and Uchiyama 2007), which

matches the most common size of nauplii in our study, so older naupliar stages of *O. similis* may have been the most important contributors to the cyclopoid nauplii pool. The observation that late naupliar stages were most abundant in Greenland fjords in February (Zamora-Terol et al. 2013) supports our interpretation. However, it is unlikely that all cyclopoid nauplii were *O. similis*. *Triconia borealis* was quite common and we observed mating in this species. *Triconia borealis* seems to reproduce year-round, and large proportions of young copepodids are sometimes observed during winter (Nishibe and Ikeda 2007; Lischka and Hagen 2016). The cyclopoid nauplii we collected may have included *T. borealis* nauplii. *Pseudocalanus* spp. nauplii are between 176 and 440 µm (Ogilvie 1953). Large nauplii were rare in our samples, so *Pseudocalanus* spp. probably contributed little to the calanoid nauplii community.

Metridia longa are not mature during winter (Tande and Grønvik 1983), but *Microcalanus* spp. are ripe during winter (Norrbin 1991; Kosobokova and Hirche 2016), and *Microcalanus* nauplii measure 80 to 210 µm (Ogilvie 1953). Using (1938) visually recorded *Microcalanus* spp. nauplii in February in East Greenlandic fjords. The high abundances of small calanoid nauplii, particularly at offshore stations where *Microcalanus* spp. were abundant, suggest that *Microcalanus* spp. may have been a major contributor to the calanoid nauplii pool at some of our sampling stations. Other copepod species may have contributed to the nauplii pool, and future studies should include molecular identification of the nauplii to identify their species (Fujioka et al. 2015). Nauplii could have hatched from dormant eggs, the development of which was slow under winter conditions (Mauchline 1998), but it is unlikely that the hatching of resting eggs would have been triggered during winter.

Meroplankton

Presence of meroplankton in our samples open the possibility of some reproductive activity in benthic species during winter. Meroplankton from various taxa have been reported to be present in Arctic and sub-Arctic fjords during the polar night, although at lower abundances than in spring or summer (Hannerz 1956; Blake 1969; Kuklinski et al. 2013; Stübner et al. 2016; Michelsen et al. 2017; Weydmann-Zwolicka et al. 2021). We recorded eight times more polychaete larvae and a similar or higher abundance of bivalve veliger in Rijpfjorden and on the shelf north of Svalbard than previously reported in other Svalbard fjords during the polar night (Kuklinski et al. 2013; Weydmann-Zwolicka et al. 2021), making these taxa the dominant component of the meroplankton community in Rijpfjorden. In contrast, meroplankton was dominated by bryozoans, gastropods, and eggs and embryos of a range of other taxa in Isfjorden and Adventfjorden, Svalbard, although bivalve veliger and polychaete larvae were also present (Stübner et al. 2016; Weydmann-Zwolicka et al. 2021). The benthic communities were mainly composed of bivalves and polychaetes during the polar night in Rijpfjorden and Adventjorden, but the most abundant species within these taxa varied (Pawłowska et al. 2011; Morata et al. 2015). The different benthic communities in each fjord likely explain the difference in the meroplankton species composition. The diversity of meroplanktonic communities during winter indicates that winter reproduction may occur in various species among a wide range of benthic taxa. Some species have larvae with substantial energy reserves, i.e., lecithotrophic larvae, which may have been produced before winter, but planktotrophic larvae are also found during winter (Michelsen et al. 2017; Weydmann-Zwolicka et al. 2021). Reproduction during winter may be a strategy to ensure survival of early life stages in a period when both predation pressure and inter-specific competition with other larvae are low, even though food availability may be low and the risk of death by starvation may be quite high.

Conclusion

We studied the zooplankton communities of the western Barents Sea and fjords around Svalbard in January during the Arctic polar night and focused on the age structure of the seven most abundant small and large copepod species. Communities were dominated by copepod nauplii and small copepods, and depicted active communities driven by reproductive activity and winter development of copepods and meroplankton. Three overwintering strategies were observed. *Calanus* spp. spends winter as immature late-stage copepodids. *Microsetella norvegica* overwinters as adults, which could be advantageous as a preparation for egg production in spring. *Microcalanus* spp. were mainly CI–CIII, suggesting recruitment, and *Microcalanus* is probably a contributor to the naupliar pool present during winter. *Pseudocalanus* spp. and *O. similis* reproduce during winter, although egg production rates appear to be low. For these two species, winter is likely mainly used for growth and development. *Metridia longa* probably adopts a similar strategy. Taking the above into account, we propose that the winter nauplii assemblage mostly consists of older stages of *O. similis*, *Pseudocalanus* spp., and possibly *M. longa*, and younger and older naupliar stages of *Microcalanus* spp. and possibly *T. borealis*.

The presence of meroplankton during winter suggests that some benthic species (mainly polychaetes and bivalves) may be reproducing during this time. Although winter is a season of decreased activity for many zooplankton species, some may rely on the reduced predation pressure or the food produced during previous season to boost recruitment leading to high abundances of larval and young stages in winter:

nauplii, young copepodids and planktonic larvae. Our study highlights winter as being more than a resting period for small copepods, and contributes to strengthen the perception of a non-dormant Arctic winter.

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Author contributions CBJ and CS conceived and designed the study. CBJ and MD conducted the field sampling. CBJ, MO, and SK did the lab analyses. CBJ and MD made the figures. CBJ wrote the manuscript. All authors commented, reviewed, and approved the manuscript.

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Data availability Abundance data for all species are available in an online repository https://www.gbif.org/dataset/76ef1883-c32a-49bb-a36c-2752af1b4e95. In this manuscript, it is referred as "Barth-Jensen et al. 2022".

Declarations

Conflict of interest The authors declare that they have no conflict of interest.

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Paper III

Coralie Barth-Jensen, Camilla Svensen, Øystein Varpe, Estelle Coguiec, Peter Glad, Théo Beroujon, Svein Kristiansen, Marja Koski.

High contribution of small copepods to zooplankton secondary production in Norwegian high-latitude coastal fjord ecosystems.

Manuscript

High contribution of small copepods to zooplankton secondary production in Norwegian high-latitude coastal fjord ecosystems

Coralie Barth-Jensen, Camilla Svensen, Øystein Varpe, Estelle Coguiec, Peter Glad, Théo Beroujon, Svein Kristiansen, Marja Koski.

Key words: population ecology; sub-Arctic; age structure; population dynamics; *Calanus finmarchicus*; *Metridia longa*; *Oithona similis*; *Microsetella norvegica; Microcalanus pusillus*

Abstract

Copepod species of < 2 mm in body length can be a large part of the zooplankton biomass and although these small copepods may be important contributors to secondary production, they are seldom the target of production studies. Here, we investigate the seasonal biomass and production of three small copepod species, the cyclopoid *Oithona similis*, the pelagic harpacticoid *Microsetella norvegica* and the calanoid *Microcalanus pusillus*, in three north-Norwegian fjords (Balsfjord 69.4°N, Altafjord 70.1°N and Porsangerfjord 70.1-70.9°N). Small copepods were sampled in the upper 100 m with Go-Flo bottles or 64 µm-mesh net over the two-year period 2015-2017. We used two independent methods to estimate secondary production: the specific egg-production rate and a temperature-dependent model. *M. norvegica* had the highest biomass year-round (up to 25 mg C m^{-3}), which was comparable to the biomass of the five-times larger copepod *Calanus finmarchicus*. Large production estimate differences were found for the small copepods, with ≤ 0.1 mg C m^{-3} d^{-1} using the specific egg-production rate or ≤ 2.0 mg C m^{-3} d^{-1} using the temperature-dependent model, to which *M. pusillus* and *M. norvegica* contributed the largest part, respectively. The copepods increased their reproductive output at the onset of the spring bloom, suggesting population dynamics that rapidly utilize pulsed food. Presence in the upper water column and fast response to fluctuations in food supply might be key components to the success of small copepods in high-latitude ecosystems.

Introduction

Arctic and sub-Arctic fjords are often highly productive, both in terms of primary (Archer et al. 2000, Juul-Pedersen et al. 2015) and secondary production (Madsen et al. 2001). At high latitudes, most of the secondary production occurs during the spring bloom, with copepods,

krill, and amphipods as major contributors (McBride et al. 2014). Spring production by large copepod species, such as *Calanus* spp., is high (Koski 2007), with these species having a phenology and reproductive strategy tightly linked to the spring phytoplankton bloom (Madsen et al. 2001, Søreide et al. 2010, Varpe 2012). For example, *Calanus finmarchicus* is mainly herbivorous, reproduces during spring and summer and enters diapause during winter (Conover 1988, Varpe 2012). Smaller copepod species of < 2 mm in body length tend to be omnivorous (Wickstead 1962, Turner 2004), can reproduce for longer periods, and contribute significantly to annual secondary production (Madsen et al. 2008, Basedow et al. 2014, Svensen et al. 2019). These species include the pelagic harpacticoid *Microsetella norvegica* that reproduces during spring and summer (Svensen et al. 2018, Barth-Jensen et al. 2020), the cyclopoid *Oithona similis* that reproduces year-round, and the calanoid *Microcalanus* spp. that also reproduces year-round, but with a peak production in late fall or winter (Norrbin 1991, Lischka & Hagen 2016, Barth-Jensen et al. 2022). In addition to these species, numerically dominant copepods in sub-Arctic fjords include *Metridia longa* (Grønvik & Hopkins 1984). *M. longa* is comparable to *Calanus* spp. in size, but is omnivorous and does not hibernate but stays active and reproduces year-round (Falk-Petersen et al. 1987).

Climate change is expected to lead to increased presence and proportion of boreal species, favoring cosmopolitan and Atlantic species like *C. finmarchicus* in high-latitude ecosystems (Weydmann et al. 2014, Feng et al. 2018, Møller & Nielsen 2019). Boreal species can produce more than one generation per year at higher temperatures, leading to higher reproductive output (Weydmann et al. 2015, Renaud et al. 2018, Middelbo et al. 2019). The frequency of autumnal blooms is projected to increase (Ardyna et al. 2014), which could also be advantageous for small copepods such as *O. similis* that remain reproductively active through autumn (Lischka & Hagen 2005). In contrast, true Arctic species such as *Calanus glacialis* and *Pseudocalanus minutus* may suffer temperature inhibition or be unable to adjust their seasonal timing, and become less competitive than the boreal species (Søreide et al. 2010, Pasternak et al. 2013, Ershova et al. 2016). There seems to be some evidence of this from observations of a gradual change within the copepod community in different regions of the Arctic, like in Disko Bay, Greenland, and in the Barents Sea (Weydmann et al. 2014, Møller & Nielsen 2019, Freer et al. 2022).

An increased proportion of small copepod species could have consequences for the ecosystem, including possible changes in carbon sequestration, recycling of nutrients, ecosystem productivity and trophic dynamics (Steinberg et al. 1994, Shoemaker et al. 2019,

Mayor et al. 2020, du Pontavice et al. 2021). Although the population dynamics of *O. similis* have been documented (e.g., Lischka & Hagen 2005, Dvoretsky & Dvoretsky 2009), those of *M. norvegica* and *Microcalanus* spp. are still poorly known, even though they are highly abundant in many Arctic ecosystems (but see Arendt et al. 2013, Lischka & Hagen 2016, Svensen et al. 2018). The few estimates available indicate that these species can account for a high proportion of the secondary production in temperate and Arctic ecosystems (Uye et al. 2002, Madsen et al. 2008, Basedow et al. 2014). *M. norvegica* is particularly interesting, because this copepod may have a large impact on carbon export and sequestration through its feeding on marine snow (Koski et al. 2007, Koski et al. 2021). We investigated the seasonal dynamics, timing of reproduction and secondary production of the three small copepod species *M. norvegica*, *O. similis* and *Microcalanus* spp. in three north-Norwegian fjords, and compared them to the larger copepod species *C. finmarchicus* and *M. longa*. We hypothesized that the small copepod species contribute significantly to the biomass and annual secondary production in these fjords, particularly in the seasons when the large copepods are less active (i.e., the autumn and winter), and that the variation in biomasses of the small copepod species are related to the seasonal changes in temperature and phytoplankton biomass.

Material and Methods

Study areas

Field sampling was conducted in three high-latitude Norwegian fjords: Balsfjord (69°N), Altafjord (70°N) and Porsangerfjord (70°N, Fig. 1). An approximate monthly sampling was carried out in Balsfjord between August 2015 and August 2016 (Table 1), and was continued in Balsfjord, Altafjord and Porsangerfjord five times between December 2016 and October 2017. The full annual cycle was covered in all fjords (Table 1).

The three fjords have Arctic characteristics in terms of light and temperature and display strong seasonal patterns in irradiance and primary production. Balsfjord and Porsangerfjord are highly productive fjords, support fisheries and are spawning and nursery areas for commercially important species (Hopkins et al. 1989, Eilertsen & Frantzen 2007, Larsen 2010). The ecosystem of Altafjord is less studied, but it supports a mussel fishery (Frantzen 2007). Balsfjord and the inner basin of Porsangerfjord have shallow sills, which restrict the exchange of deep water from the Norwegian Coastal Current, whereas Altafjord and the outer

and central basin of Porsangerfjord are subjected to more frequent water mixing due to deeper sills (Svendsen 1995, Mankettikkara 2013).

The sampling station in Balsfjord (Svartnes) is located inside the sills in the deepest part of the fjord (180 m depth), with monthly average temperatures ranging from 1.3 to 8.6 °C (Eilertsen & Skarðhamar 2006). Three stations were sampled in Porsangerfjord: Porsangerfjord Inner (105 m depth) situated at the innermost part of the fjord, Porsangerfjord Central (195 m depth) in the middle basin and Porsangerfjord Outer (220 m depth) in the outer basin. The inner station is characterized by Arctic water masses with temperature down to −1.7 °C (Wassmann et al. 1996), whereas the two other stations are subjected to frequent water exchanges with temperatures ≥ 2°C (Eilertsen & Skarðhamar 2006, Mankettikkara 2013). The sampling station in Altafjord (411 m depth) is in an area with frequent water exchanges from the Norwegian Coastal Current (Mankettikkara 2013). Monthly mean temperature in Altafjord varies between 2.2°C and 10.5°C (Eilertsen & Skarðhamar 2006).

Sampling and hydrography

During each cruise, a hydrographical profile of the water column (temperature, salinity, density, and fluorescence) was taken using a conductivity, temperature, and depth profiler (CTD, SeaBird Electronics). We complemented the hydrographical dataset from our cruises with hydrographical profiles collected between 2015 and 2017 at the same stations as part of the monitoring program Havmiljødata (https://dataverse.no/dataverse/nmdc). Temperature and fluorescence were averaged over the upper 100 m.

Samples for Chlorophyll *a* (Chl *a*), particulate organic carbon and nitrogen (POC and PON) and nutrients (nitrate + nitrite, phosphate, and silicate) were collected from August 2015 to August 2016 in Balsfjord at 5, 20, 50, and 150 m using Go-Flo bottles (20 L, General Oceanics, USA). Chl *a*, POC and PON samples from December 2016 to October 2017 in all fjords were collected at 0, 10, 20, 50 and 100 m using Niskin bottles (8 L, General Oceanics, USA). The water samples for Chl *a* and POC and PON analysis were kept dark and cool until arrival at the laboratory. To analyze for nutrients, 60 mL of seawater were collected into acid-washed (4% HCl) plastic vials and kept cool and frozen at -20°C within 2-4 h after collection. The seasonal variations in fluorescence followed closely those of the total Chl *a* in Balsfjord (Fig. 2B). Therefore, the fluorescence data from the CTD was used as a relative measure of the Chl *a* concentration in Altafjord and Porsangerfjord (Fig. S1, Table 2).

The small copepod species (*Microcalanus* spp., *O. similis*, and *M. norvegica*) were collected from the Go-Flow bottles at 5, 20, 50, and 150 m depths (sample volume of 17.5 L) from August 2015 to August 2016, filtered onto a 20 µm-sieve and transferred to plastic bottles. The large copepods (*C. finmarchicus* and *M. longa*) were collected using two vertical WP-2 net tows (Hydro-Bios, Germany, 180 µm-mesh, 0.25 m^2 opening, 0.3-0.4 m s^{-1} towing speed) from 50 m to surface and from 170 m to 50 m. All copepod samples were kept cold until arrival at the laboratory within 2 h, where the samples were fixed with buffered formalin (4% final concentration). The sampling method for small copepods was modified from December 2016 and onwards because the volume of the Go-Flo proved insufficient to quantitatively sample *Microcalanus* spp. Therefore, a WP-2 net (64 µm-mesh, 0.5 m s^{-1} towing speed) was used from 100 m to surface instead of the Go-Flo for the sampling in 2016-2017. These samples were fixed onboard with 4% formalin.

Sample analyses

Nutrients were analyzed by standard seawater methods using a Flow Solution IV Analyzer (O.I. Analytical, USA; (Hodal et al. 2012). The analyzer was calibrated using reference seawater from Ocean Scientific International Ltd., UK. The three values obtained for each nutrient were averaged, and the detection limit was used when measured values were less than the detection limit (0.02 mmol m^{-3} for nitrate and nitrite, 0.01 mmol m^{-3} for phosphate and 0.07 mmol m^{-3} for silicic acid).

Three 100 mL aliquots were filtered for total Chl *a* on GF/F filters (glass-fiber filters), and 300 mL were filtered on a 10-µm Millipore filters for Chl *a* >10 µm. Chl *a* was extracted with methanol in the dark for 16 hours, following a modified method of Strickland and Parsons (1972), and analyzed using a newly calibrated fluorometer (10-AU Turner Designs, California, USA). Three 400 mL aliquots were filtered for POC and PON on pre-combusted GF/F filters. POC and PON filters were frozen at -20°C for later analysis with CHN auto-analyzer (Reigstad et al. 2008). The concentrations of nutrients, Chl *a*, POC and PON in the upper 100 m were averaged for each sampling event.

For the identification of copepods, sub-samples were examined until a total of 300 individuals of the target species (*M. norvegica*, *O. similis* and *Microcalanus* spp.) or the entire sample were counted. In addition, *Calanus finmarchicus* and *Metridia longa* were identified and enumerated in Balsfjord in 2015-2016. All copepods were identified to developmental stages,

using a stereomicroscope (Zeiss Discovery.V20), at 75 to 150 magnification. *Microcalanus* spp. potentially includes both *M. pygmaeus* and *M. pusillus*, and visual differentiation of the species is challenging (Koszteyn et al. 1991). However, in previous studies, genetic identification has confirmed that only *M. pusillus* has been present in Balsfjord and around Svalbard (Barth-Jensen et al. 2020, Coguiec et al. 2021, Ershova et al. 2021) and we therefore assumed that the species in this study was *M. pusillus*.

The prosome length (*M. pusillus*, *O. similis*, *C. finmarchicus* and *M. longa)* or total length (*M. norvegica*) was measured for 30 to 60 copepodids of each stage (CI-CIII, CIV-CV, males, and females), using a microscope with a fitted eyepiece with an ocular micrometer (precision of 7 µm). Small copepods were measured from samples of all three fjords from December 2016 and March, April, August, and October 2017, while *C. finmarchicus* and *M. longa* were measured from Balsfjord samples between August 2015 and August 2016.

Estimates of secondary production

For the egg-carrying copepods (*O. similis* and *M. norvegica*) and for *M. pusillus*, the potential secondary production was calculated using two approaches: (1) based on multiplying the weight-specific egg production rate of the female with its total biomass, assuming that the weight-specific egg-production rate equals the juvenile somatic growth rates (Berggreen et al. 1988), and (2) based on the temperature-dependent growth rates according to Huntley and Lopez (1992), multiplied with the total biomass. For *C. finmarchicus* and *M. longa* only the temperature-dependent growth rates were used.

To estimate the egg production rate for the egg-carrying *O. similis* and *M. norvegica*, undamaged egg sacs from Balsfjord samples (2015-2016) were dissected using a fine needle and the numbers of eggs per egg sac were counted and averaged per sampling date (*O. similis*: n = 1-5, *M. norvegica*: n = 15-30). For other sampling dates and fjords, the total abundance of egg sacs (egg sacs m^{-3}) was multiplied with the mean number of eggs per egg sac in Balsfjord from the closest calendar day, giving the total abundance of eggs (*E*, eggs m^{-3}) of the entire populations of *O. similis* and *M. norvegica*. The weight-specific egg production rates (*SEP*, d^{-1}) of the population were then calculated following equation (1) of Sabatini and Kiørboe (1994):

$$SEP = \frac{E}{F} \times HR \times \frac{Wegg}{Wfemale} \qquad (1)$$

where F is the abundance of females (ind. m^{-3}), W_{egg} is the carbon content of an egg (µg C), and W_{female} is the carbon content of a female (µg C). Female carbon contents were calculated from the prosome length, according to conversions from Satapoomin (1999) for *M. norvegica* and Sabatini and Kiørboe (1994) for *O. similis* (Table S1). Egg carbon contents were taken from Barth-Jensen et al. (2020). *HR* (d^{-1}) is the temperature-dependent hatching rate according to Barth-Jensen et al. (2020), except for *O. similis* at temperatures ≤ 1°C where *HR* was calculated based on Nielsen et al. (2002).

To estimate the total abundance of eggs for *M. pusillus*, the abundance of females was multiplied by the average daily egg production rate (4.3 ± 5.9 eggs $female^{-1}$ d^{-1}) from Balsfjord, which varied only little across the reproductive seasons (Figure 5 in (Barth-Jensen et al. 2020). The average daily egg production rate was assumed to be zero from 1st October to 31st December, following the seasonal cycle in production of *M. pusillus* proposed by Norrbin (1991). The SEP was calculated by multiplying the total abundance of eggs with the egg carbon content (Barth-Jensen et al. 2020) and dividing by female carbon content, using the conversion by Klein Breteler et al. (1982), Table S1).

The weight-specific growth rate of all five copepod (g, d^{-1}) was calculated following the temperature-dependent model from Huntley and Lopez (1992):

$$g = 0.0445 \times e^{0.111 \times T} \qquad (2)$$

where T is the temperature averaged over the surface 100 m.

The weight-specific growth rate was multiplied by the total biomass (mg C m^{-3}) of each species. The carbon contents of each copepodid stage was calculated from published length-to-carbon-weight conversions, including that of Madsen et al. (2001) for *C. finmarchicus* and Hirche and Mumm (1992) for *M. longa* (Table S1). Copepod biomass and production estimates are for the upper 100 m.

Seasonality in the fjords

The secondary production was presented as seasonal means. To define the timing of seasons, a non-metric cluster analysis was performed for environmental parameters (i.e., the average temperature, nitrate + nitrite, phosphate, silicate, total Chl *a*, POC and PON concentrations over the upper 100 m) for the monthly data from Balsfjord from August 2015 to August 2016. The analysis was run with complete linkage and chi-square distances for Bray-Curtis

similarities, using R version 4.1.0 (R Core Team 2021). No data transformation was performed. Following the grouping formed by the cluster analysis, a dendrogram was created (Fig. 2A) and used with the environmental data (Fig. 2B) to guide the delimitation of the seasons, which were thereafter applied to all fjords. The seasons were divided into fall (August 31st to October 31st), winter (November 1st to March 31st), pre-bloom (April 1st to April 14th), spring bloom (April 15th to May 31st) and summer (June 1st to August 30th, Fig. 2). To simplify comparison between fjords, we assumed that the timing of seasons in Balsfjord were comparable in Altafjord and Porsangerfjord, as the three fjords are at approximately same latitude and are subjected to water influx from the Norwegian Coastal Current. This assumption is likely only partially correct, because the three fjords have different hydrological features (Eilertsen & Frantzen 2007).

The annual production (mg C m^{-3} yr^{-1}) of each species was calculated as an integration of the seasonal mean of the daily production over each season. As the spring bloom was not sampled in 2017, we used the pre-bloom daily production as value for the spring bloom production.

Results

Seasonality in Balsfjord, Altafjord and Porsangerfjord

The fall and winter in Balsfjord were characterized by decreasing water temperatures from an autumn maximum of 7.0°C to a late-winter minimum of 2.9°C (Fig. 2B, Fig. S1). The nutrient concentrations increased during the autumn and reached their maxima by the end of winter at 7.4 mmol m^{-3} for nitrate + nitrite, 0.5 mmol m^{-3} for phosphate and 5.4 mmol m^{-3} for silicate. During the same period, the total Chl *a* concentration decreased from 0.58 mg m^{-3} to 0.07 mg m^{-3} (Fig. 2B). Increasing temperatures were observed during the pre-bloom in early April (Fig. 2B) and this coincided with marked decreases in nutrient concentrations and a sharp increase in Chl *a*. Chl *a* peaked in early May (2.79 mg m^{-3}; Fig. 2B) and decreased rapidly thereafter. POC and PON concentrations were highest during the spring Chl *a* peak (292 mg m^{-3} and 44 mg m^{-3} respectively, Fig. 2B). In summer, water temperatures continued to increase (Fig. S1), while the nutrient concentrations stayed low at ≤ 3.2 mmol m^{-3} for nitrate + nitrite, ≤ 0.3 mmol m^{-3} for phosphate and ≤ 1.5 mmol m^{-3} for silicate (Fig. 2B). A second Chl *a* peak occurred at the end of August 2016 (1.44 mg m^{-3}, with 87% consisting of Chl *a* < 10 µm; Fig. 2B), but was not observed in other years (Fig. S1). The POC concentration remained high during summer.

The three fjords shared similar seasonal temperature fluctuations in the upper 100 m (Fig. S1): the temperature minima were reached in late-winter, and the temperature maxima were observed in October. Altafjord and Porsangerfjord Outer were the warmest stations with temperature ranges of 3.9 – 8.8°C and 4.3 – 8.1°C, respectively (Table 2), while Porsangerfjord Inner was coldest with a temperature range of -0.6 – 4.1°C. Fluorescence sharply increased between early April and early May in Porsangerfjord (Fig. S1) as was seen in Balsfjord, indicating the spring bloom, with the highest fluorescence at the inner station (Table 2). However, in Altafjord, the spring bloom seemed to occur earlier, as the peak fluorescence appeared in early April (fluorescence at 1.28, Table 2, Fig. S1). A late August fluorescence peak was detected in Porsangerfjord Outer in 2017.

Population dynamics and biomass of copepods

The five copepod species were common year-round in Balsfjord, but their biomasses and population dynamics differed (Fig. 3). The total biomass of *O. similis* ranged from < 0.1 to 2.3 mg C m^{-3} (Fig. 3). The population biomass of *O. similis* was dominated by CI-CV copepodids in 2015-2016, while females contributed the greatest proportion of the biomass in 2016-2017, even though female biomass was similar in both years (Fig. 3). Total *O. similis* biomass gradually diminished during the fall to reach a minimum in April, then increased to a summer maximum. Eggs sacs were observed year-round, with peaks in spring and late-summer, followed by an increase in the biomass of CI-CIII, indicating that *O. similis* had two generations per year.

Microsetella norvegica was abundant in Balsfjord, with a biomass that occasionally reached ≥ 10 mg C m^{-3}. The peak biomass of *M. norvegica* was higher in 2015-2016 (≤ 25 mg C m^{-3}, Fig. 3) than in 2016-2017 (≤ 8 mg C m^{-3}, Fig. 3), and the biomass of young copepodid stages CI-CIII was higher in June-October 2015-2016 than in 2016-2017 (Fig. 3). Both females and males were present year-round, although females dominated with a maximum biomass of 17 mg C m^{-3} in April 2016. Egg-carrying females were only present between April and August in Balsfjord, with the highest biomass in April (4 mg C m^{-3}, Fig. 3). Biomasses of juvenile stages CI-CV peaked between June (2016) and August (2015 and 2017), with CI-CIII present between April and October, and CIV-CV between May and December. Therefore, *M. norvegica* likely had only one generation developing from the eggs during the spring bloom to adults by mid-winter.

M. pusillus had a lower biomass in Balsfjord than *O. similis* and *M. norvegica* with a biomass that was ≤ 0.5 mg C m^{-3} (Fig. 3). This hindered a proper quantification of this species in the Go-Flo samples (data not shown). The population was dominated by females, though all copepodid stages of *M. pusillus* were present throughout the year (Fig. 3). Young copepodids CI-CIII were found mainly in March and April and were followed by an increase of CIV-CV in the summer and fall. It thus appeared that *M. pusillus* had one main generation per year.

The biomass of *C. finmarchicus* in Balsfjord varied between 1 and 18 mg C m^{-3} (Fig. 3). Copepodids CIV-CV dominated the upper 100 m during most of the year, except from March to May when female biomass was greatest (Fig. 3). Males and females mainly occurred between February and May and always at low biomass (≤ 1.2 mg C m^{-3}). Young *C. finmarchicus* copepodids were observed between April and August with a peak biomass in early May (≤ 1.7 mg C m^{-3}, Fig. 3). *C. finmarchicus* likely produced one generation every year.

The total biomass of *M. longa* was < 0.7 mg C m^{-3}, and all copepodid stages were present year-round (Fig. 3). Males dominated during fall and winter (≤ 0.3 mg C m^{-3}), while females were most common in spring (≤ 0.4 mg C m^{-3}, Fig. 3). The spring bloom (mid-April) marked the start of an increase in CI-CIII, which culminated in May (≤ 0.1 mg C m^{-3}, Fig. 3), followed by an increase in CIV-CV peaking during summer (≤ 0.3 mg C m^{-3}, Fig. 3). It seems likely that *M. longa* produces one main generation every year. The cumulated biomass of *O. similis*, *M. norvegica*, *C. finmarchicus* and *M. longa* in Balsfjord varied between 4 and 30 mg C m^{-3} in 2015-2016, with large copepods dominating the total biomass only at 6 out of 14 samplings (in winter and spring).

The biomasses and the seasonal stage compositions of small copepod species in Altafjord and Porsangerfjord were comparable to those in Balsfjord (Fig. 3 and 4). *M. norvegica* had highest biomass of small copepods, with a maximum biomass up to 8 mg C m^{-3} in Porsangerfjord Inner (Fig. 4), while *O. similis* had biomass ≤ 1.2 mg C m^{-3} and *M. pusillus* biomass was always ≤ 0.6 mg C m^{-3} (Fig. 4). The biomasses of the small copepod populations were low at the end of the winter and the pre-bloom, building up during spring and summer (Fig. 4). Females were the dominant stage year-round, although males constituted large proportions of the *M. norvegica* populations while being scarce in *O. similis*. Egg-carrying *M. norvegica* females were only detected in April during the early spring bloom in Altafjord (23% of females) and in August in Porsangerfjord (12-14% of females). For *O. similis*, egg-carrying females were present year-round and egg sac abundances peaked in April in Altafjord, August

in Porsangerfjord Central and Outer, and October in Porsangerfjord Inner (Fig. 4). For all seasons, the young copepodid stages CI-CIII were the least commonly observed developmental stage of all species (Fig. 4). The CI-CIII of *O. similis* and *M. norvegica* were mostly observed in August and October, whereas the CI-CIII of *M. pusillus* were present throughout the year. The biomass of *O. similis* CIV-CV increased from summer to winter in all fjords, contrasting with the relatively low biomass and proportions of CIV-CV in *M. norvegica*. The CIV-CV of *M. pusillus* represented ≥ 24% of the populations in Porsangerfjord except in March when CI-CIII biomass was greater.

In summary, all fjords presented a similar succession of small copepods with one main generation per year, except for *O. similis* which appeared to have two annual generations. The year-round presence of CI-CIII of *O. similis*, *M. pusillus* and *M. longa* suggested a prolonged reproductive period compared to that of *M. norvegica* or *C. finmarchicus*, which appeared to mainly reproduce in spring and early summer.

Copepod secondary production

The two methods used to calculate the secondary production of small copepods gave large differences in the seasonal production estimates: in all three fjords the production based on the temperature-dependent model was generally an order of magnitude higher than the estimates based on specific egg-production rate (Fig. 5 and 6). Irrespective of method, the production in Balsfjord was lowest in fall and winter (≤ 0.01 mg C m^{-3} d^{-1} based on the specific egg-production rate, ≤ 0.7 mg C m^{-3} d^{-1} based on the temperature-dependent model) and highest during summer (≤ 0.1 mg C m^{-3} d^{-1} based on the specific egg-production rate, ≤ 2.0 mg C m^{-3} d^{-1} based on the temperature-dependent model, Fig. 5A and 5B). The annual production of small copepods in 2015-2016 was 20 mg C m^{-3} yr^{-1} (specific egg-production rate) or 322 mg C m^{-3} yr^{-1} (temperature-dependent model), which was 3-7 times higher than in 2016-2017 (3 mg C m^{-3} yr^{-1} according to the specific egg-production rate or 102 mg C m^{-3} yr^{-1} according to the temperature-dependent model, Fig. 7A). This was due to the low copepod biomass in 2016-2017. In Altafjord and Porsangerfjord, the daily production of small copepods was equally low to that of Balsfjord in 2016-2017 for both methods at all seasons (Fig. 6). The annual production was low, 2 – 3 mg C m^{-3} yr^{-1} (specific egg-production rate), and 13 – 52 mg C m^{-3} yr^{-1} (temperature-dependent model) in Altafjord and Porsangerfjord, respectively (Fig. 7B).

Specific egg-production estimates followed the seasonality of egg production for each species: *M. norvegica* was the most productive species from the pre-bloom to the summer (maximum 0.09 mg C m^{-3} d^{-1}), while the production of *O. similis* and *M. pusillus* was lower but distributed throughout the year in Balsfjord in 2015-2016 (maximum 0.04 and 0.01 mg C m^{-3} d^{-1} respectively, Fig. 5A). However, *M. pusillus* dominated the seasonal production in 2016-2017 in all fjords (≤ 0.01 mg C m^{-3} d^{-1}, Fig. 5A and 6). This led to an overall dominance of the annual small copepod production by *M. norvegica* in 2015-2016 (61 and 92%, Fig. 7A) while *M. pusillus* contributed ≥ 63% in 2016-2017 (Fig. 7A and 7B). The temperature-dependent model indicated a dominance of *M. norvegica* production in all fjords (≤ 1.4 mg C m^{-3} d^{-1}), followed by *O. similis* (Fig. 5B and 6). Production of *M. pusillus* estimated using the temperature-dependent model was very low (≤ 0.03 mg C m^{-3} d^{-1}, Fig. 5B and 6), even during fall and winter. The annual production of small copepods was dominated by *M. norvegica* and *O. similis* (Fig. 7A and 7B). The two methods used to estimate secondary production indicated not only different rates of production, but also different seasonal dynamics and differences in the relative importance of the species.

According to the estimates from the temperature-dependent model, the production of the large copepods *C. finmarchicus* and *M. longa* (≤ 0.9 mg C m^{-3} d^{-1}) was equal to or lower than that of the small copepods *O. similis* and *M. norvegica* throughout the year (Fig. 5B and 5C). The maximum production of large copepods was reached in the fall, while it was minimal during the pre-bloom. Although we did not estimate the production of large copepods based on the size-specific egg production, it is likely that this method would have resulted in a maximum production during the spring bloom, when the numbers of eggs and small developmental stages peaked. The large copepod annual production was 180 mg C m^{-3} yr^{-1}, with *C. finmarchicus* contributing to 96% of the production (Fig. 7A).

Discussion

Our results confirmed the year-round presence and reproduction of *O. similis* and *M. pusillus* in all fjords, and the restriction of *M. norvegica* reproduction to the spring and summer (Dvoretsky & Dvoretsky 2009, Koski et al. 2014, Lischka & Hagen 2016). *M. norvegica* therefore appeared more dependent on the spring bloom, similar to *Calanus* spp., than the other two species, which might have had broader diets (Svensen & Kiørboe 2000, Pond & Ward 2011). In addition, our results demonstrate the importance of small copepods to

secondary production in Arctic and sub-Arctic environments, as shown by Madsen et al. (2008). However, a comparison of estimates of secondary production indicate that the choice of the method will influence the calculated production, its seasonal development, and the relative importance of species, contributing to the estimates.

Biomass and production of small copepods in Arctic – a plea for the use of small mesh sizes

Use of nets with a typical mesh size of 200 µm underestimates small copepod biomass, and therefore also their overall importance in ecosystems (Hopcroft et al. 1998, Turner 2004). *Oithona* spp. has been reported to dominate the biomass of small species (Gallienne & Robins 2001), but the sampling efficiency for *O. similis* females is higher than for *M. norvegica* females. Using the equation from Nichols and Thompson (1991) provides estimates of ≤ 37% for *O. similis* and ≤ 9% for *M. norvegica* when nets of ≥ 180-µm mesh size are used for sampling. Therefore, *M. norvegica* would likely remain undetected when sampling with the 200 µm nets (Moriarty & O'Brien 2013, Svensen et al. 2018), but sampling with nets of smaller mesh sizes has provided evidence that *M. norvegica* is often found at high abundance and with large biomass in sub-Arctic and Arctic coastal ecosystems in e.g., Norway and Svalbard (Barthel et al. 1995, Pasternak et al. 2000, Halliday et al. 2001, Hirche & Kosobokova 2011, Svensen et al. 2018, Barth-Jensen et al. 2022), Greenland (Pedersen et al. 2005, Hjorth & Dahllöf 2008, Arendt et al. 2013, Koski et al. 2021) and the Chukchi Sea (Kasyan 2020). The present study confirms *M. norvegica* as a dominant species in Norwegian sub-Arctic fjords. *M. norvegica* might thus be as abundant as *Oithona* spp. in Arctic and sub-Arctic ecosystems, but be commonly underestimated because the gear used is inadequate for sampling this small and slim harpacticoid.

The biomass of large copepods is often reported as being higher than that of small copepods in surface waters, especially during spring and summer (Pasternak et al. 2000, Basedow et al. 2014, Darnis & Fortier 2014, Svensen et al. 2019). Our Balsfjord results indicate that, if sampling is adequate, estimates of small copepod biomasses can be equal to those of large copepods even in spring and summer. Priou (2015) reported maximum abundances and biomasses of *C. finmarchicus* of 69 ind. m^{-3} or 11 mg C m^{-3} in April in Porsangerfjord Inner, and of 1157 ind. m^{-3} or 119 mg C m^{-3} in November in Porsangerfjord Outer (biomass conversion using Table 4). The maximum cumulated biomass of small copepods in our study was comparable to the estimated *C. finmarchicus* biomass in Porsangerfjord Inner, but 100 times lower in Porsangerfjord Outer. Therefore, either small or large copepods may appear to

dominate in biomass in high latitude environments, likely depending on a combination of environmental factors and how biomass estimations were made.

A high biomass of small copepods is mirrored by high production. *M. norvegica* can have production rates as high as 5 mg C m^{-3} d^{-1} in temperate waters, which emphasizes that this harpacticoid copepod can be highly productive (Uye et al. 2002). Previous studies in a temperate fjord showed a summed daily production of *O. similis*, *M. norvegica* and *M. pusillus* of 2.9 – 4.4 mg C m^{-2} d^{-1} in July, which is within the range of our summer egg production estimates (Nielsen & Andersen 2002). Previous estimates of annual production of small copepods was 0.2 – 1.7 g C m^{-2} yr^{-1} in Disko Bay, Greenland, comparable to the egg production estimates in our study but lower than the temperature-dependent estimates (Madsen et al. 2008). However, our temperature-dependent estimates were four orders of magnitude lower than the 14 g C m^{-3} d^{-1} reported by Basedow et al. (2014). The production of *C. finmarchicus* during spring and summer was modelled between 0.1 and 20 g C m^{-2} in sub-Arctic fjords, and 15 g C m^{-2} in the Barents Sea (Tande & Slagstad 1992), which is in the same order as the temperature-dependent estimation. Therefore, our production estimates seem robust and fall within ranges reported for production in temperate and Arctic ecosystems.

Dahmen (1997) found that mesozooplankton production was 10-16% of the primary production, which represents an average carbon transfer through the food chain (e.g., (Węsławski et al. 2009). In Balsfjord, the annual primary production has been estimated as 120 g C m^{-2} yr^{-1} (Tande 1991), which means that 0.3 to 27% of the primary production would be transferred to small copepods, according to our production estimates integrated over the upper 100 m. Thus, we infer that the production of small-sized zooplankton can be high and may be equivalent to that of large copepods, as also seen in other studies (Basedow et al. 2014, de Melo Júnior et al. 2021). As such, small copepods may play a large role in carbon transfer from primary producers to higher trophic levels in high-latitude ecosystems, underscoring the need to direct more studies towards these species.

Environmental factors influencing species-specific trends of biomass and production

Temperature and advection: The finding of a high biomass and production of *M. norvegica* is surprising in low temperature environment, such as the inner basin of Porsangerfjord where the average temperature was mainly ≤ 5°C. Barth-Jensen et al. (2020) showed that egg development rates and hatching success of *M. norvegica* were low at temperatures < 5°C, and

M. norvegica is most common in surface waters with a temperature > 5 °C (Pasternak et al. 2000, Halliday et al. 2001, Svensen et al. 2018). Therefore, *M. norvegica* may take advantage of the surface temperatures ≥ 5°C that characterize Porsangerfjord Inner during spring and summer (Eilertsen & Frantzen 2007, this study). It is also possible that the high biomass of *M. norvegica* in the inner basin was a result of advection of individuals from outer locations due to the eddy circulation observed in Porsangerfjord which facilitates retention in the inner basin during summer (Frantzen 2007).

Primary production: *M. norvegica* and *O. similis* rely on the spring bloom and the summer to achieve high production, which is expected for income-breeding species (i.e., fuels reproduction through feeding; Varpe et al. 2009). We noted that the earlier spring bloom in Altafjord may resulted in proportions of egg-carrying *M. norvegica* females increasing earlier in the year than in other fjords where the spring bloom started later. This seems to underscore the reliance of *M. norvegica* on the spring bloom to initiate reproduction. The copepod may be able to exploit the phytoplankton production rapidly, although feeding likely occurs on newly formed aggregates instead of suspended phytoplankton per se (Koski et al. 2005, Barth-Jensen et al. 2022, Koski & Lombard 2022). The success of *M. norvegica* at low temperature may rely on its ability to respond rapidly to resource change during its peak reproductive season. An alternative successful strategy is to distribute production throughout the year, as seen in *O. similis*. This enables a species to exploit the resources made available by an autumn bloom for a possible winter recruitment of early life stages (Lischka & Hagen 2005, Barth-Jensen et al. 2022).

The finding of the highest production of *M. pusillus* during fall and winter appears to contrast with the species description as an omnivorous income breeder (Norrbin 1991). *M. pusillus* shows two main reproductive seasons in Kongsfjord, Svalbard, and our sampling schedule may have missed the June-July production peak (Lischka & Hagen 2016). Irrespective, *M. pusillus* does not seem dependent on the spring bloom and could take advantage of the fall and winter to grow and proliferate, at a time when there are few competitors and predators. This also noted for the sibling species *M. pygmaeus* (Marshall 1949, Lischka & Hagen 2016, Barth-Jensen et al. 2022). The differences in times of peak production likely show that the three small copepods have different strategies that lead to their success in high-latitude fjords. A diversity of strategies point to small copepods being heterogeneous group, and this makes modelling a complex and taxing exercise.

Methods of biomass and production estimates

The differences in the life histories of the small copepods introduced large differences to the estimates of seasonal secondary production depending on the method used to assess production: while the specific egg-production rate followed closely the reproductive patterns of each species, the temperature-dependent model varied as a function of temperature. Whether one should use specific egg production rates, temperature-dependent growth rates or a combination of both to model and estimate production need to be considered in verbatim to factors that determine egg production and juvenile growth rates. Juvenile growth rates are assumed to be mainly temperature limited, although food limitation can occur (Klein Breteler et al. 1982, Berggreen et al. 1988, Richardson & Verheye 1999, Hygum et al. 2000), whereas reproduction tends to be mainly dependent on food concentration (Miralto et al. 1998, Koski & Kuosa 1999, Castellani et al. 2007). Juveniles of *M. norvegica* seem to grow at a similar rate to adults at similar food levels (Uye et al. 2002), though this does not hold for all copepods (Klein Breteler et al. 1982, Hirst & Bunker 2003, Leandro et al. 2014).

Madsen et al. (2008) used both methods to estimate production of small copepods in Greenland, and found maximum daily productions comparable to our specific egg-production estimates without large differences between methods. The similarity between estimates from the two methods might be explained by the low temperature in Disko Bay (-1.6 to 3.4°C) that induced long development times and therefore low specific egg-production rate and modelled growth rates (Madsen et al. 2008). In studies from temperate areas, temperature-dependent production was estimated to be twice that calculated using the egg ratio model (Dahmen 1997) and 5-fold higher than specific egg production rate estimates (Nielsen & Andersen 2002). This suggests that the temperature-dependent model may overestimate the production at higher temperatures and / or in food limited situations, and therefore may not be well-suited to assess production in most environments. In Balsfjord, the temperature-dependent estimates give an annual production equal to 8 to 27% of the primary production for small copepods or up to 42% including the large copepods. Such a high ratio of copepod:primary production is unrealistically high, but stresses that small copepods could be responsible for a large portion of the total copepod production.

Secondary production calculated from species-specific egg production rate is often lower than when using other methods (e.g. (Nielsen & Andersen 2002, Madsen et al. 2008), which suggests that juvenile growth rates are underestimated if based on the weight-specific egg production rates (Leandro et al. 2014). Therefore, both methods have their limitations, particularly for small copepods species where our knowledge on the environmental

dependencies of egg production and growth rate is sparse. It would therefore appear that a combination of using a temperature-dependent model for juveniles along with a weight-specific egg production model is a pragmatic and parsimonious way to get secondary production estimates for these understudied species.

Another question to be considered is the importance of an accurate estimates of growth rate and biomass for modelling. For example, in the present study estimates of the copepod biomass could vary markedly between the two sampling years. The question is whether this was due to real inter-annual variation or due to sampling methods and protocols. According to Nichols and Thompson (1991), the sampling efficiency of a 64-µm mesh net should be 100% for copepods with a width ≥ 103 µm (e.g., *M. norvegica* or *O. similis* female). However, *M. norvegica* CI-CIII have a width between 66 and 100 µm (Diaz & Evans 1983), which should result in a 57-99% retention efficiency by a 64-µm mesh net. Sampling method may therefore explain some of the inter-annual differences in biomass and stage-compositions of CI-III observed in Balsfjord for *M. norvegica* and *O. similis* but should not have had a major inference on estimates of female biomass. Therefore, biomass differences observed between years appear to have been real and not artefacts. They were probably driven by inter-annual fluctuations in environmental parameters, as is common in copepod populations (Abramova & Tuschling 2005, Arendt et al. 2013).

Perspective

Biological productivity in high-latitude ecosystems is thought to be fueled by the phytoplankton spring bloom, but the increasing appearance of late summer blooms can lead to a need to modify this view (Wassmann 2011, Ardyna et al. 2014). The late summer bloom is largely composed of smaller autotrophs that may be preyed upon by small copepods (Eilertsen et al. 1981, Riisgaard et al. 2014). Therefore, these secondary blooms could be beneficial to the small copepod species that are still reproducing at that time of the year (i.e., *O. similis* and *M. pusillus*). In addition, the though young life stages of larger copepods such as *M. longa* or *C. glacialis* can also feed on smaller phytoplankton (Forest et al. 2011). It is possible that an increase in prey availability in the fall would result in a shift in the biomass ratio between large and small copepods in high-latitude ecosystems, though the extend of any shift might be under the influence of the timing of the secondary bloom, predator-prey interactions and mortality rates of the secondary producers.

Spring blooms seem to be occurring earlier in some parts of the Arctic, as a result of an earlier stabilization of the water column via sea-ice melt or temperature increase (Stabeno & Overland 2001). In Altafjord, the small copepods showed their ability to adapt to an early spring bloom. In the future, changes in the timing and progression of primary production due to climate change could promote reproduction and development of small copepods, while creating possible mismatches for large copepods (Søreide et al. 2010). Under such circumstances small copepods would likely comprise a larger part of total secondary production.

Therefore, the Arctic of the future might include changes in the phenology of copepod population dynamics and the ratio between small and large copepods. However, because the production of both small and large copepods can be similar at a specific location, a shift towards small copepods may not always imply a less productive ecosystem. Nevertheless, small copepods impact the carbon cycle, the recycling of nutrients and other ecosystem processes differently to large copepods. Our study stresses the need for a broader understanding of the functional role and the productivity of small copepods, how environmental forcing could have an influence on small copepod populations and how any changes could impact Arctic marine ecosystems.

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Contributions

The design of the study was made by CBJ and CS. The sampling was done by CBJ, EC, PG and CS. The sample analysis was run by CBJ, EC, PG, TB and SK. The manuscript was written by CBJ, and all authors contributed to its edition and review.

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Figure legends

Fig. 1 Location of the sampling stations in three sub-polar Norwegian fjords: Balsfjord (Svartnes), Altafjord (Alta) and Porsangerfjord (Inner, Central and Outer).

Fig. 2 (A) Cluster dendrogram (based on chi-square distances) and (B) Environmental data averaged in the upper 100 m (including temperature, fluorescence, and concentrations of nitrate + nitrite, phosphate, silicate, total Chl *a*, Chl $a \geq 10$ μm, POC and PON) at Svartnes, Balsfjord, collected during the cruises between August 2015 and August 2016. The 2016-05-31 cruise was only used for temperature and fluorescence.

Fig. 3 Biomass (mg C m^{-3}) and stage composition of *O. similis*, *M. norvegica*, *M. pusillus*, *C. finmarchicus* and *M. longa* in Balsfjord between August 2015-August 2016 (left) and December 2016-October 2017 (right). Note the difference in the biomass scale (*y*-axis) between species.

Fig. 4 Biomass (mg C m^{-3}) and stage composition of *O. similis*, *M. norvegica* and *M. pusillus* in Altafjord and Porsangerfjord between December 2016 and October 2017. The biomasses of Porsangerfjord Central and Outer were averaged. Note the difference in the biomass scale (*y*-axis) between species, and for *M. norvegica* in Porsangerfjord Inner.

Fig. 5 Daily secondary production (mg C m^{-3} d^{-1}) of the copepods (A and B) *O. similis*, *M. norvegica*, *M. pusillus*, and (C) *C. finmarchicus* and *M. longa* in Balsfjord averaged for each season between August 2015 and October 2017. The production were estimated from (A) the specific egg-production rate, and (B and C) the temperature-dependent model from Huntley and Lopez (1992).

Fig. 6 Daily secondary production (mg C m^{-3} d^{-1}) of the copepods *O. similis*, *M. norvegica* and *M. pusillus* in Altafjord and Porsangerfjord, averaged for each season between December 2016 and October 2017. The production were estimated from (left) the specific egg-production rate, and (right) the temperature-dependent model from Huntley and Lopez (1992).

Fig. 7 Annual production (mg C m^{-3} yr^{-1}, right axis) and contribution of each species to the annual production (%, left axis) for *O. similis*, *M. norvegica*, *M. pusillus*, *C. finmarchicus* and *M. longa* in (A) Balsfjord and (B) Altafjord and Porsangerfjord. Both estimation methods used are displayed: SEPR = specific egg production rate; Model = temperature-dependent model from Huntley and Lopez (1992).

Figure S1. Temperature (°C) and fluorescence variations in Balsfjord, Altafjord and Porsangerfjord from hydrographical profiles collected between 2015 and 2017 including this studies' cruises and published datasets from the Havmiljødata monitoring program (https://dataverse.no/dataverse/nmdc).

Tables and captions

Table 1. Location, sampling depth, sampling date, and gear used in the different stations.

Fjord	Station	Coordinates	Depth (m)	Sampling dates (DD/MM)	Gear for copepod sampling
Balsfjord	Svartnes	69° 22.947’ N, 19° 05.414’ E	180	**2015:** 31/08 - 24/09 - 29/10 - 19/11 - 15/12	Go-Flo 20µm, WP-2 180µm
				2016: 16/02 - 07/03 - 05/04 - 19/04 - 03/05 - 19/05 - 31/05* - 27/06 - 23/08	Go-Flo 20µm, WP-2 180µm
				2016: 07/12	WP-2 64µm
				2017: 16/03 - 07/04 - 15/08 - 19/10	WP-2 64µm
Altafjord	Altafjord	70° 06.570’ N, 23° 08.644’ E	410	**2016:** 06/12	WP-2 64µm
				2017: 15/03 - 05/04 - 18/10	WP-2 64µm
Porsangerfjord	P. Inner	70° 07.200’ N, 25° 11.000’ E	105	**2016:** 05/12	WP-2 64µm
				2017: 14/03 - 04/04 - 16/08 - 17/10	WP-2 64µm
	P. Central	70° 30.700’ N, 25° 35.000’ E	195	**2016:** 05/12	WP-2 64µm
				2017: 14/03 - 04/04 - 16/08 - 17/10	WP-2 64µm
	P. Outer	70° 52.500’ N, 26° 17.050’ E	220	**2016:** 05/12	WP-2 64µm
				2017: 14/03 - 04/04 - 16/08 - 17/10	WP-2 64µm

* Sampled only for hydrographical data.

Table 2. Average (± SD) of the temperature (°C) and fluorescence in the upper 100 m in Balsfjord, Altafjord and Porsangerfjord for the different seasons. Data were collected during this study and during the Havmiljødata monitoring program from 2015 to 2017 (https://dataverse.no/dataverse/nmdc). P. stands for Porsangerfjord.

		Fall	Winter	Pre-bloom	Spring bloom	Summer
Temperature (°C)	**Svartnes**	7.1 ± 0.2	4.5 ± 1.4	3.6 ± 0.4	4.1 ± 0.6	6.3 ± 0.4
	Alta	8.8	5.3 ± 1.6	3.9 ± 0.5	4.1 ± 0.3	6.1 ± 0.8
	P. Outer	8.1 ± 0.1	5.6 ± 1.3	4.3 ± 0.1	4.3 ± 0.2	7.8 ± 0.8
	P. Central	7.2 ± 0.3	4.5 ± 1.4	2.8 ± 1.1	3.3 ± 1.0	6.2 ± 0.8
	P. Inner	4.1 ± 0.1	1.1 ± 1.7	-0.6 ± 0.3	0.5 ± 0.5	3.0 ± 0.6
Fluorescence	**Svartnes**	0.26 ± 0.06	0.11 ± 0.04	0.80 ± 0.17	1.45 ± 0.55	0.51 ± 0.33
	Alta	0.31	0.13 ± 0.08	1.28 ± 0.34	0.91 ± 0.29	0.43 ± 0.15
	P. Outer	0.33 ± 0.07	0.09 ± 0.03	0.30 ± 0.10	1.45 ± 0.10	0.66 ± 0.27
	P. Central	0.28 ± 0.04	0.09 ± 0.03	0.48 ± 0.30	1.88 ± 0.08	0.31 ± 0.03
	P. Inner	0.26 ± 0.01	0.11 ± 0.02	0.33 ± 0.10	2.78 ± 1.42	0.28 ± 0.06

Table 3. Average number of eggs per egg sacs (± SD) in Balsfjord between October 2015 and August 2018 for *O. similis* and *M. norvegica*. The number in parenthesis is the number of observations (*n*).

Date	*O. similis*	*M. norvegica*	Reference
2015-10-29	6 (1)		This study
2016-04-19		9 ± 2 (30)	This study
2016-05-03	17 ± 6 (5)	11 ± 1 (15)	This study
2016-05-19	20 ± 4 (2)	12 ± 1 (30)	This study
2016-05-31	16 ± 6 (5)	12 ± 2 (30)	This study
2016-06-27	17 ± 4 (5)	12 ± 3 (30)	This study
2017-06-09	20 ± 9	11 ± 2	Barth-Jensen et al. (2020)
2017-06-19	23 ± 9	10 ± 3	Barth-Jensen et al. (2020)
2017-08-15	17 ± 7	9 ± 3	Barth-Jensen et al. (2020)
2018-03-01	8 ± 3		Barth-Jensen et al. (2020)
2018-03-12	9 ± 2		Barth-Jensen et al. (2020)
2018-05-03		10 ± 1	Barth-Jensen et al. (2020)
2018-06-11		12 ± 3	Barth-Jensen et al. (2020)
2018-08-24		9 ± 2	Barth-Jensen et al. (2020)

Table 4. Length (mean ± SD) and biomass of eggs and copepodids of *O. similis*, *M. norvegica*, *M. pusillus*, *C. finmarchicus* and *M. longa* measured during this study. Copepodid length was converted to carbon weight using regressions from Table S1. Egg carbon weight was taken from Barth-Jensen et al. (2020).

Species	Stage	Length (µm)	Carbon weight (µg C)
M. norvegica	Female egg sacs	524 ± 22	0.554
	Female	509 ± 18	0.536
	Male	483 ± 12	0.505
	C V - C IV	437 ± 19	0.450
	C I - C III	334 ± 42	0.330
	egg		0.015
O. similis	Female egg sacs	514 ± 23	0.678
	Female	488 ± 24	0.607
	Male	422 ± 11	0.444
	C V - C IV	395 ± 17	0.385
	C I - C III	284 ± 39	0.189
	egg		0.014
M. pusillus	Female	521 ± 21	1.598
	Male	507 ± 14	1.488
	C V - C IV	421 ± 24	0.894
	C I - C III	287 ± 46	0.314
	egg		0.019
M. longa	Female	2332 ± 114	78
	Male	1778 ± 177	34
	CV	1373 ± 250	16
	CIV	1273 ± 205	13
	CIII	987 ± 114	6
	CII	757 ± 58	3
	CI	542 ± 39	1
C. finmarchicus	Female	2839 ± 295	199
	Male	2801 ± 87	189
	CV	2499 ± 217	126
	CIV	1955 ± 191	52
	CIII	1727 ± 420	34
	CII	1122 ± 181	7
	CI	841 ± 104	3

Table S1. Length (*L*, µm) to carbon weight (*W*, µg C) conversion regressions of the copepodids CI to adults used for the secondary production calculations.

Species	Regression	Reference
O. similis	$W = 9.4676 \times 10^{-7} \times L^{2.16}$	Sabatini and Kiørboe (1994)
M. norvegica	$\ln(W) = 1.15 \times \ln(L) - 7.79$	Satapoomin (1999)
M. pusillus	$W = 6.12 \times 10^{-8} \times L^{2.7302}$	Klein Breteler et al. (1982)
C. finmarchicus	$W = 4.8 \times 10^{-3} \times L^{3.5687}$	Madsen et al. (2001)
M. longa	$W = 6.05 \times 10^{-3} \times L^{3.0167}$	Hirche and Mumm (1992)

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Figures

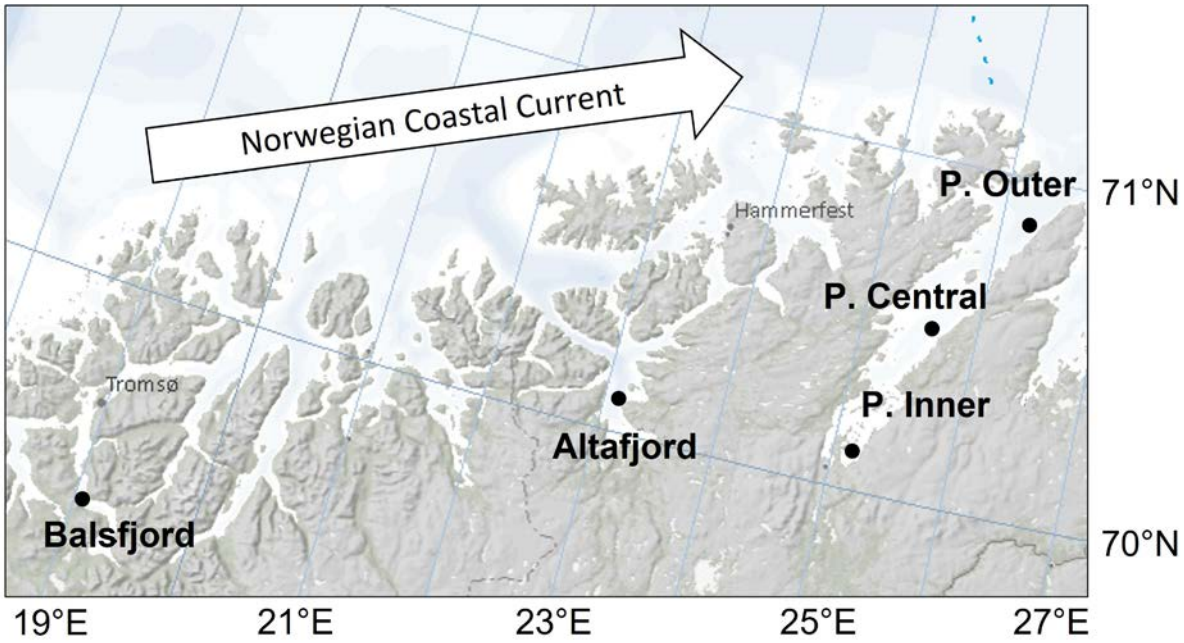

Figure 1. Location of the sampling stations in three sub-polar Norwegian fjords: Balsfjord (Svartnes), Altafjord (Alta) and Porsangerfjord (Inner, Central and Outer).

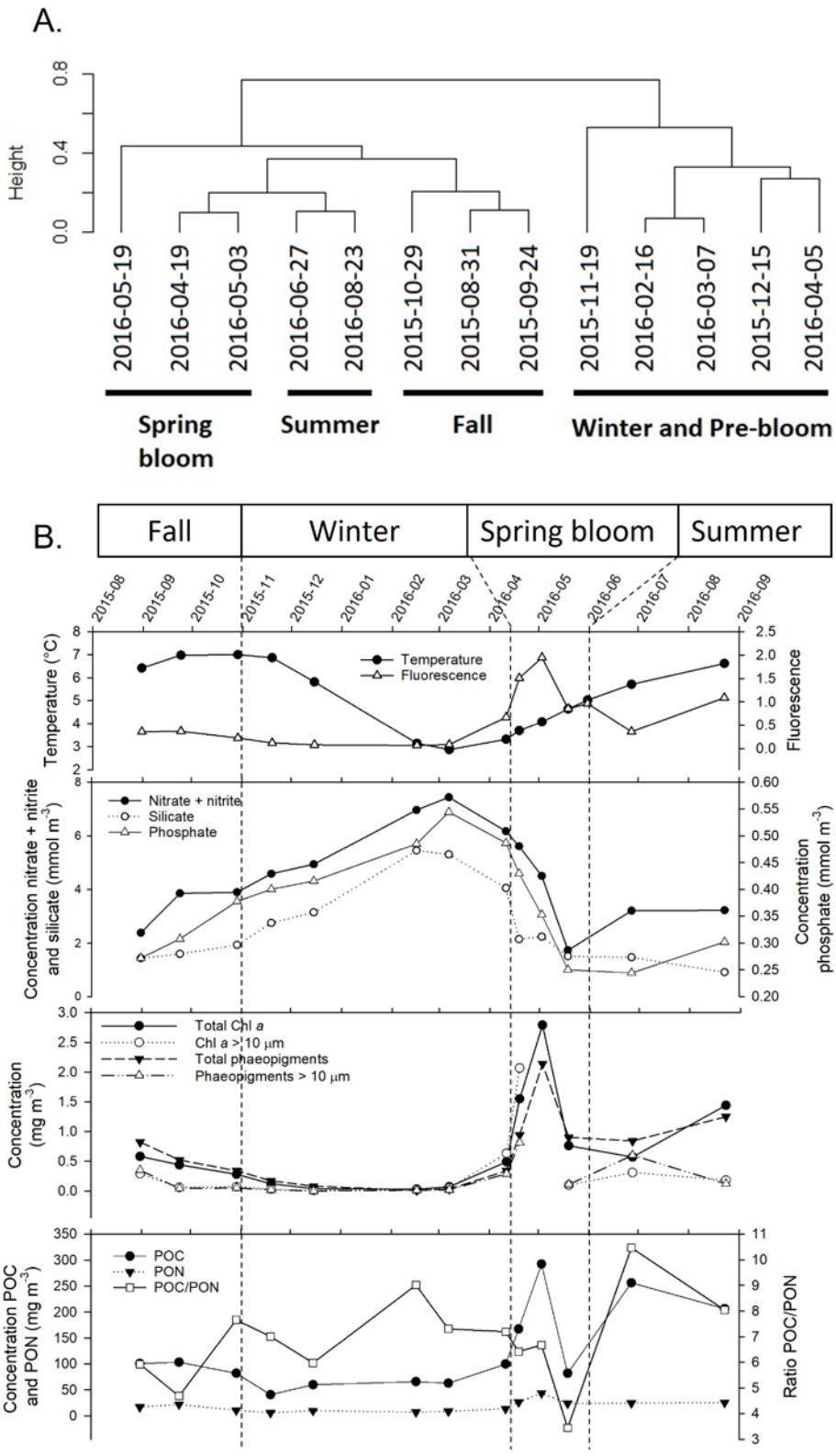

Figure 2. (A) Cluster dendrogram (based on chi-square distances) and (B) Environmental data averaged in the upper 100 m (including temperature, fluorescence, and concentrations of nitrate + nitrite, phosphate, silicate, total Chl a, Chl a ≥ 10 µm, POC and PON) at Svartnes, Balsfjord, collected during the cruises between August 2015 and August 2016. The 2016-05-31 cruise was only used for temperature and fluorescence.

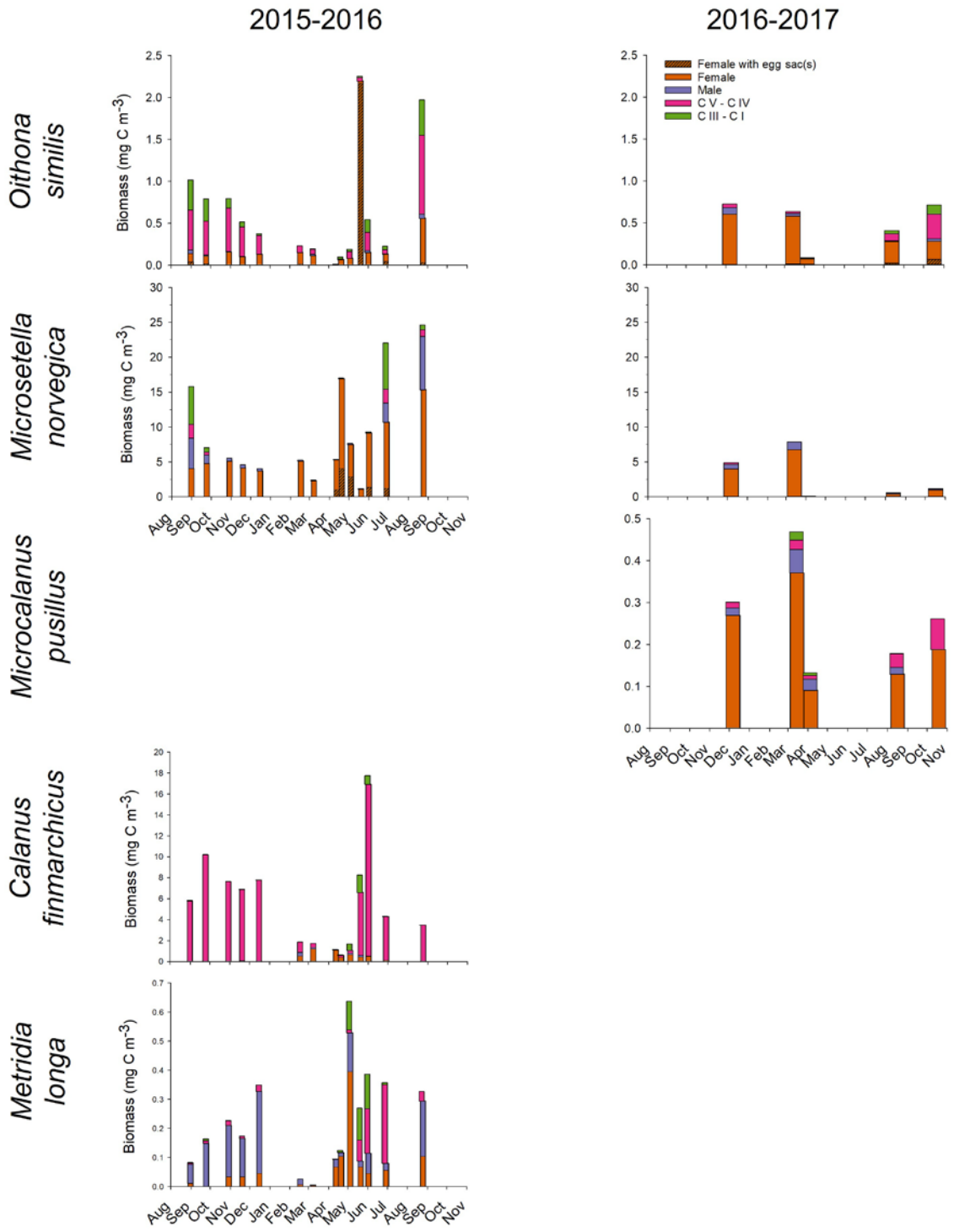

Figure 3. Biomass (mg C m^{-3}) and stage composition of *O. similis*, *M. norvegica*, *M. pusillus*, *C. finmarchicus* and *M. longa* in Balsfjord between August 2015-August 2016 (left) and December 2016-October 2017 (right). Note the difference in the biomass scale (*y*-axis) between species.

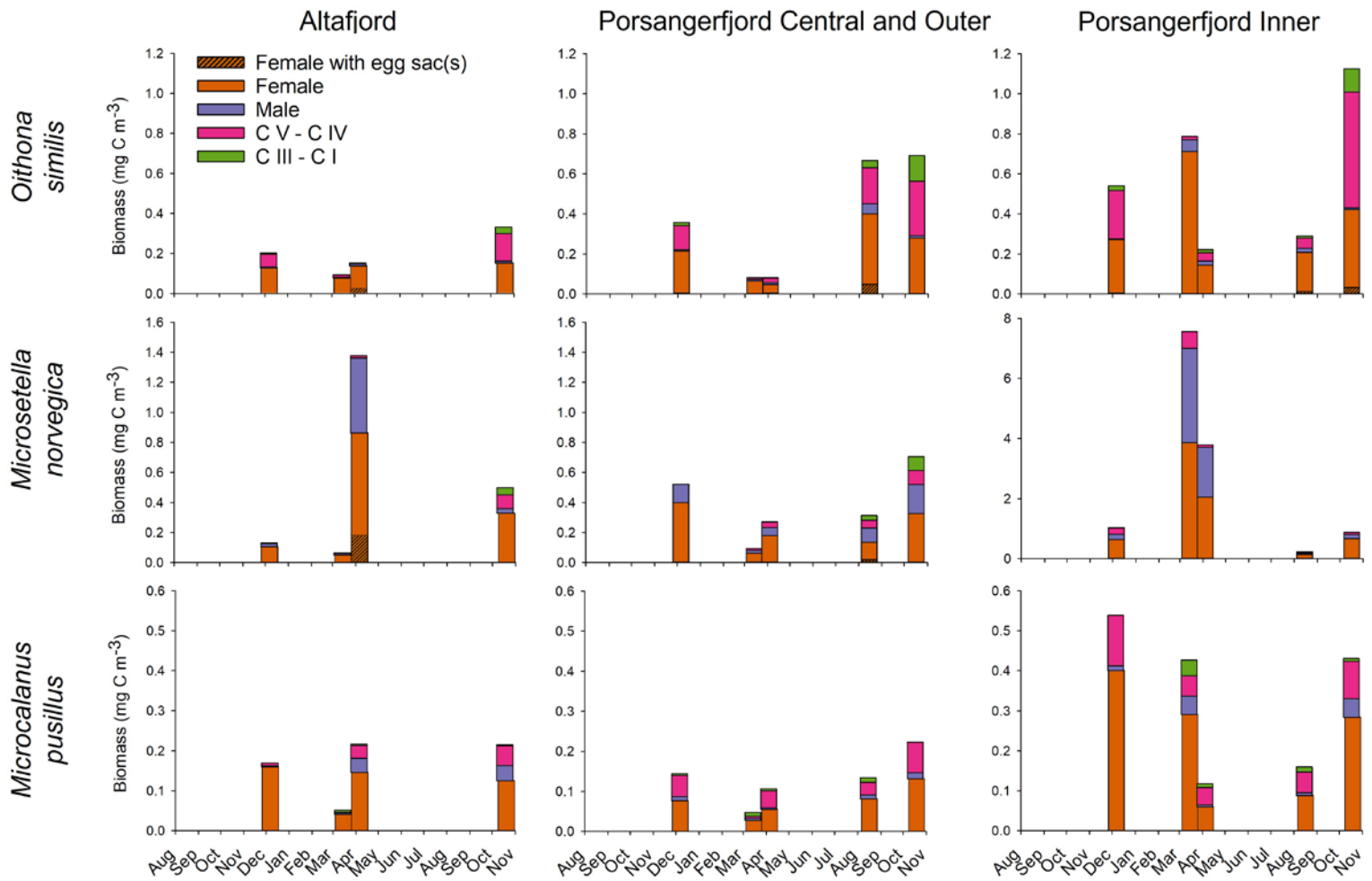

Figure 4. Biomass (mg C m^{-3}) and stage composition of *O. similis*, *M. norvegica* and *M. pusillus* in Altafjord and Porsangerfjord between December 2016 and October 2017. The biomasses of Porsangerfjord Central and Outer were averaged. Note the difference in the biomass scale (*y*-axis) between species, and for *M. norvegica* in Porsangerfjord Inner.

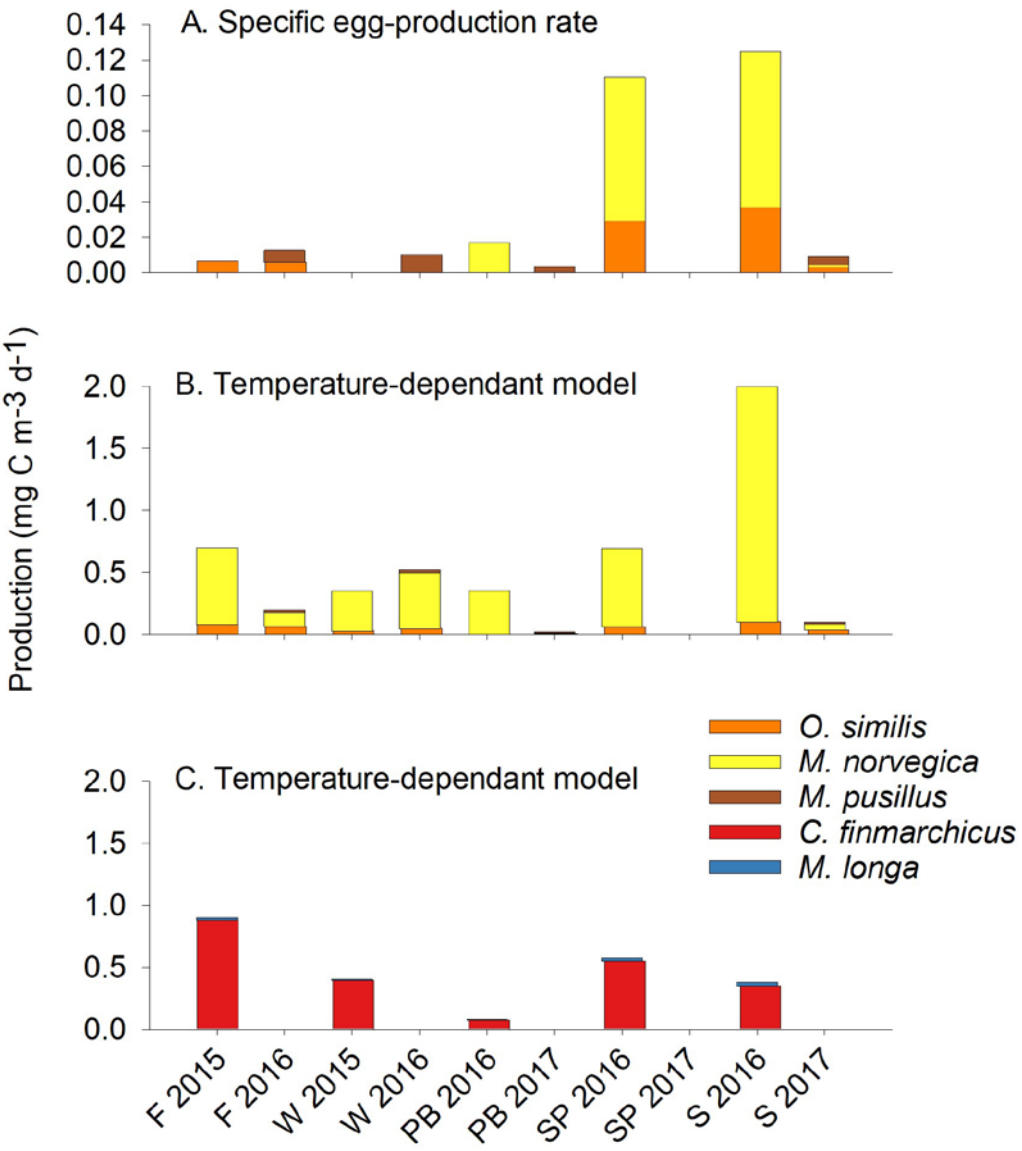

Figure 5. Daily secondary production (mg C m-3 d-1) of the copepods (A and B) *O. similis*, *M. norvegica*, *M. pusillus*, and (C) *C. finmarchicus* and *M. longa* in Balsfjord averaged for each season between August 2015 and October 2017. The production were estimated from (A) the specific egg-production rate, and (B and C) the temperature-dependent model from Huntley and Lopez (1992).

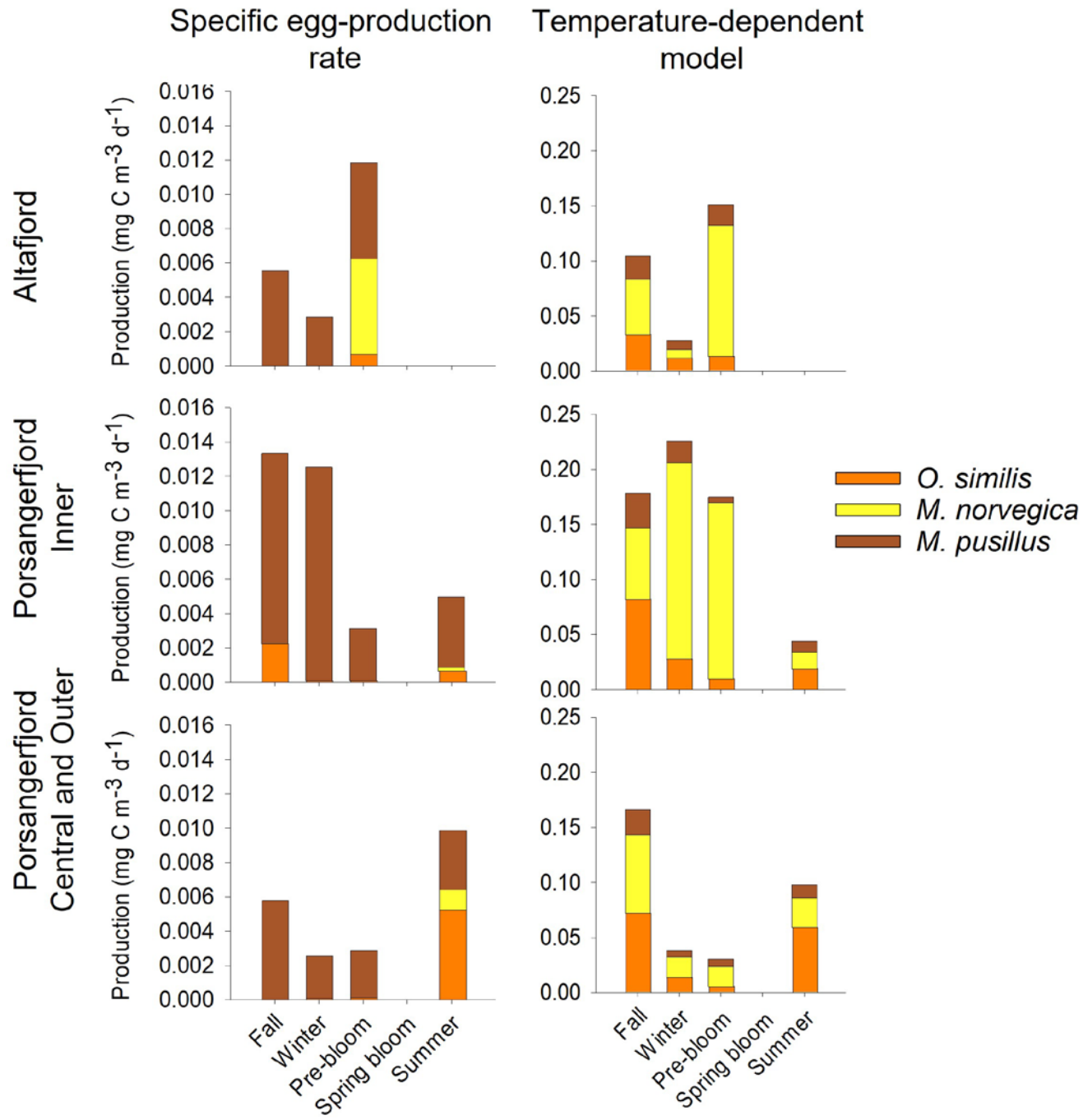

Figure 6. Daily secondary production (mg C m^{-3} d^{-1}) of the copepods *O. similis*, *M. norvegica* and *M. pusillus* in Altafjord and Porsangerfjord, averaged for each season between December 2016 and October 2017. The production were estimated from (left) the specific egg-production rate, and (right) the temperature-dependent model from Huntley and Lopez (1992).

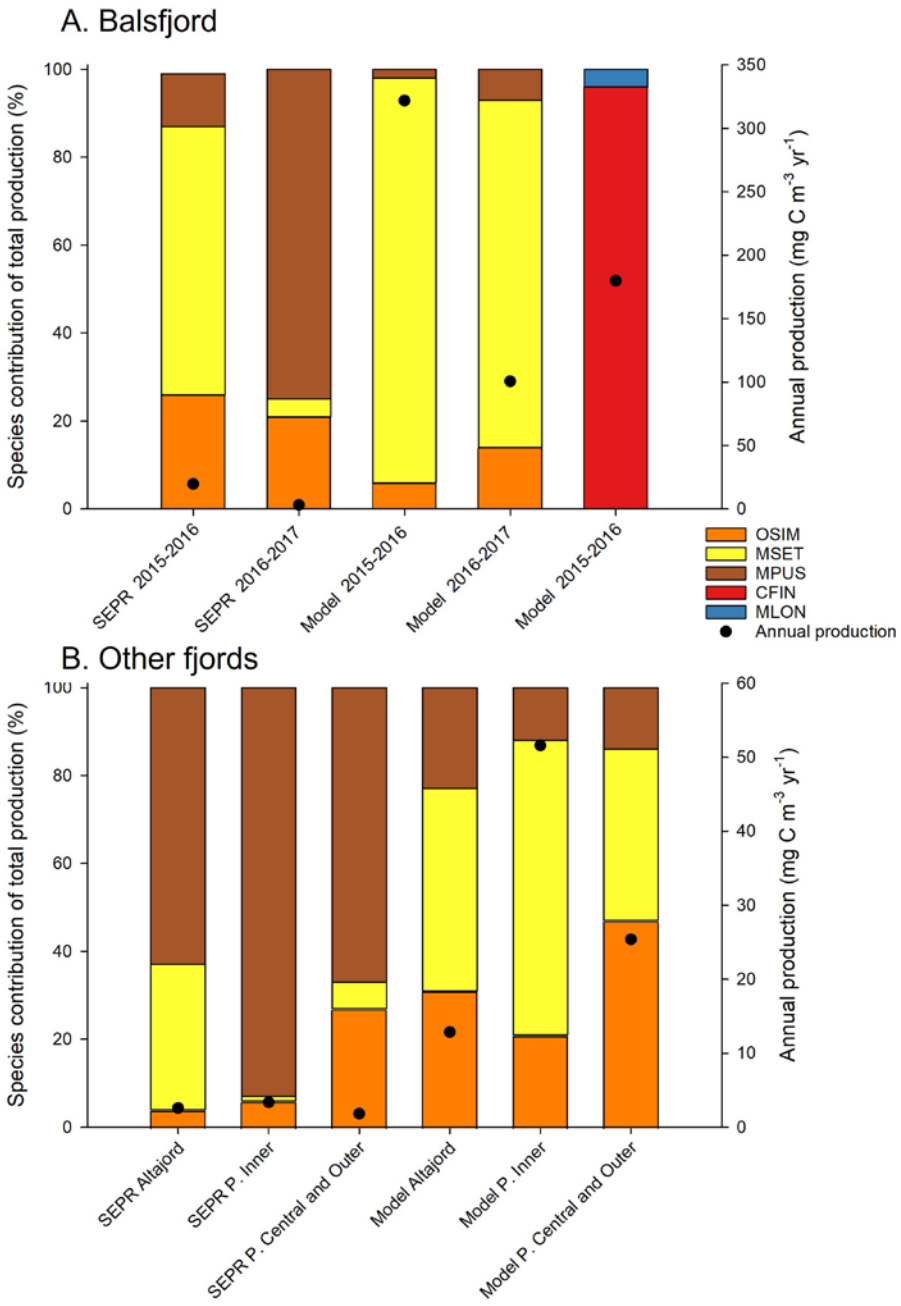

Figure 7. Annual production (mg C m^{-3} yr^{-1}, right axis) and contribution of each species to the annual production (%, left axis) for *O. similis*, *M. norvegica*, *M. pusillus*, *C. finmarchicus* and *M. longa* in (A) Balsfjord and (B) Altafjord and Porsangerfjord. Both estimation methods used are displayed: SEPR = specific egg production rate; Model = temperature-dependent model from Huntley and Lopez (1992).

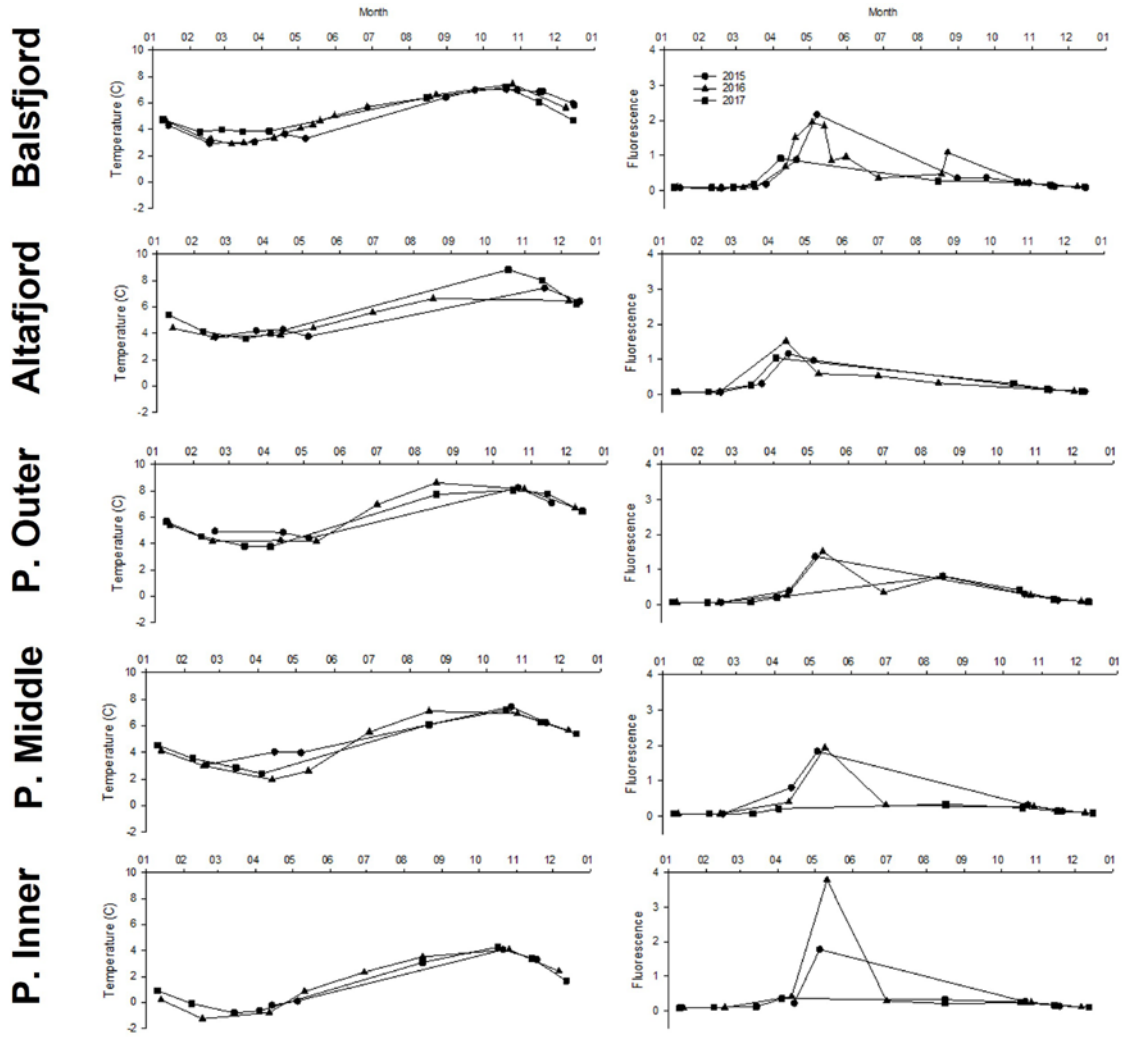

Figure S1. Temperature (°C) and fluorescence variations in Balsfjord, Altafjord and Porsangerfjord from hydrographical profiles collected between 2015 and 2017 including this studies' cruises and published datasets from the Havmiljødata monitoring program (https://dataverse.no/dataverse/nmdc).