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Aggregate-colonizing copepods in a glacial fjord: Population dynamics, vertical distribution and allometric scaling of growth and mortality rates of *Microsetella norvegica* and *Oncaea* spp.

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ABSTRACT

Most global analysis on the role of copepods in food web efficiency or carbon sequestration ignore the harpacticoid or poecilostomatoid copepods that are under-estimated in traditional zooplankton surveys and understudied with respect to their ecology and behavior. Nevertheless, when small-mesh-size nets are used these groups appear to dominate zooplankton abundance and sometimes even biomass from Arctic to tropical seas. We studied the seasonal succession of abundance, body size, vertical distribution, reproduction, growth and mortality of two aggregate-colonizing copepods, *Microsetella norvegica* and *Oncaea* spp. in a glacial fjord, to investigate the allometric scaling of their vital rates and the correlation between their reproduction, mortality and vertical distribution and environmental variables. Although both species are known to feed on marine snow, they differed in population dynamics, vertical distribution and environmental tolerance. Also, in contrast to most sac-spawning copepods, both *M. norvegica* and *Oncaea* spp. had a high specific mortality of eggs and early naupliar stages, and the allometric scaling of their egg size and growth differed from calanoid and cyclopoid copepods. Our results suggest that these non-calanoid copepods do not necessarily share the same habitat or respond similarly to the environment, and that our understanding of the allometric scaling of copepods is incomplete if we do not consider these copepod groups. *M. norvegica* and *Oncaea* spp. form by virtue of their high abundance an important part of oceanic food webs, and should be included if we are to understand the future of the ocean ecosystems.

1. Introduction

Copepods play different key roles in marine ecosystems, as a link from primary producers to fish, as recyclers of nutrients and as exporters of carbon from the surface ocean to depth (Steinberg & Landry 2017). How copepods influence these global processes is, however, dependent on the ecology and behavior of species. Recent analysis considering key traits of copepod groups and their contribution to the community revealed that different copepod communities can have a widely-variable effect on the ecosystem services, for instance on the carbon sequestration in the North Atlantic (Brun et al. 2019). Most of the global analyses, however, only consider the well-known larger calanoid copepods, ignoring the small cyclopoid, harpacticoid and poecilostomatoid copepods that pass the traditionally-used 200 μm zooplankton nets and are thus under-estimated in the most zooplankton surveys (Turner 2004).

Pelagic harpacticoid *Microsetella norvegica* and poecilostomatoid oncaeid copepods such as *Oncaea* spp. and *Triconia* spp. are abundant copepod species, which have some common features that distinguish them from most calanoid and cyclopoid copepods. First, they have a low activity level resulting in a relatively-low metabolic rate (Paffenhöfer 2006, Nishibe & Ikeda 2008). Second, their success in obtaining high abundance appears to be due to a low mortality, rather than a high reproductive rate (Paffenhöfer 1993). Third, their consumption rates are low, and their diet mainly consists of other particles rather than suspended phytoplankton (Alldredge 1972, Turner 1986) and the size range of their food might therefore deviate from the typical predator–prey size ratio in pelagic food webs. Fourth, size-specific scaling of their metabolic rates, such as egg size or respiration rate, appears

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different from calanoid and cyclopoid copepods (Böttger-Schnack & Schnack 2005, Nishibe & Ikeda 2008), although only a few measurements exist to verify this.

Both *Microsetella norvegica* and *Oncaea* spp. can be extremely abundant in widely-varying environments. For instance, *M. norvegica* can dominate the zooplankton abundance and / or biomass as well in the subtropical Sea of Japan (Uye et al. 2002) as in arctic and sub-arctic fjords (Arendt et al. 2010, Svensen et al. 2019) and the northwest Atlantic (Dugas & Koslow 1984). *Oncaea* spp. is abundant in subarctic Pacific Ocean (Nishibe & Ikeda 2004), Arctic Ocean (Kosobokova & Hirche, 2000), tropical Red Sea (Böttger-Schnack & Schnack 2005) and Andaman Sea (Satapoomin et al. 2004), among other places. Despite this, only a handful of studies exist on their population dynamics and reproduction. These studies suggest that the reproduction of *M. norvegica* is restricted to summer (Uye et al. 2002, Svensen et al. 2018, Barth-Jensen et al. 2020), while the sub-arctic oncaeids have low but continuous reproduction throughout the year (Nishibe & Ikeda 2007). The reproduction and growth of *M. norvegica* appear to be controlled by temperature (Uye et al. 2002, Barth-Jensen et al. 2020), while no correlation has been shown between *Oncaea* spp. reproduction and temperature, possibly because oncaeid copepods include > 100 species (World Register of Marine Species), which not only inhabit different geographic locations, but also different depth layers (Nishibe & Ikeda 2004 & 2007).

General concepts of reproductive traits of copepods have been developed without information from oncaeids (Böttger-Schnack & Schnack 2005) or *Microsetella norvegica*, and the global models on copepod mortality, reproduction, growth or development rates typically do not include representatives from these important groups (Kiørboe & Sabatini 1995, Hirst & Bunker 2003, Bunker & Hirst 2004, Kiørboe & Hirst 2014). As a consequence, we do not know if the relationships between the vital rates and body size, temperature and chl-*a* typically observed for calanoids and cyclopoids are also valid for these groups. The one existing study on the reproductive traits of oncaeids (Böttger-Schnack & Schnack 2005) does not suggest so. These species are also not represented in trait-based models describing global copepod distribution, its future changes, or the effect of copepods on ecosystem services (Brun et al. 2019). This is problematic, taking into account that the size structure of the copepod community is expected to change (decrease) in relation to increasing temperature and chl-*a* concentration (Rice et al. 2015, Balazy et al. 2018, Svensen et al. 2019), and that *M. norvegica* and *Oncaea* spp. play an important role in the degradation of marine snow (Alldredge 1972, Ohtsuka et al. 1993, Green & Dagg 1997) and therefore in the efficiency of the global carbon pump (Sanders et al., 2014).

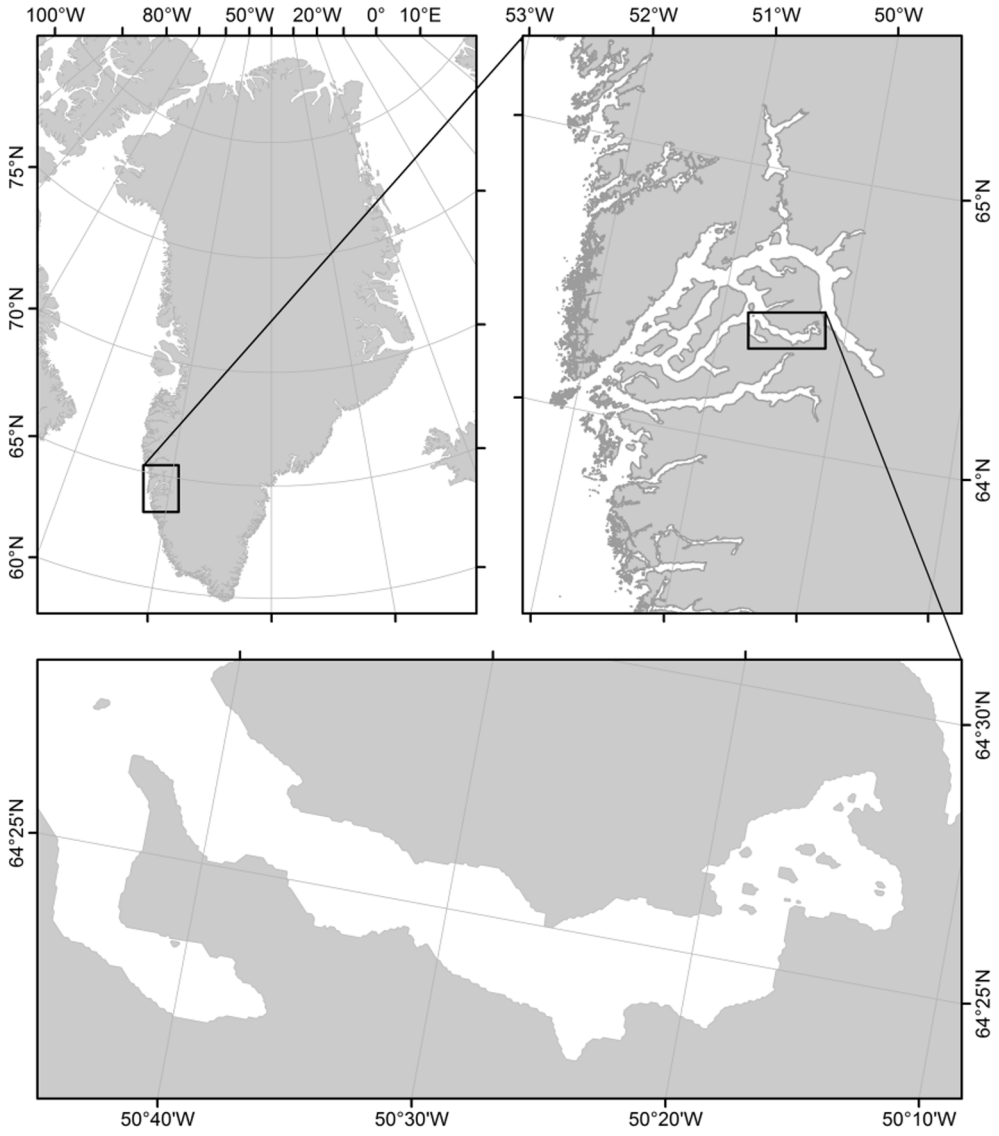

Fig. 1. The map of the study area, showing the four sampling stations in the fjord branch Kapisigdlit in West Greenland.

Here we analyzed the seasonality in development of vertical distribution, abundance, body size, reproduction, growth rate and mortality of *Microsetella norvegica* and *Oncaea* spp. spp. in a glacial fjord, to 1) compare the succession and environmental control of these groups and 2) establish the allometric scaling of their egg size, growth and mortality rates. Our results shed light on the importance of these species in the arctic ecosystem both now and in the future, and provide insights into their traits and size-specific rates that can be used in modelling zooplankton community composition and its effect on ecosystem services such as carbon sequestration.

2. Material and methods

2.1. Sampling

Sampling was conducted from March 24 to August 5, 2010, in the fjord branch Kapisigdlit located in the inner part of the Godthåbsfjord system, West Greenland (Fig. 1; Mortensen et al. 2011). Sampling was conducted onboard the vessel *Lille Masik*, a small tugboat modified to carry out scientific work, except for 16-18th July when sampling was conducted onboard the *R/V Dana* (National Institute for Aquatic Resources, Denmark). Sampling was carried out every 7 to 10 days along a transect spanning the length of the 25 km long fjord branch (Fig. 1), resulting in 15 cruises. The transect was composed of 6 designated stations, 4 of which were used in the present study; namely Stations 2, 4, 5 and 6 (Table 1). Station 2 was located close to the mouth of the fjord branch while Station 5 was located on the slope leading up to a shallow inner creek at the end of the fjord branch in which Station 6 was positioned (Fig. 1). Station 4 was located on an old monitoring station used by Smidt (1979) in the middle of the fjord. On every third cruise (6 times during this study) the main station, Station 4, was sampled for 24 h at 6:00, 12:00, 18:00 and 00:00 while on the other cruises hydrography and mesozooplankton sampling were carried out at 18:00 local time. At Stations 2, 5 and 6 the exact timing of the sampling varied between cruises.

Table 1
Sampling stations, their coordinates and maximum depths (m), sampling depths, sampled parameters and gear used. All stations were sampled 14–15 times between March 24th and August 5th; every third cruise on Station 4 included sampling at dawn, dusk, day and night. Sampling depths for WP2 are indicated in italics, whereas the other depths indicate sampling by Multinet.

Station	Position	Max. depth	Sampling depth	Variables	Gear
2	64° 26 N, 50° 39 W	180	*0–100*; [1]0–50, 50–100, 100–150	Hydrography, mesozpl	CTD, Multinet, WP2
4	64° 25 N, 50° 22 W	240	[2]0–50, 50–100, 100–150, 150–200, 200–235	Hydrography, Chl-*a*, mesozpl, protozoans	CTD, Multinet
5	64° 25 N, 50° 18 W	120	*0–75*; [3]0–50, 50–100	Hydrography, mesozpl	CTD, Multinet, WP2
6	64° 26 N, 50° 15 W	80	*0–50*; [4]0–10, 10–20, 20–30, 30–40, 40–50	Hydrography, mesozpl	CTD, WP2, Multinet

[1]Sampling in 3 depth strata on 24.3., 22.4., 18.5., 17.6. and 6.7.
[2]Sampling on 18.6. at 25-m intervals (10 depth strata)
[3]Sampling in 2 depth strata on 22.4., 18.5., 17.6. and 6.7.
[4]Sampling in 5 depth strata on 10.5., 24.5. and 3.6.

2.2. Hydrography and chlorophyll-a

On every cruise, vertical distributions of salinity and temperature were recorded using a Seabird CTD (SBE 19 plus). Casts were done down to approximately 10 m above the sea floor. In addition, at Station 4, water samples were taken for chlorophyll-*a* analysis at eight depths: 1, 10, 20, 50, 75, 100, 150 and 250 m, using a Niskin sampler. Water samples for chl-*a* were carefully filtered and size fractionated into total (Whatman GF/F) and > 10 μm (10 μm mesh sized nylon net) filters. Chl-*a* was extracted for 12–24 h in 96% ethanol, and measured using a Turner TD-700 fluorometer (Riisgaard et al. 2014).

2.3. Population dynamics and vertical distribution

At Station 4, mesozooplankton was sampled from five depth layers using a Hydrobios Multinet (type Mini, opening 0.25 m^2) equipped with 50 μm mesh nets. At other stations the Multinet was used for depth-resolved samples on 3–5 sampling dates, while a WP-2 net (opening 0.28 m^2) with a 50 μm mesh size equipped with a non-filtering cod-end was used at other times (Table 1). On one occasion (3rd June) the WP-2 net was towed at an angle of 30-45° due to bad weather conditions; as the sampling volume was unclear, the abundance data on this date was omitted. All nets were hauled with a speed of 0.2–0.3 m s^{-1}. The sampled volumes were calculated by multiplying the opening area of the net with the distance that the net was hauled. Samples were preserved in buffered formalin (4% final concentration) immediately after recovery of the nets.

Samples containing high numbers of copepods were split into subsamples using a splitter. In each sample, approximately 400 individuals were counted (all mesozooplankton species), which resulted in 9–116 counted individuals of *Microsetella norvegica* and 3–124 of *Oncaea* spp. in each sample. However, as we mostly used depth-integrated abundances, population dynamics, size, and reproduction and mortality rates are based on several samples (Table 1), generally resulting in > 60 individuals in each development stage. Both copepods were divided into development stages, but *Oncaea* spp. was not determined to species level. In reality, *Oncaea* spp. is also likely to include the genus *Triconia*, as the species *Triconia borealis* was identified from the Godhåbsfjord samples in 2011 (Maria Grazia Mazzocchi, pers. com.). For simplicity, we will in following sections refer to all oncaeid copepods as *Oncaea* spp. All samples were analyzed in the Plankton Sorting and Identification Center in Szczecin (www.nmfri.gdynia.pl), using the identification key of Hirakawa (1974) for *M. norvegica*. Abundances of eggs, NI and females of *M. norvegica* in selected dates during the spawning season have been previously presented in Koski et al. (2014).

Vertical distribution of copepods was expressed as the weighted mean depth (WMD), which is calculated by multiplying the numbers of individuals at each depth layer (n_i; ind. m^{-3}) with its average depth (d_i), divided by the sum of all individuals (Bollens and Frost 1989):

$$\mathrm{WMD} = \frac{\Sigma n_i d_i}{\Sigma n_i} \quad (1)$$

2.4. Body size

Prosome (*Oncaea* spp.) or total (*Microsetella norvegica*) length was measured for 10 individuals of each naupliar and copepodite stage when sufficient numbers of individuals were present, with a 6 μm resolution. Carbon weights of nauplii, copepodites and adults were calculated from the length measurements according to the carbon-to-length regressions of Uye et al. (2002) for *M. norvegica* and Satapoomin (1999) for *Oncaea* spp. For comparison, the carbon weights of female stages were also estimated based on the average length to weight ratio of *M. norvegica* in a sub-arctic fjord (Svensen et al. 2018, Barth-Jensen et al. 2020) and on the average length to weight ratio of three similar-sized *Oncaea* species in sub-Arctic sea of Japan (Nishibe & Ikeda 2007 & 2008; Table A.1).

Egg-carbon content of *M. norvegica* was estimated to be 0.018 ± 0.002 μg C egg^{-1}, based on the egg diameter of 46 ± 6 μm and carbon content of *M. norvegica* eggs as in Uye et al. (2002), corrected for size. Egg-carbon content of *Oncaea* spp. was estimated to be 0.011 ± 0.001 μg C egg^{-1}, based on the female size and egg to female size ratio of 0.008 (Böttger-Schnack & Schnack 2005; Table A.1).

2.5. Reproduction and growth

In addition to developmental stages, females carrying eggs and free-egg sacs were identified and counted in the samples, as was the number of eggs per egg-sac (10 egg-sacs per sample). Egg production was calculated using the egg-ratio method (Edmondson and Winberg, 1971), by multiplying the average number of eggs per clutch (N_{eggs}) with the depth-integrated number of egg-sacs (N_{clutch}; m^{-2}), divided by the depth-integrated number of females (N_f; m^{-2}) and the temperature-specific development time of eggs (D_{eggs}).

$$Ep = \frac{N_{eggs}N_{clutch}}{N_f D_{eggs}} \quad (2)$$

Only few measurements exist on the embryonic development times of *Microsetella* or *Oncaea*, and using the functions determined for the temperate or sub-tropical species (Uye et al. 2002) result in indefinitely-long development times at the present low temperatures. Therefore, we estimated the development times using the equations from McLaren et al. (1969) and Nielsen et al. (2002) for, respectively, *Eurytemora hirundoides* and *Pseudocalanus minutus*, and *Oithona similis*, and used the average of the three obtained rates (Table A.1). Weight-specific egg production was calculated by multiplying the egg production with the egg carbon weight, divided with the female carbon weight. Clutch size and weight-specific egg production rates of *Microsetella norvegica* have been previously presented in Koski et al. (2014).

The weight-specific growth rates were calculated assuming exponential growth, from the increase in carbon weight (based on the length) between successive stages and the estimated temperature-dependent development times for each stage. The juvenile development times have not been estimated for arctic or subarctic *Microsetella norvegica* or *Oncaea* spp. To estimate the development times of different stages we first calculated the total post-embryonic development times based on two studies on other sac-spawning copepods that included low (≤5 ℃) temperatures (McLaren et al. 1989, Lee et al. 2003). Then, we averaged these two development times, and estimated the development time for each development stage based on the proportional lengths of stages according to Uye et al. (2002; Table A.1). For females, the weight-specific egg production was used as a growth rate, while males were assumed to grow (or produce spermatophores) at a rate similar to the average growth of the copepodite stages I-V.

2.6. Mortality

Mortality was calculated using the vertical life-table approach as presented in Hirst & Ward (2008). To calculate the egg mortality, we used the equation from Mullin & Brooks (1970):

$$\frac{exp^{\beta D_{egg}} - 1}{1 - exp^{-\beta D N_1}} = \frac{N_{egg}}{N_{NI}} \quad (3)$$

where β is the specific mortality of egg-NI (d^{-1}), D_{egg} is the development time of eggs (days; estimated as above), D_{NI} is the development time of NI, and N_{egg} and N_{NI} are the depth-integrated abundances of eggs and NI (ind. m^{-2}), respectively. The egg mortality was estimated by iteration. The mortalities of nauplii and copepodite stages up to CIV-CV were calculated similarly to egg mortality.

To calculate the female and male mortality we used the equation from Aksnes and Ohman (1987):

$$\beta = \frac{ln\left(\frac{N_{CV}}{N_{F/M}} + 1\right)}{D_{CV}} \quad (4)$$

where N_{CV}, N_F and F_M are the depth-integrated abundances (ind. m^{-2}) of copepodite stage 5, females and males, respectively, and D_{CV} is the development time of copepodite stage 5. To get the mortality of each sex we assumed that the 5th copepodite stage had a sex ratio of 1:1, although this assumption is not necessarily correct (Gusmão et al. 2013). Mortality rates of females and eggs of *Microsetella norvegica* have been previously presented in Koski et al. (2014).

2.7. Biomass and secondary production

Depth-integrated biomass of *Microsetella norvegica* and *Oncaea* spp. were estimated from the depth-integrated numbers of individuals multiplied by the average carbon weight of each stage. The secondary production was estimated by multiplying the biomass of each stage by their weight-specific growth rates.

2.8. Statistics

The clutch size and body size of both species were tested for differences between the sampling dates using a one-way analysis-of-variance (ANOVA). The sex ratio, proportion of spawning females and egg production rate were tested for differences between the sampling months with a one-way ANOVA, after pooling the data within each month. The tests were run for the data from Station 4 only, since the abundance of females in the other stations was variable and often low. Two-way ANOVA was used to test for the differences in the daily specific mortality between species and life-stages, after pooling the data from the four stations. A Tukey HSD test was used for all pairwise comparisons. If the assumptions for the ANOVAs were not met (normality and equal variances), the data were square-root transformed, or Kruskal-Wallis one-way ANOVA, followed by Dunn's test, were used. Spearman rank order correlation analysis was used to 1) test for correlations between egg and nauplii abundances, proportion of spawning females, clutch size, female size, sex ratio, average temperature and salinity in the weighted mean depth of females and average chl-*a*, and 2) test for correlations between stage-specific mortality, average temperature and salinity in the weighted mean depth of stages, average chl-*a* and chl-*a* > 10 μm, depth-integrated abundance of late copepodite and adult stages (CIV-VI) and depth-integrated abundance of large calanoid copepods.

In addition, allometric scaling of weight-specific growth and daily specific mortality were tested by linear regressions, after $\log_{10}$ transformation of the growth and mortality rates and body sizes (in carbon). Correlations between weight-specific growth rates of different stages (including reproduction) and chl-*a* were tested by linear regressions, as were the correlations between the ratio of the abundance of NI to F and temperature. NI to F was used as an indication of reproduction / growth, since the calculations of growth and reproduction rates included temperature-dependent development times and were therefore not independent of temperature.

3. Results

3.1. Hydrography and chl-a

In late March when sampling was initiated, the water column was well mixed along the fjord with cold, saline, nutrient-rich water throughout the euphotic zone (Fig. 2). The chl-*a* concentration was relatively low (0.5–1 μg Chl-*a* L^{-1}) and evenly distributed in the upper 40 m. In late April a weak halocline established, and additional heat was trapped in the surface layer. The stratification stimulated the phytoplankton growth that depleted the nitrate to < 0.5 μM (Riisgaard et al.

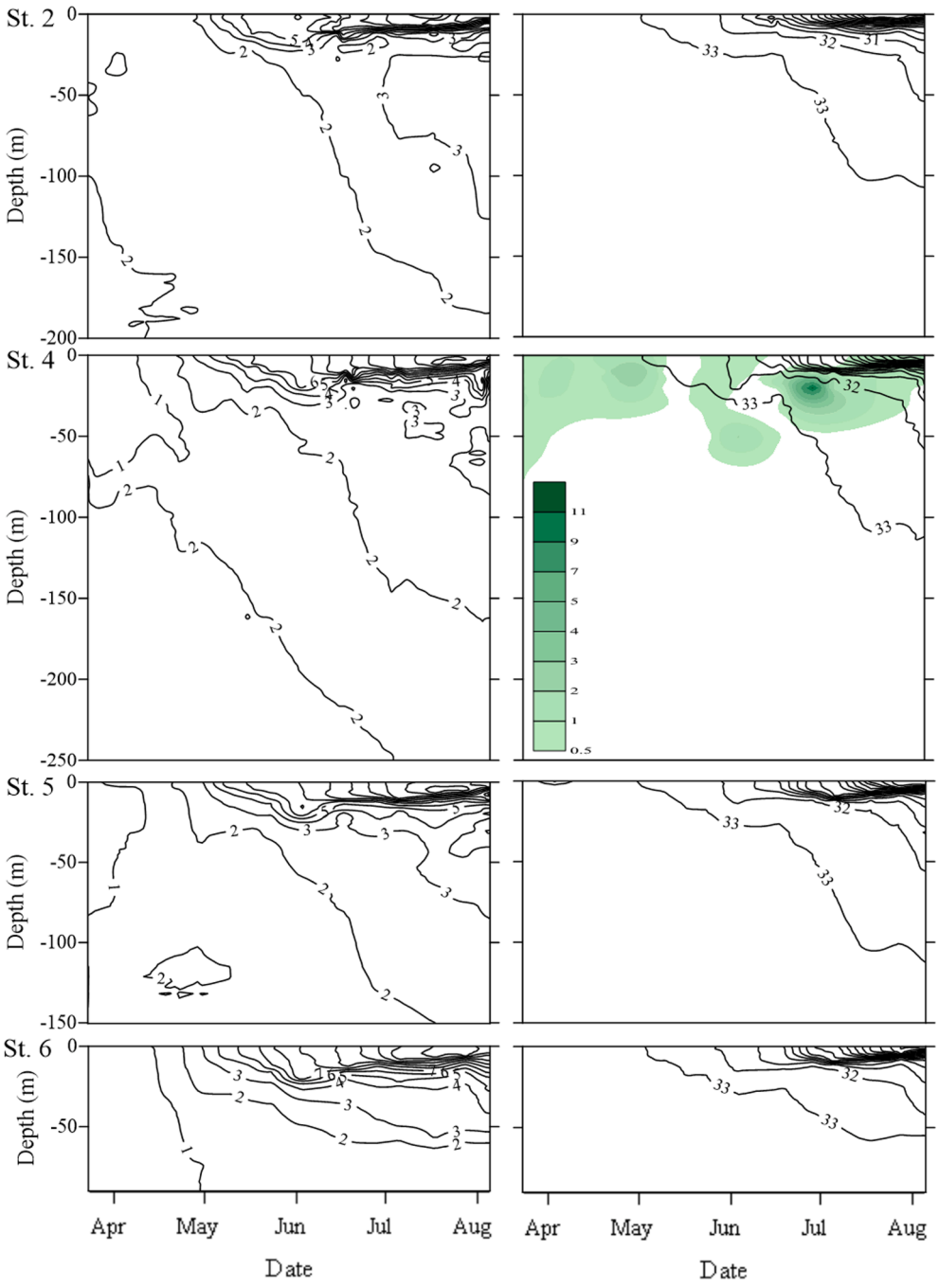

Fig. 2. Vertical distribution of temperature (left panel), salinity (right panel) and chl-*a* (only Station 4; green color shading) at Stations 2, 4, 5 and 6 from March to August.

2014), in association with the peak of the first bloom at 3 μg Chl-*a* L^{-1} (Fig. 2).

During May and the first part of June, melt water was added to the surface layer from the runoff from land, succeeded by a seasonal pulse of freshwater discharge in association with the ice breakup of the Kapsidglit River around June 20th. Hereafter the surface salinity rapidly decreased from 31 to 16 ppm in the beginning of August. The melt water established a strong halocline, strengthened by a thermocline caused by warming of the brackish surface plume that reached > 13 °C on the last sampling of August 5th. After the depletion of nitrate above the pycnocline, a subsurface bloom developed that peaked at 12 μg Chl *a* L^{-1} on June 26th (Fig. 2).

3.2. Population dynamics and vertical distribution

In late March at the time of the first sampling, most of *Microsetella norvegica* population consisted of late copepodite stages or adults (Fig. 3a) that resided at a depth of > 150 m (Fig. 4a). In April-May the weighted mean depth of the population decreased (Fig. 4a), with the simultaneous strong decrease in the numbers of late copepodites and adults, particularly at Station 4 (Fig. 3a). From May to July most individuals remained in the upper 25 m (Fig. 4a), where the peak abundances of eggs, early and late naupliar stages and early and late copepodite stages followed each other in June-July (Fig. 3a). The abundance of adult stages increased again in the beginning of August (Fig. 3a), concurrent with a slight indication of increasing weighted

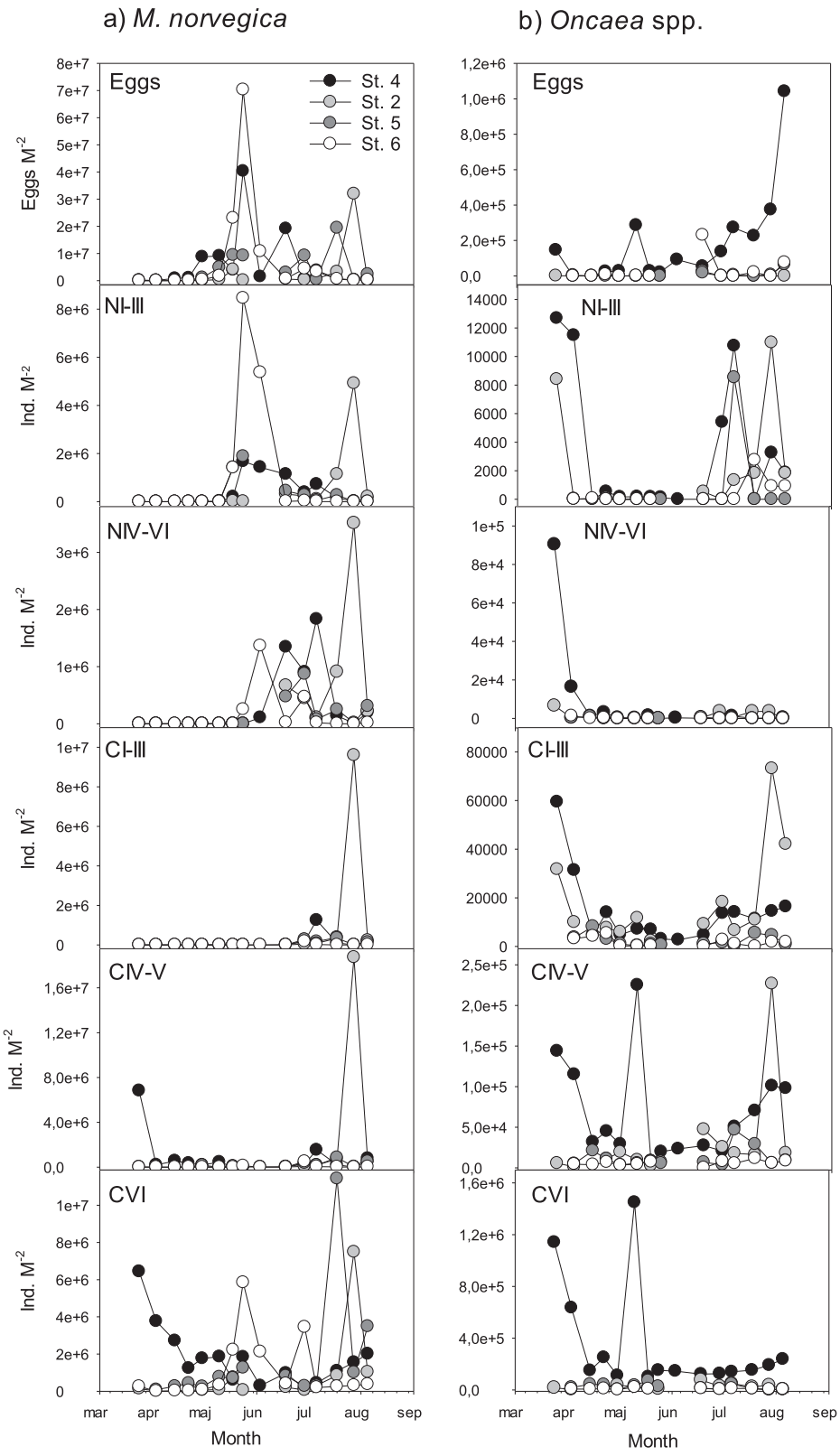

Fig. 3. Seasonal changes in the depth-integrated abundances of eggs, naupliar stages I-III and IV-VI, copepodite stages I-III and IV-V, and adults (ind. m^{-2}) of a) *Microsetella norvegica* and b) *Oncaea* spp. at the four stations. Note different scales of the egg and nauplii abundances.

mean depth (Fig. 4a). It thus appeared that *M. norvegica* reproduced while residing close to the surface, whereas the dominance of late copepodite and adult (mainly female) stages and the deep weighted mean depth of the population in early spring indicated overwintering at depth in these life stages. Although this development was clearest at station 4, the early nauplii were restricted to the period after mid-May and the early copepodites to the period after mid-June at all stations, supporting the observation of a relatively-restricted reproductive

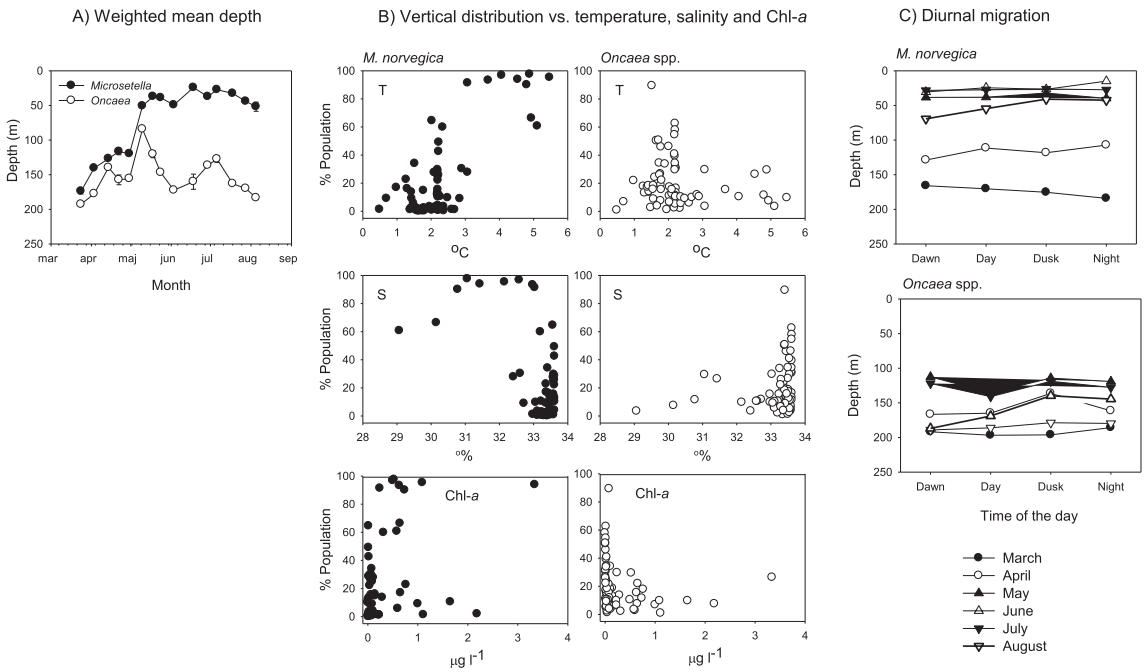

Fig. 4. A) Seasonal changes in weighted mean depth (m) of *Microsetella norvegica* (solid circles) and *Oncaea* sp. (open circles) at station 4, (B) vertical distribution (% population) of both species as a function of temperature (T; ℃), salinity (S) and chl-*a* concentration (µg L^{-1}) and (C) diurnal changes in the weighted mean depth of both species. The diurnal changes in weighted mean depth are based on the 6 sampling times with four daily samples (see Methods); the error bars in (A) represent the standard error of four diurnal samples.

period.

Similar to *Microsetella norvegica*, the *Oncaea* spp. population in early spring consisted mainly of adults (Fig. 3b), located below 150 m (Fig. 4a), although eggs, nauplii and copepodites were also present in low numbers (Fig. 3b). However, the population development was less clear than that of *M. norvegica*. Although first eggs appeared at the start of May, the numbers of nauplii and copepodites remained low throughout the summer, and the numbers of eggs only increased substantially in late summer (Fig. 3b). The occasional peak abundances of early nauplii and copepodites at Station 2 in early August were more likely due to advection events than the population dynamics, particularly since the abundances of all life-stages of *M. norvegica* had a similar peak at the same date (Fig. 3). After an initial decrease in the weighted mean depth of the population to ca. 100 m in April, the weighted mean depth of the population increased back to 150–200 m in June-August (Fig. 4a). This was mainly due to the adult stages residing in deeper waters, while nauplii and copepodites remained closer to the surface (Fig. A.1).

The vertical distribution of *M. norvegica* appeared to be connected to temperature, with the highest proportion of the population observed at the highest temperature (Fig. 4b), probably reflecting the upward migration at the time of the developing thermocline. In contrast, temperature did not influence the vertical distribution of *Oncaea* spp., and neither salinity nor chl-*a* had any effect on the vertical distribution of either of the species. However, it appeared that a low salinity of 29 did not have a negative influence on the distribution of *M. norvegica*, while *Oncaea* spp. rarely occurred at the salinities < 33 (Fig. 4b). While *M. norvegica* did not perform a daily vertical migration at any of the sampling times, the vertical distribution of *Oncaea* spp. seemed to be shallower at dusk and / or at night than during the day, particularly in late spring and early summer (Fig. 4c).

3.3. Seasonal changes in body size

Changes in body size suggested that several generations of *Microsetella norvegica* were present during the year (Fig. 5a). The CV copepodites and adults in early spring (25.3.-14.4.) and late summer (18.7.-5.8.) were significantly larger than the same life-stages during most sampling times between late April and mid July (Kruskal Wallis ANOVA; $H_{12} = 279$ for CV, $H_{14} = 418$ and 278 for F and M, respectively, $p < 0.001$; Dunn's method, $p < 0.05$), with exceptions of 24.5. and 29.6. when the average size of copepods was similar to early spring and late summer individuals. The body size indicated two generations: Large individuals in March-April potentially representing the overwintering generation, small individuals in May-July representing the summer generation and large individuals in late summer potentially providing the next overwintering generation (Fig. 5a).

Also, *Oncaea* spp. body size changed significantly between the months (Kruskal-Wallis ANOVA; $H_{14} = 176$, 186 and 125 for CV, F and M, respectively; $p < 0.001$; Fig. 5b). Similar to *Microsetella norvegica*, larger individuals were typically observed in spring (13–14.4.) and late summer (18.7.-5.8.) and smaller individuals in most dates in-between, although the differences were smaller, and not always consistent between the life-stages. For instance, whereas the females in late summer were significantly larger than the females in May-June (Dunn's method; $p < 0.05$), size of CV did not differ between the early and late summer (Fig. 5b).

With both species, the length of the first naupliar stage was typically related to the size of the females, with an average NI: female size ratio of 0.3 ± 0.01 for *Microsetella norvegica* and 0.2 ± 0.01 for *Oncaea* spp. (Fig. 5), irrespective of the season. If both NI and female sizes were expressed as carbon, the NI: female size ratio was 0.11 ± 0.01 for *M. norvegica* and 0.012 ± 0.004 for *Oncaea* spp.

3.4. Reproduction and growth

The sex ratio of *Microsetella norvegica* varied over the months, but females always dominated the population, with the average F: M ratios increasing from 4.3 ± 2.6 in March-April to 7.5 ± 6.7 in May-June and 17.5 ± 22.6 in July-August (mean $\pm$ SD of all the stations). The F: M ratios at Station 4 were lower and more stable than in the other stations where the variation between the dates increased later in the season

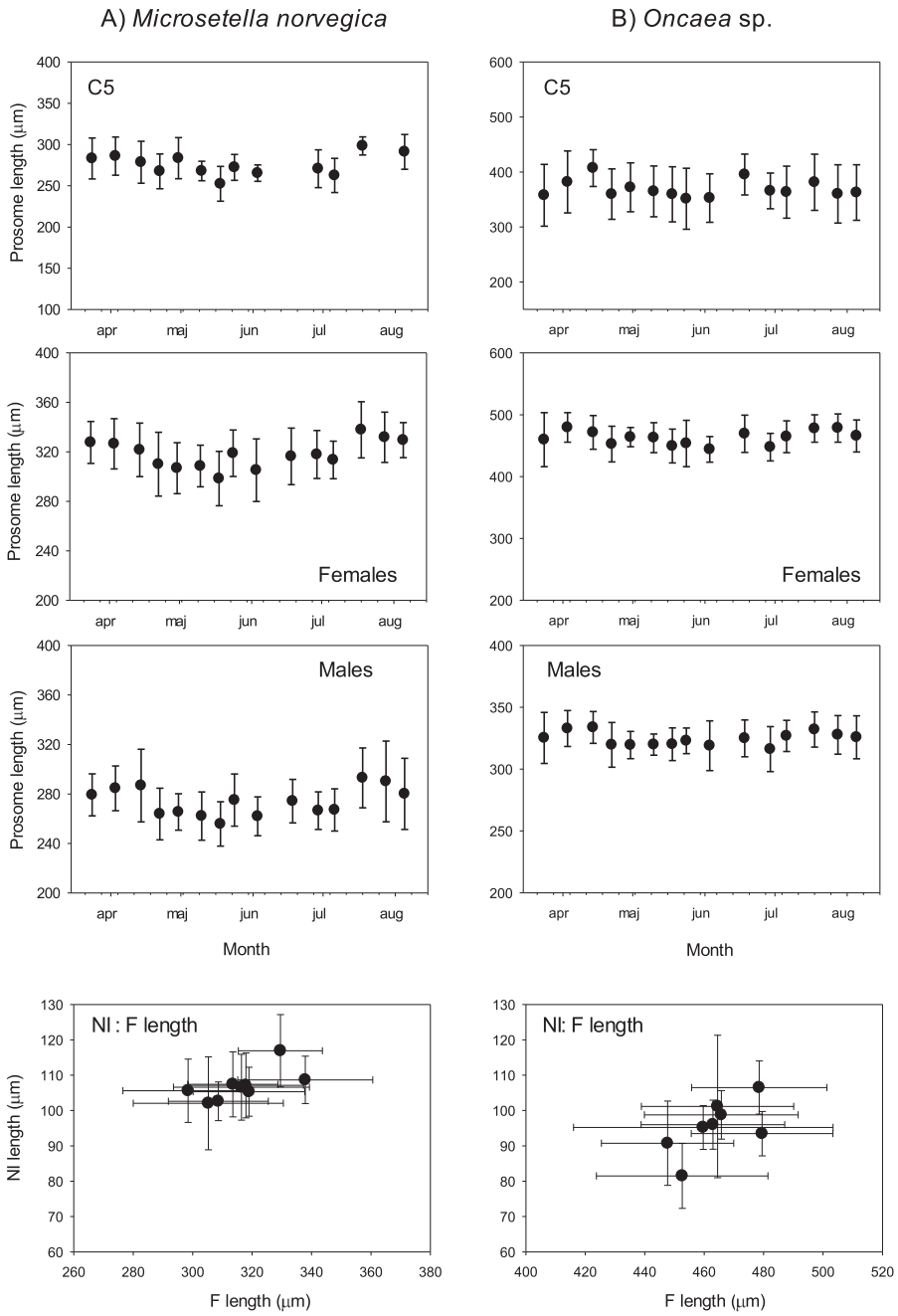

Fig. 5. Seasonal changes in the length (µm; mean ± SD) of the 5th copepodite stages, females and males as well as the length of the first naupliar stage (NI) as a function of female length of A) *Microsetella norvegica* and B) *Oncaea* sp. (at Station 4). The average (±SD) of the NI: F size ratio is indicated in the figure. Note the different scales of the x-axis.

(Table 2). In contrast to *M. norvegica*, the largest part of the *Oncaea* spp. population consisted of males, with F: M ratio fluctuating between 0.2 ± 0.14 in March-April, 0.16 ± 0.08 in May-June and 0.51 ± 0.43 in July-August (mean ± SD of all the stations). The seasonal changes in the F: M ratio of *Oncaea* spp. were similar at all stations, with the proportion of females increasing in late summer (Table 2).

Microsetella norvegica reproduction at the four stations is presented in detail elsewhere (Koski et al. 2014), so only a short summary will be given here. The peak reproduction of *M. norvegica* occurred in May-July, while females with eggs were less common earlier (March-April) or later (late July-August). During the peak spawning season the amounts of egg-sacs frequently exceeded the amounts of females, resulting in peak egg-sac to female ratios of > 1. The average clutch size of *M. norvegica* was 8.8 ± 1.3 eggs clutch^{-1}, with little variation between dates or stations. The egg production during the spawning season varied from 1 to ca. 5 eggs f^{-1} d^{-1} (Table 2; Koski et al. 2014).

Oncaea spp. reproduction had a different seasonal development than that of *Microsetella norvegica*, with both clutch size and proportion of spawning females increasing toward the end of the summer (Table 2). The average clutch size of *Oncaea* spp. increased from 12 ± 1.8 eggs clutch^{-1} in March-April to 16 ± 2.6 eggs clutch^{-1} in July-August. The proportion of spawning females at station 4 increased from < 10% in early summer up to 60% in late summer, resulting in egg production fluctuating from 0.1 up to ca. 1 egg f^{-1} d^{-1} (Table 2). At the other stations the percentage of spawning females was based on a generally-low abundance of females, and therefore was variable (Table 2).

The numbers of eggs and first naupliar stages of *Microsetella norvegica* were related to the proportion of spawning females (Spearman

Table 2
Average sex ratio, percentage of spawning females (%), clutch size (eggs clutch^{-1}) and egg production (eggs f^{-1} d^{-1}) of *Microsetella norvegica* and *Oncaea* spp. during spring (March-April), early summer (May-June) and late summer (July-August) at the four sampling stations (mean ± SD of the sampling dates). (-) No data.

Station	Sex ratio		Spawning females		Clutch size		Egg production	
	M. norvegica	*Oncaea*	*M. norvegica*	*Oncaea*	*M. norvegica*	*Oncaea*	*M. norvegica*	*Oncaea*
Station 2								
March-April	2.2 ± 1.7	0.08 ± 0.02	0.4–35	0–20	8.6 ± 1.9	12 ± 2.1	0.1 ± 0.2	0.2 ± 0.2
May-June	6.0 ± 6.6	0.18 ± 0.06	35–109	0–13	8.1 ± 0.8	12	1.5 ± 0.6	0.1 ± 0.1
July August	27 ± 30	0.40 ± 0.31	1.4–79	0–1.2	9.8 ± 1.6	18	1.5 ± 1.0	0.01 ± 0.02
Station 4								
March-April	4.1 ± 1.7	0.31 ± 0.19	1.5–94	0–6	8.1 ± 0.2	13 ± 1.6	0.1 ± 0.7	0.1 ± 0.1
May-June	3.3 ± 3.5	0.21 ± 0.08	67–450	9–37	8.8 ± 0.6	15 ± 1.1	4.9 ± 3.6	0.6 ± 0.4
July August	4.2 ± 0.8	0.48 ± 0.02	2–120	27–61	8.4 ± 0.8	17 ± 1.2	1.0 ± 1.6	1.3 ± 0.7
Station 5								
March-April	6.1 ± 3.3	0.16 ± 0.07	0–83	1–8	8.8 ± 0.8	14	0.4 ± 0.6	0.06 ± 0.1
May-June	8.6 ± 6.6	0.12 ± 0.04	61–410	0–30	8.9 ± 1.3	–	4.3 ± 4.3	0.2 ± 0.3
July August	30 ± 31	0.43 ± 0.49	4–19	0–100	8.6 ± 0.9	–	0.4 ± 0.2	1.0 ± 1.8
Station 6								
March-April	4.4 ± 1.1	0.23 ± 0.08	0–69	0–22	9.2 ± 0.5	10	0.4 ± 0.5	0.07 ± 0.02
May-June	11.2 ± 8.3	0.09 ± 0.08	22–103	0–3	9.8 ± 2.5	–	1.7 ± 1.0	0.02 ± 0.03
July August	9.2 ± 8.6	0.73 ± 0.69	7–191	0–100	8.8 ± 0.5	14	2.0 ± 3.0	1.1 ± 1.6

correlation coefficient 0.782 and 0.588 for eggs and NI; $p < 0.001$) rather than to the clutch size ($p > 0.05$), and profited from higher temperature (0.426 for both eggs and NI; $p < 0.01$), lower salinity (-0.306 and −0.453; $p < 0.05$ and < 0.01 for eggs and NI, respectively) and, in case of the NI abundance, also from a higher chl-*a* concentration (0.614; $p < 0.05$; Table A.2). For *Oncaea* spp., NI abundance was not related to the proportion of spawning females ($p > 0.05$), but both egg and NI abundances were related to the clutch size (0.577 and 0.479; $p < 0.001$ and < 0.05 for eggs and NI, respectively) and to the F: M ratio (0.538 and 0.343; $p < 0.001$ and < 0.05 for eggs and NI, respectively; Table A.2). In contrast to *M. norvegica*, the F:M ratio of *Oncaea* spp. was always < 1, and the reproduction only increased in late summer when the sex-ratio was more balanced (Table 2). Neither temperature nor salinity had any effect on the abundance of *Oncaea* spp. eggs, but the abundance of NI was positively correlated to temperature (0.376; $p < 0.01$; Table A.2).

Microsetella norvegica and *Oncaea* spp. had similar average growth rates of 0.07–0.11 μg C (μg C)$^{-1}$ d^{-1} for nauplii I-V and 0.03–0.06 μg C (μg C)$^{-1}$ d^{-1} for copepodites (Table 3). The last naupliar stage (NVI) of both species had a negative growth rate. In contrast, there was a large difference in female growth rates (weight-specific egg production) between species, which averaged 0.07 μg C (μg C)$^{-1}$ d^{-1} for *M. norvegica* but only 0.003 μg C (μg C)$^{-1}$ d^{-1} for *Oncaea* spp. (Table 3), mainly due to the small size of *Oncaea* spp. eggs (Fig. 5). The growth rates of *M. norvegica* nauplii and copepodites decreased with the body size, without large differences in the slope between the developmental stages (Fig. 6). In contrast, whereas the growth rate of *Oncaea* spp. nauplii had a similar scaling to the body size as *M. norvegica*, the growth rate of *Oncaea* spp. copepodites decreased much faster with increasing body size. Body size explained between 20 and 44% of the variation in growth rate (Table 4). The weight-specific egg production of neither species was related to female size (Fig. 6, Table 4). The growth or weight-specific egg production rates of neither of the species or any of the life-stages (nauplii, copepodites or adults) were related to chl-*a* concentration (linear regression $R^2 \leq 0.04$; data not shown). Also, there was no connection between the ratio of NI to F (as an indication of reproduction) and temperature for either *M. norvegica* or *Oncaea* spp. (linear regression $R^2 \leq 0.04$; data not shown).

3.5. Mortality

Mortality of *Microsetella norvegica* typically decreased with increasing life-stage, with an average specific mortality of 0.5 ± 0.3 d^{-1} for eggs, 0.1–0.2 d^{-1} for different naupliar stages and ≤ 0.05 d^{-1} for different copepodite stages (with an exception of CII-III; Fig. 7). The mortality of most stages was highest in the spring – early summer, with a second peak in mortality for some stages in late summer. Particularly male mortality was high in July-August with rates up to 0.1 d^{-1}. Egg mortality was always significantly higher than female mortality, and did not follow a similar seasonal development. In general, temperature, total

Table 3
Weight-specific growth of nauplii (NI-V and NVI), copepodites (CI-V) and females (Egg production EP; μg C (μg C)$^{-1}$ d^{-1}) of *Microsetella norvegica* and *Oncaea* spp. averaged for each sampling month and for all stations, and their production to biomass ratio (P / BM) at the four sampling stations, averaged for each sampling month (mean ± SD). The average and range of the values are for the whole sampling period. (-) Missing data.

	Growth			EP	P / BM			
	NI-V	NVI	CI-V	F	St. 2	St. 4	St. 5	St. 6
M. norvegica								
March-April	–	–	0.03 ± 0.01	0.01 ± 0.02	0.009 ± 0.01	0.01 ± 0.02	0.01 ± 0.02	0.01 ± 0.02
May	0.07 ± 0.05	–	0.03 ± 0.01	0.13 ± 0.11	0.007 ± 0.05	0.12 ± 0.01	0.08 ± 0.02	0.09 ± 0.03
June	0.08 ± 0.05	−0.09 ± 0.4	0.04 ± 0.02	0.12 ± 0.13	0.02 ± 0.003	0.06 ± 0.04	0.08 ± 0.05	0.04 ± 0.03
July-August	0.07 ± 0.04	−0.10 ± 0.2	0.05 ± 0.02	0.05 ± 0.07	0.03 ± 0.01	0.02 ± 0.01	0.02 ± 0.01	0.06 ± 0.08
Average	**0.07 ± 0.05**	**−0.09 ± 0.3**	**0.04 ± 0.02**	**0.07 ± 0.10**	**0.03 ± 0.03**	**0.05 ± 0.06**	**0.04 ± 0.04**	**0.05 ± 0.05**
Range	**0.03–0.09**	**−0.02- −0.14**	**0.01–0.09**	**0–0.46**	**0.003–0.12**	**0.002–0.23**	**0.001–0.11**	**0.001–0.11**
Oncaea spp.								
March-April	0.06 ± 0.05	−0.004 ± 0.02	0.06 ± 0.03	0.0005 ± 0.0006	0.03 ± 0.01	0.04 ± 0.01	0.03 ± 0.004	0.03 ± 0.003
May	0.06 ± 0.04	0.005 ± 0.02	0.06 ± 0.02	0.002 ± 0.005	0.02 ± 0.004	0.03 ± 0.01	0.03 ± 0.003	0.03 ± 0.01
June	0.07 ± 0.04	0.05	0.06 ± 0.02	0.005 ± 0.004	0.02 ± 0.003	0.04 ± 0.01	0.03 ± 0.01	0.02 ± 0.01
July-August	0.11 ± 0.10	−0.03 ± 0.004	0.06 ± 0.03	0.006 ± 0.007	0.03 ± 0.001	0.03 ± 0.02	0.03 ± 0.02	0.03 ± 0.004
Average	**0.07 ± 0.07**	**−0.003 ± 0.03**	**0.06 ± 0.03**	**0.003 ± 0.005**	**0.03 ± 0.005**	**0.04 ± 0.01**	**0.03 ± 0.01**	**0.03 ± 0.01**
Range	**0–0.34**	**0–0.05**	**0–0.16**	**0–0.02**	**0.02–0.03**	**0.01–0.06**	**0.01–0.05**	**0.01–0.04**

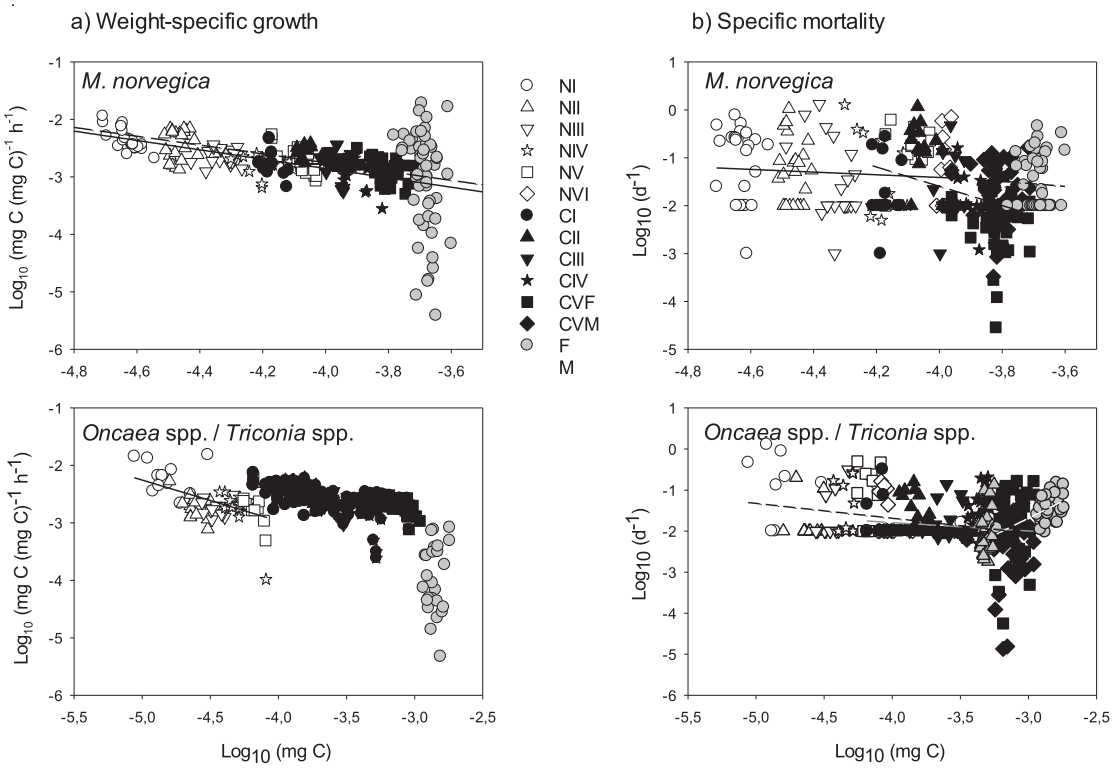

Fig. 6. Log10 of a) the weight-specific growth rate (mg C (mg C)$^{-1}$h^{-1}) and b) the daily specific mortality (d^{-1}) of *Microsetella norvegica* and *Oncaea* spp. as a function of log10 of the body size (mg C ind.$^{-1}$). Different symbols represent different life-stages. (Open symbols) naupliar stages (NI-VI), (closed symbols) copepodite stages (CI-V), (grey symbols) adults (F and M). NVI stage is not included in a) due to their negative growth rates. In b), zero mortality rates are replaced with a mortality of 0.01 d^{-1}, so that the zero rates read as −2 on the y-axis. The significant linear regressions between the growth or mortality rates and body size (Table 4) are indicated in the figure.

Table 4
Parameters from linear regressions relating the $\log_{10}$ of the offspring (NI) size to $\log_{10}$ of the female size (both in mg C ind.$^{-1}$) and the $\log_{10}$ of the weight-specific growth rates (mg C (mg C)$^{-1}$h^{-1}) and the specific mortality rates (d^{-1}) of each development stage to the $\log_{10}$ of their average body sizes (mg C ind.$^{-1}$; Fig. 7). (n) Number of observations, (NS) not significant, (MS) marginally significant ($p < 0.1$), (**) and (***) significant at the levels of $p < 0.01$ and $p < 0.001$, respectively.

	Offspring to female ratio (mg C NI^{-1}: mg C F^{-1})			Weight-specific growth to size (mg C (mg C)$^{-1}$h^{-1}: mg C ind.$^{-1}$)			Specific mortality to size (d^{-1}: mg C ind.$^{-1}$)		
	a	b	R^2 (n)	a	b	R^2 (n)	a	b	R^2 (n)
M. norvegica									
NI-V				−6.1	−0.81 ± 0.08	0.44 (119)***	NS		
CI-V				−5.8	−0.77 ± 0.14	0.20 (117)***	−9.6	−2.01 ± 0.45	0.12 (151)***
F				NS			NS		
M							NS		
All	−2.5	0.56 ± 0.15	0.38 (27)***	−5.7	−0.72 ± 0.08	0.21 (290)***	−4,3	−0.68 ± 0.13	0.07 (378)***
Oncaea spp.									
NI-V				−5.8	−0.71 ± 0.14	0.27 (67)***	NS		
CI-V				−3.9	−0.38 ± 0.04	0.33 (173)***	−2.6	−0.20 ± 0.12	0.013 (216)MS
F				NS			3.3	1.6 ± 0.5	0.19 (46)**
M							11.3	4.1 ± 2.4	0.07 (39)MS
All	−2.7	0.75 ± 0.32	0.30 (15)*	−4.4	−0.45 ± 0.05	0.26 (265)***	−2.3	−0.16 ± 0.06	0.02 (374)**

chl-*a* or the presence of large calanoid species had little influence on the mortality of *M. norvegica* (Spearman correlation; $p > 0.05$). However, the mortality of NI-NIV was significantly negatively correlated to chl-*a* in the > 10 μm size fraction (-0.778–0.927; $p < 0.05$), whereas the mortality of some naupliar stages (NI, NIV, NVI) seemed to be positively correlated to salinity (0.394–0.578; $p < 0.05$; Table A.3).

Oncaea spp. mortality followed similar trends as *Microsetella norvegica* mortality, with decreasing mortality with increasing life-stage. However, the mortality of NI at 0.3 ± 0.4 d^{-1} was substantially higher than that of *M. norvegica* NI, while the mortality of most other nauplius stages was lower at 0.02–0.07 d^{-1} (Fig. 8). Copepodites and females had average mortality rates similar to *M. norvegica* at ≤ 0.05 d^{-1}, but *Oncaea* spp. male mortality was approximately two times higher than the male mortality of *M. norvegica* (Figs. 7 and 8). Similarly to *M. norvegica*, *Oncaea* spp. eggs had a significantly higher mortality than *Oncaea* spp. females. *Oncaea* spp. mortality was not consistently related to temperature, salinity, chl-*a* or the presence of large copepods ($p > 0.05$). However, the mortality of eggs and males was positively correlated to temperature (0.519 and 0.384 for eggs and males, respectively; $p < 0.05$) and negative to salinity (-0.623 and −0.493 for eggs and males, respectively; $p < 0.05$; Table A.3).

Thus, there were significant differences in the mortality both between the two species (2-way ANOVA; $F_{1,\ 263} = 12.3$; $p < 0.001$) and between the development stages ($F_{12,\ 263} = 19.8$; $p < 0.001$), with a

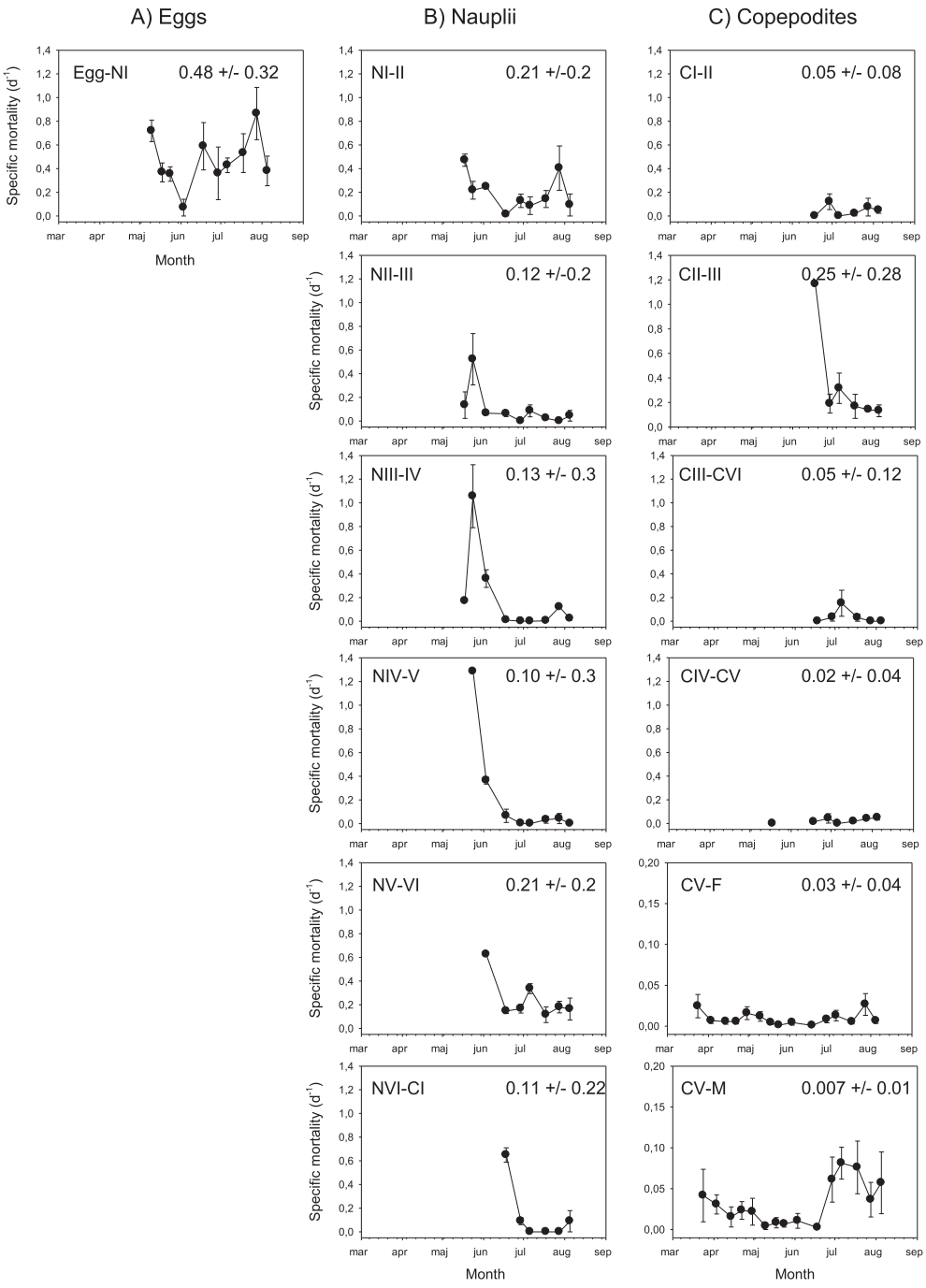

Fig. 7. Seasonal changes in the average specific daily mortality of A) eggs, B) nauplii and C) copepodites of *Microsetella norvegica* (d^{-1}; mean ± SE of the four sampling stations). The average of each development stage (±SD) is indicated in the figure.

significant interaction between the two ($F_{12,263} = 3.3$; $p < 0.001$). The difference between species was mostly due to the lower mortality of *Oncaea* spp. NIII, NIV and CII than the corresponding stages of *M. norvegica* (Tukey HSD; $p < 0.05$). The difference between life-stages resulted from the significantly-higher mortality of *M. norvegica* eggs and *Oncaea* spp. eggs and NI compared to other stages (Tukey HSD; $p < 0.01$).

Whereas the mortality of nauplii was not related to their body size, the mortality of both *Microsetella norvegica* and *Oncaea* spp. copepodites decreased with increasing body size, but much more so for *M. norvegica* than for *Oncaea* spp. Also, whereas the adult mortality of *M. norvegica* was not related to body size, the mortality of both female and male *Oncaea* spp. increased with increasing body size (Fig. 6). However, body size in all cases explained < 20% of the variation in mortality (Table 4), which also varied between the seasons and stations (Figs. 7 and 8).

3.6. Biomass and secondary production

The peak biomass of *Microsetella norvegica* was ca. 7, 3.5, 2.5 and 1.5 g C m^{-2} at Stations 2, 4, 5 and 6, respectively (Fig. 9). The biomass peak occurred in different months at different seasons: while females and late copepodites made up most of the peak biomass in early spring at Station 4, the peak biomass at Stations 2 and 5 occurred in late summer and consisted mostly of late copepodites and adults probably belonging to the new overwintering generation. The biomass of *Oncaea* spp. was typically less than half of *M. norvegica*, though in early spring both

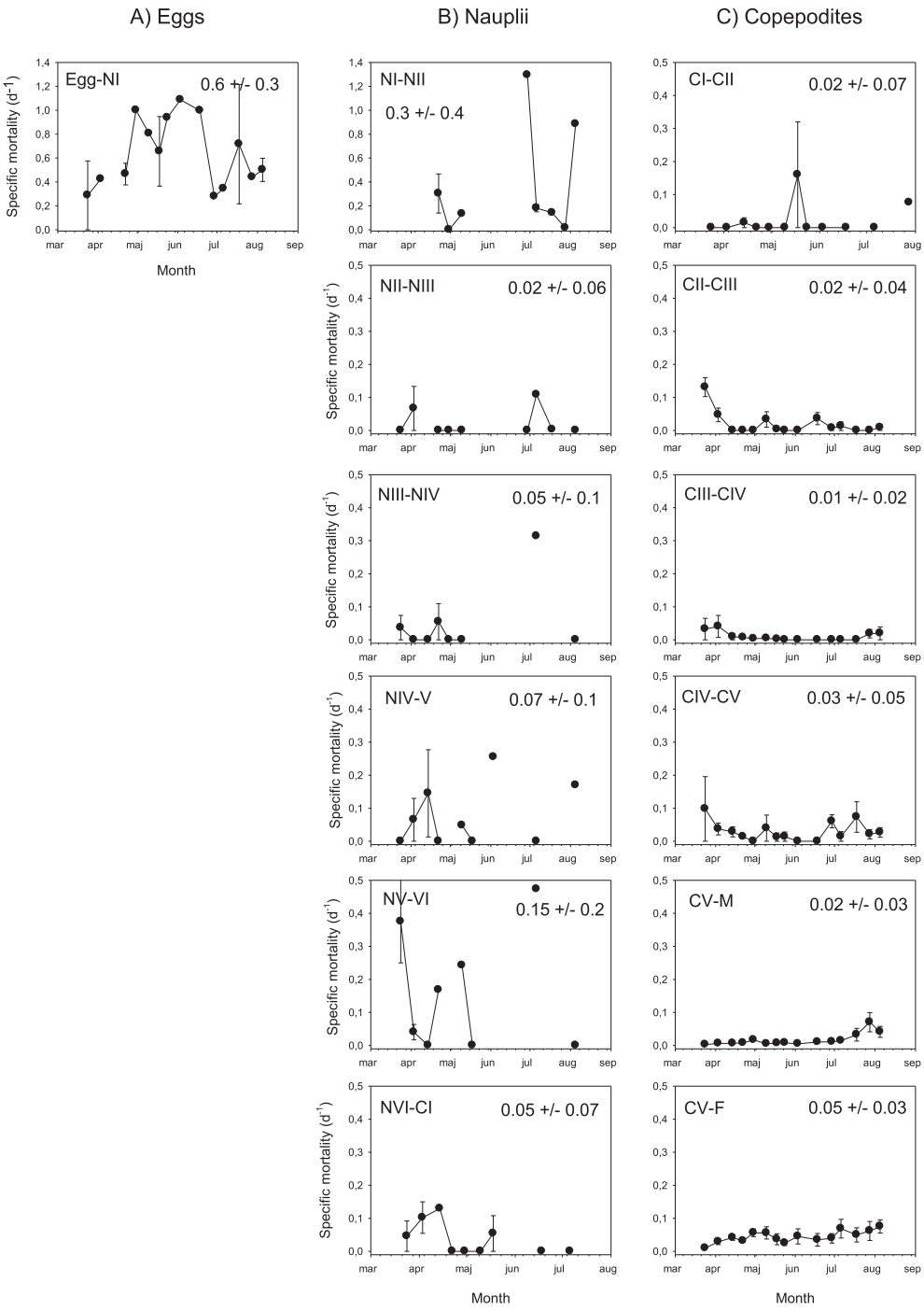

Fig. 8. Seasonal changes in the average specific daily mortality of A) eggs, B) nauplii and C) copepodites of *Oncaea* spp. (d^{-1}; mean ± SE of the four sampling stations). The average of each development stage (±SD) is indicated in the figure.

species had similar biomasses (with the exception of Station 4 where *M. norvegica* dominated).

The total secondary production of *M. norvegica* over the study period varied between 1.5 and 3.8 g C m^{-2} (5 months)$^{-1}$, while the production of *Oncaea* spp. was ca. half of that at Station 2, but>10 times lower at the other stations (Table 5). For *M. norvegica* most of the secondary production was due to female egg production, and thus peaked during the reproductive season (Fig. 9). In contrast, most of the secondary production of *Oncaea* spp. was due to the growth of late copepodite stages and males, and did not follow the seasonal development of female egg production. The production to biomass ratio was typically ≤ 0.12 for *M. norvegica*, while the production to biomass ratio of *Oncaea* spp. was ca. half of that (0.06; Table 4).

4. Discussion

4.1. Calculation of mortality, growth and secondary production

Calculations of mortality rate, growth rate and secondary production relied on the measured numbers of individuals and their mean lengths as well as on the calculated development times and carbon contents. These calculations could potentially result in erroneous estimates of mortality and growth rates, if the temperature dependency of the development times or the carbon to length ratios were deviating from the utilized

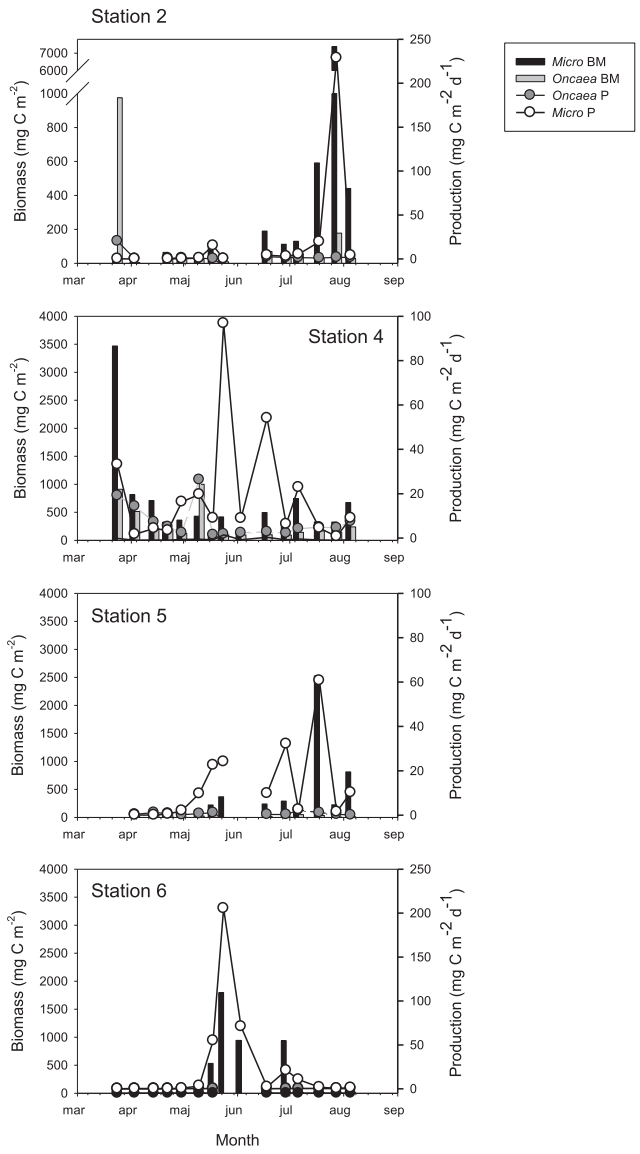

Fig. 9. Seasonal changes in depth-integrated biomass (BM; mg C m^{-2}; columns) and secondary production (P; mg C m^{-2} d^{-1}; symbols) of *Microsetella norvegica* and *Oncaea* sp. in the four sampling stations in Kapisigdlit.

Table 5
Total secondary production of *Microsetella norvegica* and *Oncaea* spp. from the end of March to the beginning of August at the four sampling stations (g C m^{-2} (5 months)$^{-1}$).

	M. norvegica	Oncaea spp.
Station 2	2.3	0.9
Station 4	2.9	0.3
Station 5	1.5	0.08
Station 6	3.8	0.03

literature equations.

The estimates of the development times of *Microsetella norwegica* and *Oncaea* spp. were not based on data obtained with the same species, but relied on the temperature-dependence of the development of other Arctic and sub-Arctic sac-spawning copepods (see Methods). The juvenile development times varied < 5%, irrespective of the equation that was used (Table A.1), and therefore had little effect on the calculations of mortality and growth rates. However, the calculated egg development times varied by ca. 30%, so that if the development times were calculated following the temperature-dependent egg development of *Oithona similis* (Nielsen & Andersen 2002), the egg development times were substantially longer than if they were calculated following the temperature-dependent development times of *Eurytemora* sp. or *Pseudocalanus* spp. (McLaren et al. 1969; Table A.1). The egg development times had a direct effect on mortality rates, so that the mortality rate calculated using the development times based on *Oithona similis* was on average 25% lower and the mortality rate calculated based on the development time of *Pseudocalanus* spp. on average 25% higher than the average mortality rates (Fig. A.2), although the overall trends, including the seasonality, remained the same. Although we do not know the exact temperature-dependence of *M. norvegica* and *Oncaea* spp. egg development, all equations resulted in a proportional decrease in development time with increasing temperature (0.44–0.48 days per degree Celsius) that was comparable to the temperature-dependent decrease in *M. norvegica* egg development measured by Uye et al. (2002) at higher temperatures (0.41 days per degree Celsius), indicating that the development times (and thus mortality rates) were realistic estimates.

There exists only one study of the length-specific carbon content of *Microsetella norvegica* that covers all development stages (Uye et al. 2002). However, Svensen et al. (2018) and Barth-Jensen et al. (2020) measured the carbon content of sub-arctic *M. norvegica* females in different months, and estimated it to be 0.18–0.51 μg C ind.$^{-1}$, which on average corresponded to 0.0007 ± 0.0002 μg C μm^{-1}. Using this length-specific carbon content resulted in carbon weights that were on average 16 ± 4 % higher than the weights based on the carbon to length regression of Uye et al. (2002; Table A.1). If all developmental stages were assumed to be 16% larger than the carbon weights obtained by Uye et al. (2002), the total secondary production of *M. norvegica* would have been elevated by 9.6 ± 1%, and the production to biomass ratio would have been reduced by 6 ± 1 %. For *Oncaea* spp. no study apart from Satapoomin et al. (1999) that would have measured both the lengths and carbon content of individuals was identified, but comparison of the body lengths of three sub-arctic oncaeoid species reported in Nishibe & Ikeda (2007) and the carbon contents of the same species in Nishibe & Ikeda (2008) suggested a carbon content of 0.002 ± 0.001 μg C μm^{-1}. Using this ratio resulted in ca. 30% reduction of the female carbon weight. Assuming a similar reduction for all developmental species, the secondary production of *Oncaea* spp. could have been somewhat overestimated. Nevertheless, mortality, growth and secondary production estimates appeared relatively robust to the changes in the temperature-dependency of development times and carbon to length ratios, and the overall trends on these rates were thus assumed to be reliable.

4.2. *Effect of temperature and chl-a on reproduction and growth*

Irrespective of both being small aggregate-colonizing copepods, *Microsetella norvegica* and *Oncaea* spp. differed in their seasonal succession, their response to environmental factors and their internal controls of reproduction. A recent study detailed the seasonal development of *M. norvegica* in a sub-arctic fjord, indicating overwintering of adult stages at depth, ascent in spring, and reproduction in the surface layer in summer (Svensen et al. 2018). Our results confirm this pattern which has also been observed in other sub-arctic fjords (Arendt et al. 2013). Temperature has emerged as the controlling factor for the reproduction of *M. norvegica* in previous studies, although with local adaptations (Uye et al. 2002; Barth-Jensen et al. 2020). Whereas *M. norvegica* from a temperate area could decrease its hatching and development time linearly with increasing temperature (Uye et al. 2002), the response of the hatching time of a sub-arctic *M. norvegica* to temperature was bell-shaped, peaking at temperatures of 6–8 °C (Barth-Jensen et al. 2020). Also, *M. norvegica* from the sub-tropics had substantially-larger maximum clutch size and weight-specific egg production rates (Uye et al. 2002) than measured in the arctic fjords (Svensen et al., 2018, this study), although all studies confirmed the potentially-high reproduction rates that could account for the high biomass observed in several studies

(Dugas & Koslow 1984, Arendt et al. 2013, Svensen et al. 2018). In contrast to expectations of low metabolic rates and low mortality, *M. norvegica* appears to build up and maintain a high biomass through high reproduction rate. Although temperature clearly exerts some control over reproduction, *M. norvegica* also appears capable of boosting its egg production when conditions are favorable by shedding egg-sacs before they have hatched (Koski et al. 2014).

In contrast to *Microsetella norvegica*, *Oncaea* spp. reproduction was not related to temperature, and most of the population remained in the colder waters below the surface layer. Although the oncaeid copepods were not identified to species, the relatively even size, vertical distribution and seasonal development suggested that most of the organisms belonged to one or a few species, most likely to *Triconia borealis*, which was also identified in previous samples from the area (M. Mazzocchi, pers. comm.). *Triconia borealis* has been described to mainly occupy the upper 250 m of the water column with a deeper distribution of adult stages in winter than in summer, and to reproduce year-round but with peak biomass and reproduction during summer-fall (Gislason 2003, Nishibe & Ikeda 2007, Lischka & Hagen 2016, Middelbo et al. 2019). We observed similar succession and vertical distribution, although the high abundance of early developmental stages in early spring also indicated overwintering and/or reproduction at depth.

The population of oncaeids was always dominated by males, similar to most other studies (Nishibe & Ikeda 2007, Lischka & Hagen 2016), but the egg production ($\leq$1.3 eggs f^{-1} d^{-1}) was lower and clutch size smaller (max. 18 eggs $clutch^{-1}$) than what has previously been reported for *Oncaea* spp. These earlier studies measured production of 5 to 15 eggs / nauplii day^{-1} in temperatures $\geq$ 20 °C and at high food concentrations (Paffenhöfer 1993, Fyttis et al. 2015) and a clutch size of 46–70 eggs $clutch^{-1}$ (Nishibe, pers comm, cited in Böttger-Schnack & Schnack 2005, Nishibe & Ikeda 2007). Assuming a Q_{10} of 2.5–3, the egg production in our study was however comparable to these rates, and suggested that the proportion of females rather than food limitation was controlling the reproduction in this glacial fjord.

If the weight-specific growth and reproduction rates of *Oncaea* spp. and *Microsetella norvegica* were compared to the global model describing growth and reproduction rates of copepods as a function of temperature and chl-*a* (Bunker & Hirst 2004), a few trends emerged. First, the weight-specific reproduction of *M. norvegica* during the reproductive season was up to 10 times higher than the predicted weight-specific reproduction of either broadcast or sac-spawning copepods in corresponding temperatures. Second, population dynamics controlled *M. norvegica* reproduction, and the only reproductive rates that were lower than expected based on the temperature only, were those outside of the reproductive season (early spring or late autumn). Third, the global models might not capture well the reproduction at low temperatures predicting only small differences in the temperature range that covered the whole growing season for our study area. In contrast, weight-specific growth rates of *M. norvegica* juveniles corresponded well to the temperature-specific in situ rates of sac-spawning copepods, whereas the weight-specific growth rates of *Oncaea* spp. were more similar to in situ rates of broadcast spawning copepods or food-replete laboratory rates of sac-spawners. This would suggest that whereas juvenile growth rates of *M. norvegica* and *Oncaea* spp. do not deviate substantially from the global rates of calanoid and cyclopoid copepods, weight-specific egg production rates do. Also, whereas no indication of food limitation was evident for *M. norvegica* egg production, the juvenile growth rather followed the food limited in situ rates than the food-replete laboratory rates.

4.3. High mortality of early development stages

The specific mortality rates of *Microsetella norvegica* and *Oncaea* spp. were more similar to previous estimates for broadcast-spawning copepods than for egg-carrying copepods. For instance, the high average egg mortality of $\geq$ 0.5 d^{-1} was similar to that of *Calanus* spp. on Georges Bank (Ohman et al. 2002), and the high average mortality of the first naupliar stage (0.2–0.3 d^{-1}) corresponded well to rates measured for early *Calanus* spp. nauplii in the North Sea (Eiane & Ohman 2004). Typically, the mortality rates of sac-spawning copepods (e.g., *Oithona* spp.) are lower ($\leq$0.1 d^{-1}; Ohman et al. 2002, Eiane & Ohman 2004, Thor & Nielsen 2008, Hirst & Ward 2008), and mortality rates of carried eggs are similar to mortality rates of females (Ohman et al. 2002). For *M. norvegica* the difference in egg and female mortality could be explained by the shedding of egg-sacs before they hatch (Koski et al. 2014) or by an environmental factor affecting egg hatching. Although not observed in this study, egg hatching can be influenced by temperature (Barth-Jensen et al. 2020), maternal investment (Koski et al., 2020), nutritional quality of food (Dutz et al. 2008) and deleterious compounds (Ianora et al. 2003). Although it was not possible to demonstrate a direct connection between egg mortality and temperature, the restriction of spawning and nauplii occurrence of *M. norvegica* to the surface water of > 5 °C during the summer fit with the observed optimum temperature for hatching of *M. norvegica* eggs (6–8 °C; Barth-Jensen et al. 2020).

The stage-specific patterns of mortality were similar in both *Microsetella norvegica* and *Oncaea* spp., with the highest mortality in eggs and early nauplii, elevated mortality in NV-VI, lower mortality in copepodite stages and higher mortality of CV males than CV females. Neither of the species therefore seemed to suffer elevated mortality during the metamorphosis (NVI-CI), as observed in several freshwater copepods (Marion et al. 2016). Hirst & Ward (2008) suggested that the early mortality of first naupliar stages could reflect the poor ability of these stages to locate food patches or to avoid predation. Our data did not provide any evidence of density-dependent mortality of naupliar stages, but the mortality of most naupliar stages of *M. norvegica* was negatively correlated to the concentration of chl-*a* at the > 10 μm size fraction, suggesting that food limitation by phytoplankton could have occurred for these stages. With the exception of the first naupliar stage, naupliar mortality of *Oncaea* spp. was much lower than that of *M. norvegica*, and did not correlate with chl-*a* concentration. Although both *M. norvegica* and *Oncaea* spp. are known to feed on marine snow (Alldredge 1972, Ohtsuka et al. 1993, Koski et al. 2020), *M. norvegica* nauplii have also been shown to ingest phytoplankton (Uye et al. 2002), and chl-*a* has been observed in *M. norvegica* guts (Koski et al. 2020). The only existing study on the feeding of *Oncaea* spp. nauplii demonstrated consistent feeding on bacteria (Roff et al. 1995) and also the vertical distribution of *Oncaea* spp. nauplii below the euphotic zone suggested other food sources than live phytoplankton. It could be that the higher mortality in *M. norvegica* nauplii compared to *Oncaea* spp. was due to starvation.

The male mortality of *Oncaea* spp. was lower than the female mortality, and the mortality of CV male stages was lower than the mortality of CV females in both species. This is the opposite of the observations with many egg-carrying copepods where the high male mortality is suggested to be a trade-off of the mate-searching behavior (Hirst & Ward 2008, Hirst et al. 2010). For *Oncaea* spp. the male and CV male mortalities correlated positively with temperature and negatively with salinity, which could emphasize the general sensitivity of *Oncaea* spp. to environmental conditions. Since females of these species typically resided deeper in the water column, they would have experienced less fluctuations in temperature and salinity. In contrast, predation could have been female-biased in both species, due to the larger size and higher visibility of egg-carrying females, also suggested by the increase in mortality with the size in adult *Oncaea* spp. Apart from chaetognaths (unpubl. data) many species of predatory larval fish were abundant in the study area from the end of May (Swalethorp 2013). Although *M. norvegica* and *Oncaea* spp. were not the primary prey of larval fishes they were observed in the stomachs of all species (Swalethorp et al. 2014, 2015). One exception was larval capelin, which were highly abundant from mid-June, and fed extensively on the naupliar stages of *M. norvegica* (Malanski et al. 2020), right around the time that we observed a spike in nauplii mortality.

4.4. Allometric scaling of growth and mortality rates

In principle, reproduction is a tradeoff between the quantity and the quality of eggs, both of which have the potential to reduce mortality under different environmental conditions (Neuheimer et al. 2015). In calanoid copepods and other crustaceans, the size of the offspring tends to increase in proportion to female size (Kiørboe & Sabatini 1995, Neuheimer et al. 2015). The size of the first naupliar stage of *Microsetella norvegica* and *Oncaea* spp. scaled to the female body size with exponents of 0.56 and 0.75, respectively, indicating that the egg size did not increase in proportion to the female size. The scaling of NI to female size resembled the exponent of 0.62 for sac-spawners in Kiørboe & Sabatini (1995), although the NI size of *Oncaea* spp. appeared to increase faster with female body size than the NI size of *M. norvegica*. Also, the size ratio of NI to females differed from the typical offspring to female ratios for broadcast and sac-spawners (as compiled by Kiørboe & Sabatini 1995) in both *Oncaea* spp. and *M. norvegica*, with *Oncaea* spp. NI being approximately half the size and *M. norvegica*, ca. five times larger than the offspring of typical sac-spawning copepods. This low NI to female size ratio of *Oncaea* spp. has been reported previously (Böttger-Schnack & Schnack 2005) and is not far off from the average crustacean offspring to female-size ratio of 100 (Neuheimer et al. 2015). The ratio for *M. norvegica* was about half of that reported in previous studies (Uye et al. 2002, Svensen et al. 2018, Barth-Jensen et al. 2020), and ten times lower (8.8 ± 0.7) than the expected ratio of 100. Neuheimer et al. (2015) suggested that a low offspring to female size ratio could result from parental care for instance in the form of high lipid content of eggs, from strong seasonality that would force the offspring size to be larger to allow earlier maturation, or from strong density-dependent cannibalism. All of these could be valid factors influencing *M. norvegica* offspring size in glacial fjords where the main reproduction takes place within a short time period at the surface layer (Svensen et al. 2018, this study), and where the predation on eggs is also likely to be high. In contrast, the reproductive season of *Oncaea* spp. seems to be less seasonal, with most of the population remaining at depth, which could suggest less need to produce large eggs.

The weight-specific growth rates of *Microsetella norvegica* and *Oncaea* spp. nauplii decreased with increasing body size, with a high exponent of −0.71–0.81. In comparison, the exponent of *Oncaea* spp. juveniles was lower (-0.38), and more similar to what has been demonstrated in previous studies that ether did not record a substantial decrease in the specific growth rates with size or estimated exponents of $\leq$ -0.3 (Kiørboe & Sabatini 1995, Hirst & Lampitt 1998, Kiørboe & Hirst 2014). Although the scaling of specific growth rate varies between juvenile and adult copepods, sac- and broadcast-spawners and food limited and-food replete populations from −0.42 to > 0 (Hirst & Bunker 2004), the slope of the decrease in *M. norvegica* and *Oncaea* spp. was exceptionally high. The decrease in the growth rate with body size could indicate increasing food limitation in the larger individuals / development stages as suggested by Hirst & Bunker (2003), or it could just reflect the differences in the allometric scaling over development. Whatever the reason, it was clear that allometric scaling of growth in *M. norvegica* and *Oncaea* spp. was different from calanoid and cyclopoid copepods. Systems that are dominated by these two species might therefore deviate from the predicted size structure of modelled systems where they are not considered.

Mortality of the nauplii was not influenced by the body size in either of the copepod species, but the mortality of *Microsetella norvegica* copepodites decreased with increasing body size with a high exponent of −0.68, while it increased for adult *Oncaea* spp. with an exponent of 1.6. It should be noted that there was a lot of scatter around the regressions, and only a small proportion of mortality was explained by the body size. Despite the high variability, it appeared that the mortality of *M. norvegica* copepodites was more influenced by the body size in comparison to *Oncaea* spp. copepodites (exponent of −0.2), where the allometric scaling of juveniles resembled that from previous studies on calanoid and cyclopoid copepods, which showed little or no size-dependency in sac-spawning species (slope of −0.04; Hirst & Kiørboe 2002). It is not clear why the specific mortality of *Oncaea* spp. adults increased with increasing body size, but since the group may have consisted of different species, the scaling could be affected by species-specific mortality rates resulting from e.g., differences in depth distribution. Similar to growth rates, allometric scaling of mortality rates in *M. norvegica* and *Oncaea* spp. appears different from calanoid and cyclopoid copepods. Since these two groups are similar in size and food preferences but distinctly different from calanoid and cyclopoid copepods, allometric scaling of their vital rates provides insights into the mechanisms that govern the feeding, growth and mortality rates of copepods, and the role of environmental adaptation in this. This is the key to understanding and predicting the effects of ongoing ecosystem changes.

4.5. Climate change and aggregate-colonizing copepods

A large proportion of the secondary production in arctic fjords is due to the production of *Microsetella norvegica* and *Oncaea* spp. (Arendt et al. 2013, Svensen et al. 2018). In Kapisigdlit, these species, and particularly *M. norvegica*, always dominated the abundance by up to 95% contribution to the copepod community, and the biomass of small copepods (*M. norvegica*, *Oncaea* spp., *Oithona* spp. and *Pseudocalanus* sp.) comprised > 50% of the copepod biomass outside the early spring when *Calanus* spp. dominated (Kjellerup 2014). The relative impact of small species is expected to only increase with the projected increase in stratification of the ocean. However, climate change is likely to have different effects on *M. norvegica* and *Oncaea* spp. due to their different population dynamics, environmental tolerances and food sources, and the predicted increase in meltwater flow and temperature in the glacial fjords may favor *M. norvegica* over *Oncaea* spp. The tolerance of *M. norvegica* to low salinity appears also to fit with the general trend of biomass increase at the time of the increased freshwater flow within the fjord systems (Tang et al. 2011, Arendt et al. 2013). However, stratification will also influence the food source of *M. norvegica* and *Oncaea* spp. Assuming that these species will mainly feed on aggregated particles (Koski et al. 2020) or copepod fecal pellets (Møller et al. 2011), the food supply is likely to decrease due to decreases in large diatoms that aggregate readily (Thornton 2002), and with it a decrease in large calanoids with a high fecal-pellet size and production. According to our observations, *M. norvegica* might be more dependent on phytoplankton aggregates, and could thus be more prone to food limitation with decreasing primary production than *Oncaea* spp., which resides at greater depth and might have a broader diet spectra.

Although *Microsetella norvegica* and *Oncaea* spp. share some traits such as small size and likelihood to feed on marine snow, their biology is different, and climate change will thus have different effects on their future distributions. While the outcome of the counteracting environmental factors is uncertain, it is certain that these abundant species form an important part of oceanic food webs in the arctic and elsewhere, and therefore must be considered if we are to understand the future of the ocean ecosystems. For this we will need both to focus on the temperature and food dependency of their vital rates, and on assessing the overall importance of these small copepods for functioning of the open ocean ecosystem.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

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