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**Small copepods matter: Population dynamics of *Microsetella norvegica* in a high-latitude coastal ecosystem**

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**KEY WORDS:** *Microsetella norvegica*, harpacticoid copepod, high-latitude, seasonal population dynamics, sub-Arctic fjord

18 **ABSTRACT**

19 We investigated the population dynamics of a small and little-studied harpacticoid copepod,  
 20 *Microsetella norvegica*, in a sub-Arctic Norwegian fjord (Balsfjord 69 °N). We sampled with a 90  
 21  $\mu\text{m}$  mesh WP-2 net and a 20 L Go-Flo bottle and found that the WP-2 under-sampled all juvenile  
 22 stages. The abundance and biomass were high, peaking in June with  $9349 \times 10^3 \text{ ind. m}^{-2}$  and  $1678 \text{ mg}$   
 23  $\text{C m}^{-2}$ . *Microsetella* were most abundant in the surface, but females and males demonstrated a distinct  
 24 migration to below 50 m from October to March. Consistently, individual female body carbon content  
 25 was highest in October ( $0.39 \mu\text{g C ind}^{-1}$ ) and lowest in March ( $0.18 \mu\text{g C ind}^{-1}$ ). Males were present  
 26 throughout the year, and females with eggs were found from April to September. The average clutch  
 27 size was  $11 \pm 2 \text{ eggs female}^{-1}$ , and our study supports the observation that females can release their  
 28 egg sac before the eggs have hatched, possibly to produce a new one. With its high abundance and  
 29 biomass, a flexible reproductive strategy and specialised feeding preferences, *M. norvegica* is likely  
 30 a key species in high-latitude coastal ecosystems.

31

32 **INTRODUCTION**

33 Most harpacticoid copepods are benthic, inhabiting all types of surfaces and sediments at all depths  
 34 (Azovsky *et al.*, 2016). The majority of harpacticoid copepods are substrate-bound (Dahms & Qian,  
 35 2004), and common habitats are seagrass blade surfaces and on or within bottom sediments (Bell *et*  
 36 *al.*, 1987). However, one harpacticoid copepod species, *Microsetella norvegica*, appears especially  
 37 adapted to a pelagic lifestyle. It is frequently associated with aggregates and marine snow (Kiørboe,  
 38 2000, Koski *et al.*, 2005, Koski *et al.*, 2007), and it has been suggested to be important for regulating  
 39 the downward flux of carbon in coastal ecosystems (Green & Dagg, 1997, Koski *et al.*, 2005, Koski  
 40 *et al.*, 2007). *Microsetella norvegica* is reported as highly abundant in temperate (Uye *et al.*, 2002)  
 41 as well as sub-Arctic (Arendt *et al.*, 2013) seas, and may even be the numerically-dominant copepod  
 42 species in the mesozooplankton community (Arendt *et al.*, 2013, Dugas & Koslow, 1984). Although  
 43 *M. norvegica* has received increased attention during recent decades (Arendt *et al.*, 2013, Diaz &  
 44 Evans, 1983, Koski *et al.*, 2014, Turner, 2004, Uye *et al.*, 2002), knowledge of its biology and  
 45 ecology is still rudimentary compared to that for calanoid copepod species. One likely reason is that  
 46 *M. norvegica* is not efficiently sampled with standard plankton nets (e.g., mesh size  $180 \mu\text{m}$ ) due to  
 47 its tiny ( $< 550 \mu\text{m}$  total length) and slender bodies. On the other hand, *M. norvegica* is often recorded  
 48 in fish stomachs (Demchuk *et al.*, 2015, Falkenhaug & Dalpadado, 2014), pointing to their wide  
 49 distribution and importance as prey for fish in coastal ecosystems.

50 Balsfjord (69 °N) is a high-latitude, cold-water fjord featuring Arctic characteristics regarding  
 51 irradiance and seasonality in primary production (Eilertsen & Taasen, 1984). The fjord is semi-

52 enclosed and advection is reduced due to an entrance sill at 30 m depth, making it well suited for  
53 studies of zooplankton population dynamics. Previous studies have concluded that *Calanus*  
54 *finmarchicus* is the dominant zooplankton species in Balsfjord (Tande, 1982). However, other  
55 investigations, sampling zooplankton with Niskin water bottles (Pasternak *et al.*, 2000) or plankton  
56 nets with 64  $\mu\text{m}$  mesh size (Davis, 1976), reported high relative abundance of *M. norvegica* during  
57 all seasons, although quantitative abundances were not presented. There are presently few  
58 quantitative studies focusing on *M. norvegica* seasonal abundance in high-latitude ecosystems, and  
59 therefore its population dynamics are not well known in these areas. For instance, aspects of its  
60 reproductive strategy, such as the timing and extent of the reproductive period, clutch-size and the  
61 seasonal variation in ratio of males to females have not been fully described for high-latitudes.  
62 Furthermore, many small copepods are winter-active in the surface at high latitudes (Madsen *et al.*,  
63 2008, Møller *et al.*, 2006), but the overwintering strategy for *M. norvegica* is not well known.

64 We investigated population dynamics of *M. norvegica* in Balsfjord through monthly  
65 samplings from June 2013 to June 2014. Our main objectives were to 1) study seasonal patterns of  
66 developmental stage composition, abundance, biomass and vertical distribution and 2) determine the  
67 timing of reproduction of *M. norvegica*. In addition, we evaluated sampling efficiency for the  
68 different developmental stages of *M. norvegica* by comparing abundances obtained with a WP-2 net  
69 (90  $\mu\text{m}$  mesh) with those obtained with a 20 L Go-Flo bottle.

70

## 71 **METHODS**

### 72 **Study site and sampling**

73 The study was conducted at station Svartnes in Balsfjord (Fig. 1), northern Norway (69°22'N,  
74 19°06'E). The fjord is 5 km at its widest, 46 km long. A shallow sill at the mouth (30 m depth)  
75 separates the fjord from coastal water to seaward (Reigstad, 2000, Wexels Riser *et al.*, 2010).  
76 Balsfjord has two basins. The outermost is 130 m deep, and the innermost, where station Svartnes is  
77 located, is 185 m deep. The sun passes below the horizon between November 26<sup>th</sup> and January 18<sup>th</sup>  
78 (polar night), and stays above the horizon between May 28<sup>th</sup> and July 19<sup>th</sup> (midnight sun).  
79 Stratification of the water column generally starts in May and lasts until September (Eilertsen &  
80 Taasen, 1984). Vertical profiles of salinity, temperature, density and fluorescence were obtained for  
81 each sampling date using a CTD profiler (Seabird model 25 Sealogger) from the surface to 175 m  
82 (station depth was 180 m). Station Svartnes is part of a large hydrographic monitoring-program  
83 (<https://dataverse.no/dataverse/nmdc>), and our monthly sampling results were supplemented with  
84 additional hydrographic data from the monitoring program. Temperature data from June 2014 are  
85 missing due to malfunction of the temperature logger.

86

87 ***Microsetella norvegica***

88 Monthly samplings were conducted during daytime from June 2013 to June 2014 from R/V “Hyas”.  
89 We aimed at collecting all developmental stages of *M. norvegica*, from nauplii to adult copepodites,  
90 and therefore sampled with both a WP-2 net (Hydro-Bios, 90  $\mu\text{m}$  mesh size) and a 20 L Go-Flo bottle  
91 (General Oceanics). The WP-2 net was equipped with a filtering cod-end and a closing mechanism  
92 to allow discrete sampling from 175-50 m and 50-0 m depth ranges. The contents of the cod end were  
93 concentrated with a 90  $\mu\text{m}$  mesh sieve. Due to the small mesh-size of the WP-2 net, the towing speed  
94 was slow, 0.2-0.3 m/s. The filtration volume was calculated from wire length, and no visual  
95 indications of clogging were observed. The Go-Flo bottle collected water at 5, 20 and 50 m depth,  
96 and its contents were concentrated with a 20  $\mu\text{m}$  mesh sieve. All zooplankton samples were preserved  
97 with buffered formaldehyde at 4 % final concentration.

98 Individuals of *M. norvegica* were counted and identified using a stereo microscope (Leica  
99 MZ16) at 40 – 100 x magnification. Developmental stages were identified according to Hirakawa  
100 (1974) and Huys and Boxshall (1991). Due to their small size, *M. norvegica* nauplii were not  
101 identified to stage but counted as one group. Copepodite stages CIV and CV were not separated due  
102 to their morphological resemblance and are reported as *M. norvegica* CIV-CV. Other stages were  
103 enumerated separately. Females carrying an egg sac and detached egg sacs in the sample were also  
104 enumerated. From each subsample, a minimum of 300 individuals were counted. Subsample volumes  
105 ranged from 7 to 100 % of the entire sample. A total of 65 samples were analysed in this study. To  
106 obtain comparative estimates of the WP-2 and Go-Flo sampling efficiency in the surface layer, the  
107 Go-Flo samples were integrated from 0-50 m depth, assuming the sample depths represented the  
108 midpoint in each interval.

109 Carbon and nitrogen contents of *M. norvegica* females were determined in October, January,  
110 March and May to cover the seasonal variations in body condition. For these analyses, additional  
111 samples were collected with the WP-2 net and live animals were transported to the laboratory where  
112 600 females without egg sacs were sorted out. The females were rinsed in filtered seawater and  
113 duplicates of 300 animals from each sampling occasion were gently dropped onto combusted GF/F  
114 filters and stored frozen (-20 °C) until analysis. The organic carbon and organic nitrogen contents of  
115 females were determined on a CHN Lab-Leeman 440 elemental analyser. Results for blank filters  
116 without copepods were subtracted from those for filters containing *M. norvegica*. To obtain a length-  
117 carbon relationship, the body lengths of 50 *M. norvegica* females from the same sample were  
118 measured using a stereo microscope (Zeiss Discovery V20).

119 To achieve population biomass of *M. norvegica*, the carbon contents of all copepodite stages  
 120 were estimated from an empirical length-carbon correlation (Uye *et al.*, 2002),  
 121

$$122 \quad C = 2.65 \times 10^{-6} \times BL^{1.95}, \quad (1)$$

123  
 124 where C is the carbon content ( $\mu\text{g}$ ) and BL the total body length ( $\mu\text{m}$ ). Body lengths of at least 10  
 125 individuals of each developmental stage were measured for selected samples to cover the full seasonal  
 126 cycle. Average body lengths of all six naupliar stages were obtained from measurements of totally 55  
 127 nauplii of different stages (from June only) and applied to eq. 1. The length and width of 30 egg sacs  
 128 were measured and the sac volume was calculated assuming cylindrical shape. All 30 egg sacs were  
 129 dissected and the individual eggs were counted, the diameter was measured and the volume of  
 130 individual eggs were calculated (as volume of a sphere).

131

### 132 **Statistical analyses**

133 Differences in sampling efficiency between the WP-2 net and Go-Flo bottle for the different  
 134 developmental stages of *M. norvegica* were tested for statistical significance by applying a  
 135 nonparametric Mann-Whitney U-test for independent samples (IBM SPSS statistics version 24). Due  
 136 to the seasonal, and hence uneven, occurrence of the younger developmental stages, including nauplii,  
 137 CI, CII and CIII (Table I), these were merged and tested as one group.

138

## 139 **RESULTS**

### 140 **Hydrography**

141 The water column was stratified from late May to late November, with warm surface water (8-10 °C)  
 142 over colder water (2-4 °C) below a thermocline at 40-80 m (Fig. 2A). A core of warm, saline (32.5 g  
 143  $\text{kg}^{-1}$ ) water was present in the surface from early June, and the water masses gradually cooled from  
 144 September. During winter, from January to April, the water column was well mixed with temperatures  
 145 from 2-4 °C. Three periods with low salinity were observed: in June 2013, January 2014, and June  
 146 2014 (Fig. 2B). These events were most likely caused by snowmelt (June) and heavy snowfall  
 147 (January). The fluorescence started to increase at the beginning of April, with maxima observed in  
 148 June 2013 and in May-June 2014, indicating spring bloom conditions around 13 and 20 m depth,  
 149 respectively (Fig. 2C). Between late October and early March, the fluorescence was below the  
 150 detection limit.

151

### 152 **Comparison of sampling methods**

153 The *M. norvegica* population in Balsfjord was sampled using a WP-2 net (90  $\mu\text{m}$  mesh) and a Go-  
154 Flo water bottle (volume 20 L). When averaging all stages and samplings integrated over 0-50 m,  
155 2.2-fold higher abundance of *M. norvegica* individuals was obtained with the Go-Flo bottle, than with  
156 the WP-2 net (Table I), and the difference is statistically significant (Mann-Whitney U-test,  $p=0.024$ ).  
157 The discrepancy between the two sampling methods was statistically significant for the group of  
158 nauplii plus young copepodites CI-CIII ( $p=0.023$ ) and for CIV-CV ( $p=0.017$ ). Females and males  
159 were sampled about equally well with the Go-Flo and WP-2 ( $p > 0.5$ ). When presenting data on *M.*  
160 *norvegica* population dynamics we will use the data obtained with the Go-Flo bottle integrated from  
161 50-0 m depth, while the data obtained by WP-2 will be used to evaluate the seasonal shifts in vertical  
162 distributions of females and males.

163

#### 164 **Body lengths and female carbon and nitrogen weight**

165 The body length of all developmental stages varied seasonally and peaked in June (Fig. 3). Females  
166 had the largest body size, followed by males. The range in C and N contents for individual females  
167 throughout the sampling period were 0.18 - 0.39  $\mu\text{g C ind}^{-1}$  and 0.03 - 0.05  $\mu\text{g N ind}^{-1}$  (Table II). The  
168 individual carbon weight (mean  $\pm$  standard deviation) was highest in October ( $0.39 \pm 0.01 \mu\text{g C ind}^{-1}$ )  
169 and lowest in March ( $0.18 \pm 0.04 \mu\text{g C ind}^{-1}$ ), while the N-content varied little between the sampled  
170 months (Table II). The C:N ratio of females ranged from  $11.2 \pm 0.5$  in October to  $6.0 \pm 0.3$  in May.

171

#### 172 **Vertical distribution**

173 Females and males were present throughout the water column year-round, but with an apparent  
174 seasonal shift (Fig. 4). From May to September, the vast majority were present in the upper 50 m,  
175 and few adults were found deeper in the water column. About half of the *M. norvegica* adult  
176 population were found below 50 m from October to January. The entire population was dominated  
177 by males and females in this winter period, with a modest contribution of developmental stages CIV-  
178 CV (Table I). From March onwards, the adult population abundance increased in the upper 50 m  
179 while declining below (Fig. 4).

180

#### 181 **Population dynamics**

182 *Microsetella norvegica* was found in high abundance in the upper water column (0-50 m) of Balsfjord  
183 year-around (Fig. 5). The maximum was observed in June 2014, a total abundance of  $9349 \times 10^3 \text{ ind.}$   
184  $\text{m}^{-2}$  ( $2977 \times 10^3$  copepodites and  $6372 \times 10^3$  nauplii), and the minimum ( $418 \times 10^3 \text{ ind. m}^{-2}$ ) occurred  
185 in late January (Table I). A clear seasonal succession of developmental stages was observed in the  
186 upper 50 m (Fig. 5). Females, males and CIV-CV had high abundances throughout the year.  
187 Oviparous females were only present from April to August (Fig. 5). Interestingly, detached egg-sacs

188 were found over a longer time-period, from April to October (Fig. 5). Nauplii were present  
189 simultaneously with ovigerous females (Table II, Fig. 5). Copepodite stages CI-CIII were present  
190 from May to September with maximum observed abundances in June.

191 The integrated population biomass of *M. norvegica* above 50 m was below 400 mg C m<sup>-2</sup> in  
192 winter (November to mid-March), and building up from early spring (March) to summer (Fig. 6). The  
193 highest observed biomass, 1.7 g C m<sup>-2</sup>, was found in June 2014 (Fig. 6). Males and females made up  
194 the largest contributions to biomass, except for June when smaller stages also contributed  
195 significantly.

196

### 197 *Microsetella norvegica* fecundity

198 Males and females were present during all months investigated (Table III). The sex ratios were  
199 skewed toward females from March to June, and strongly skewed toward males in November and  
200 January (no data are available for December). In the remaining months the sex ratios were close to 1.  
201 Females with egg sacs were present from April to August, and the total number of egg sacs (sum of  
202 egg sacs attached to females and detached egg sacs in the sample) was highest in June. The fraction  
203 of detached egg-sacs ranged from 36 to 100 % of the total number of egg-sacs recorded (Table III).  
204 The total egg sacs:females ratios were in general below 1, although as high as 1.6 in May (Table III).  
205 The egg sacs:females ratios were also slightly higher than 1 in April (Table III). No relationship was  
206 found between female body length and the number of eggs in the attached egg sacs (regression  
207  $R^2=0.000005$ ,  $p=0.99$ ,  $n=30$ ), but there was a significant positive correlation between female body  
208 length and egg sac volume ( $R^2=0.47$ ,  $p<0.0001$ ) and between clutch size and the average volume of  
209 a single egg ( $R^2=0.15$ ,  $p=0.03$ ) (data not shown). The number of eggs in an egg-sac ranged from 6 to  
210 13, with a mean  $\pm$  SD of  $11 \pm 2$  eggs (Table IV). Nauplii were present in the period from April to  
211 August, with a peak of 6 372 000 nauplii m<sup>-2</sup> in June 2014 (Table I). This corresponds to a mean  
212 concentration of 127 440 nauplii m<sup>-3</sup> in the upper 50 m, or about 130 nauplii L<sup>-1</sup>.

213

## 214 DISCUSSION

215 For a species, Gaston (2008) argues that “it is rare to be common” and that “common species are  
216 typically both abundant and widespread.” There are only a few previous observations of *M. norvegica*  
217 in high-latitude Norwegian fjords, and an earlier study explicitly stated that this species is rare in  
218 Balsfjord (Hopkins, 1981). In strong contrast, we found high abundances of *M. norvegica* throughout  
219 the year, with a population peak exceeding 9 000 000 ind. m<sup>-2</sup> in the upper 50 m in June 2014. This  
220 is among the highest abundances ever reported for this species, and the first quantitative estimate  
221 including all copepodite stages and nauplii of *M. norvegica* at similarly high latitudes (69 °N).

222

223 **Microsetella norvegica – abundant and widespread?**

224 Due to its small body size, *M. norvegica* is not efficiently caught by a WP-2 with 180  $\mu\text{m}$  mesh,  
 225 which is a widely-used zooplankton sampler. By now, it is a well-known fact that copepods with body  
 226 lengths shorter than 800  $\mu\text{m}$  are significantly underestimated when sampled with 180 – 200  $\mu\text{m}$  mesh  
 227 (Gallienne & Robins, 2001), and a mesh size of 80  $\mu\text{m}$  has been suggested as suitable for sampling  
 228 small copepods in the marine environment (Riccardi, 2010). However, we found that all copepodite  
 229 stages of *M. norvegica*, except females and males, were under sampled with a 90  $\mu\text{m}$  mesh compared  
 230 to the Go-Flo bottle.

231 The high abundances of *M. norvegica* found in Balsfjord are likely common, as high numbers  
 232 have also been reported from different geographic areas (from 45 °S to 69 °N), where zooplankton  
 233 have been sampled with mesh sizes of 100  $\mu\text{m}$  or smaller (Table V). For example, *M. norvegica* is  
 234 abundant in the White Sea, Russia (Demchuk *et al.*, 2015), in Godthåpsfjord, Greenland (Arendt *et*  
 235 *al.*, 2013), in Storfjorden, Norway (Halliday *et al.*, 2001), on the Scotian Shelf, Canada (Dugas &  
 236 Koslow, 1984), in the Central North Sea (Koski *et al.*, 2007), in the Inland Sea of Japan (Uye *et al.*,  
 237 2002) and on the Patagonian Shelf, Argentina (Antacli *et al.*, 2014, Temperoni *et al.*, 2014) (Table  
 238 V). There are also a number of studies highlighting the importance of *M. norvegica* as prey for a  
 239 variety of fish species in different habitats. For example, it was found to be the preferred prey of sprat  
 240 in Hardangerfjord, Norway (Falkenhaus & Dalpadado, 2014), three-spined stickleback in the White  
 241 Sea (Demchuk *et al.*, 2015), larval jack mackerel off eastern Tasmania (Young & Davis, 1992) and  
 242 for anchovies and sardines in the north-western Mediterranean Sea (Morote *et al.*, 2010). We  
 243 therefore suggest that *M. norvegica* is one of the supposedly rare species that is actually both abundant  
 244 and widespread (*sensu* Gaston 2008) in fjords and coastal ecosystems at high and temperate latitudes.  
 245 It is, thus, a key copepod species in these ecosystems.

246

247 **Population dynamics and C/N composition**

248 During winter (October to March), the population consisted mostly of adults, with a  
 249 predominance of males. The over-wintering females did not carry eggs. About 50 % of the adult *M.*  
 250 *norvegica* population showed a distinct seasonal migration to below 50 m from October to March,  
 251 while the other half remained in the upper water column. From this observation, it is difficult to  
 252 conclude whether *M. norvegica* are winter-active or not, but we also measured a 53 % decline in body  
 253 C, a 25 % reduction in body N and a decline in C/N ratio in females from October to March. This  
 254 probably reflects low energy intake during winter, which is comparable with seasonal patterns in  
 255 carbon content and C/N ratios for both the *C. finmarchicus* in diapause and the winter-active *Metridia*



256 *longa* in Balsfjord (Grønvik & Hopkins, 1984, Tande, 1982). The decreasing carbon content and C/N  
257 ratio through the winter (Table II) could reflect both a shift in body composition from more carbon-  
258 rich lipids in autumn to relatively more nitrogen-rich proteins in early spring when the copepods  
259 prepare for reproduction. However, this assumption is based on speculation, as lipid accumulation in  
260 this species has not been confirmed. When comparing the measured (CHN analyzer) with the  
261 calculated (equation 1) carbon content of *M. norvegica* females, the calculated values were always  
262 higher but the degree of discrepancy was variable. For instance, in October the C content calculated  
263 from body length was 10 % higher than the measured concentration, whereas in March the calculated  
264 C content was almost twice the measured concentration. This also points to a relatively large  
265 difference in body condition (e.g. lipid content), while body length was relatively stable (464  $\mu\text{m}$  in  
266 October and 457  $\mu\text{m}$  March). Nevertheless, it is likely that *M. norvegica* reduce their feeding activities  
267 during winter, although their tolerance for starvation is not known. It should also be noted that in a  
268 sub-Arctic Greenlandic fjord, *M. norvegica* did not display a defined time for leaving the upper 100  
269 m (Arendt *et al.*, 2013).

270 In March, the majority of the males and females had ascended from the deeper layers and were  
271 found in close to equal numbers in the upper 50 m depth (female:male ratio from 0.7 to 1.3). Females  
272 with eggs first appeared in April, when the sex ratios strongly favoured females (Table III). Nauplii  
273 occurred from April to August, and copepodite stages CI-CIII were present from June to September.  
274 Body sizes of *M. norvegica* varied with season and all the developmental stages were largest in the  
275 warm, high production period (May-June) (Fig. 3). The decrease in body sizes observed from June to  
276 August likely results from newly moulted copepodites from the new cohort of nauplii produced in  
277 April. Based on the clearly observed distinction between the cohorts of developmental stages, we  
278 suggest that *M. norvegica* has a single generation per year in Balsfjord. This is in contrast to the  
279 suggested five or six generations per year in the significantly warmer (25 °C in summer) central part  
280 of the Inland Sea of Japan (Uye *et al.*, 2002).

281 In general, males were more abundant than females from August to March, while the sex ratio  
282 was skewed toward females in April, May and June (no data are available for July). An adult sex-  
283 ratio skewed toward males is rarely reported for pelagic copepods (Hirst *et al.*, 2010, Kiørboe, 2006).  
284 As the availability of males to fertilize females may be a limiting factor for population growth  
285 (Kiørboe, 2007), an even sex-ratio may be regarded as an advantage for the reproductive success for  
286 *M. norvegica*. It has been reported that for copepods lacking seminal receptacles the adult sex ratio  
287 is closer to 1:1, as repeated mating is necessary to allow continued fertilisation of eggs (Kiørboe,  
288 2006). Mironova and Pasternak (2017) recently described the occurrence of seminal receptacles in  
289 female *M. norvegica*. The reason for the unusual dominance of males found in this study could instead

290 be a result of differences in gender-specific mortality due to predation or starvation. Higher mortality  
 291 rates for females could have occurred, as the total abundance of females decreased from October to  
 292 early March. Predatory mortality rates in copepods are related to behavioural traits, with a higher  
 293 mortality rate among copepods for feeding-current grazers and cruise feeders than for ambush-  
 294 feeding species, with similarly greater relative mortality for males actively searching for females  
 295 (Greve *et al.*, 2017). As the behavioural traits of male and female *M. norvegica* have not yet been  
 296 described, it is not straight forward to conclude whether the possibly gender-specific mortality rates  
 297 result from differential predation. Copepods may also display gender-specific tolerance to starvation  
 298 that can partly be explained by differences in body size (Holm *et al.*, 2018). However, for copepods  
 299 such as *M. norvegica* where the females are larger than the males, this should result in lower starvation  
 300 tolerance and greater mortality rates for males than for females. An alternative explanation for the  
 301 observed sex ratios in this study is environmental sex determination (ESD). Adult sex ratios  
 302 influenced by environmental parameters, such as temperature or pheromones, have been found for  
 303 many Crustaceans, including copepods (Svensen & Tande, 1999). Clearly, more information is  
 304 needed on the gender-specific mortality rates and sex determination mechanisms in order to explain  
 305 the unusually high abundance of *M. norvegica* males throughout the year.

306

### 307 **Patterns of reproduction**

308 The spring bloom in Balsfjord starts in March and reaches a maximum in late April (Eilertsen  
 309 *et al.*, 1981). We anticipated that reproduction of *M. norvegica* would not be restricted to this short  
 310 bloom period, a strategy differing from that of *C. finmarchicus*, which spawns during a short period  
 311 of 3-4 weeks in connection to the bloom (Diel & Tande, 1992). As *M. norvegica* may feed on marine  
 312 snow particles (Koski *et al.*, 2005, Koski *et al.*, 2007), we expected prolonged reproduction outlasting  
 313 the spring bloom. Defined according to the fraction of egg-carrying females, the reproductive onset  
 314 for *M. norvegica* was in April, with its main reproductive period in May/June. However, females with  
 315 eggs were observed until September, and detached egg sacs were recorded until November. This is  
 316 in agreement with Davis (1976) and Koski *et al.* (2014), who reported that reproduction of *M.*  
 317 *norvegica* started in April and May in the surface. In Balsfjord, Davis (1976) first observed females  
 318 with eggs in late March and did not observe any carrying eggs after mid-September. Given that  
 319 concurring data, we conclude that the egg production of *M. norvegica* is triggered by the onset of the  
 320 spring bloom, but that females can continue reproducing until September. They start spawning around  
 321 the same time as the broadcast-spawning *C. finmarchicus*, and they possibly compensate for lower  
 322 production rates by prolonged spawning and egg carrying (Kjørboe & Sabatini, 1995).

323 Egg carrying copepods produce smaller clutches than broadcast spawners (Bunker & Hirst,  
 324 2004). Egg hatching is temperature-dependent (Bunker & Hirst, 2004), and for a sac-spawner the

325 production of a new egg sac must wait until hatching of eggs from a sac already carried (Koski *et*  
326 *al.*, 2014). Sac-spawning copepods are assumed to keep the egg sac until the eggs hatch. However,  
327 an unusual reproductive strategy has been suggested for *M. norvegica*. In a sub-Arctic fjord, Koski *et*  
328 *al.* (2014) found as many as 4.5-fold more egg sacs than females in May. They suggested that *M.*  
329 *norvegica* sheds its egg sacs before the eggs hatch, allowing each female to produce a new sac of  
330 eggs earlier. We made similar observations in Balsfjord, with 1.6 egg sacs per female in May. This  
331 finding is also supported by studies on *M. norvegica* gonad morphology (Diaz & Evans, 1983,  
332 Mironova & Pasternak, 2017). Diaz and Evans (1983) also observed females possessing an egg sac  
333 while simultaneously developing new eggs internally, and they suggested that *M. norvegica* spawns  
334 more than once, producing more offspring faster than more typical sac-spawning copepods. This may  
335 explain the apparent paradox that a slowly growing species like *M. norvegica* can achieve such high  
336 abundances, as already pointed out by Koski *et al.* (2014).

337

### 338 ***Microsetella norvegica* in the food web**

339 *Microsetella norvegica* reproduces relatively slowly but can build up dense populations in fjords and  
340 coastal ecosystems. In Balsfjord, the total *M. norvegica* surface biomass during spring and summer  
341 was 600 to 1700 mg C m<sup>-2</sup> and they sustain a level of 200-300 mg C m<sup>-2</sup> during winter. They are a  
342 substantial and continuously available source of energy for fish and other predators. The maximum  
343 abundance of *M. norvegica* in this study was 9 x 10<sup>6</sup> ind m<sup>-2</sup>, corresponding to 156 copepodites L<sup>-1</sup>  
344 and 127 nauplii L<sup>-1</sup>. This points to their importance not only as prey but also as grazers. They are  
345 repeatedly observed in association with aggregates (Green & Dagg, 1997, Kiørboe, 2000), and the  
346 grazing rate on discarded larvacean houses was found to be 0.14 μg C ind<sup>-1</sup> d<sup>-1</sup> in the North-Sea (Koski  
347 *et al.*, 2007). At the abundances of *M. norvegica* copepodites observed in Balsfjord, their grazing  
348 impact on marine snow could be ~ 350 mg C m<sup>-2</sup> d<sup>-1</sup> in the upper 50 m depth. In comparison,  
349 sedimentation rates in Balsfjord in June are on the order of 100 - 200 mg C m<sup>-2</sup> d<sup>-1</sup> (Reigstad &  
350 Wassmann, 1996). *Microsetella* are under-sampled with standard zooplankton nets, making it  
351 plausible to suggest that it is substantially more abundant than previously reported. We suggest that  
352 *M. norvegica* plays an essential role in the carbon cycle of fjords and coastal ecosystems, perhaps  
353 particularly so at high-latitudes.

354

### 355 **CONCLUSIONS**

356 This is the first study to report high abundances of *Microsetella norvegica* all through the year in a  
357 high-latitude fjord, specifically Balsfjord. We expected *M. norvegica* to be active through winter, but  
358 we found that about half of the adult population migrated below 50 m from October to January.

359 Furthermore, a decline in body C:N ratios from 11.2 in October to 6.0 in May indicates low energy  
360 intake during winter. Reproduction of *M. norvegica* was not limited to the spring-bloom period, as  
361 females with eggs were observed from April to September. Moreover, our study suggests that *M.*  
362 *norvegica* females shed their egg sacs before the contained clutches of eggs are hatched, thus allowing  
363 more rapid production of clutches. A prolonged reproductive period, combined with production of  
364 multiple egg sacs by each female, may compensate for the small clutch size of  $11 \pm 2$  eggs female<sup>-1</sup>.  
365 So far, few studies have specifically targeted *M. norvegica* and their role in the pelagic food webs of  
366 high-latitude waters. We argue that it is potentially a key species with high ecological impact in  
367 coastal ecosystems of temperate climates like the Mediterranean Sea and extending far to the north  
368 including the Arctic. Our results demonstrate that increasing our knowledge of the structure and  
369 function of coastal, pelagic ecosystems will require including small and less well known copepod  
370 species in our sampling schemes.

371

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379

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508 **TABLE LEGENDS**

509

510 Table I: Integrated (0 - 50 m) abundance ( $10^3$  ind.  $m^{-2}$ ) of *Microsetella norvegica* developmental  
 511 stages obtained with Go-Flo bottle (G) and WP-2 (W). Data are presented for each sampling date,  
 512 and the mean of all samplings is provided. A statistically-significant difference between abundances  
 513 obtained with Go-Flo and WP-2 is indicated by a \* ( $p < 0.05$ ). No statistically-significant difference  
 514 between samplers is indicated by “ns”.

515

516 Table II: Body length ( $\mu m$ ) of *Microsetella norvegica* females in October, January, March and May.  
 517 Carbon content ( $\mu g$  C  $ind^{-1}$ ), nitrogen content ( $\mu g$  N  $ind^{-1}$ ) and C/N ratio (atomic) is given as the mean  
 518  $\pm$  SD (N=2 filters, each containing 300 females).

519

520 Table III: Integrated (0-50 m) seasonal abundance of ( $10^3$  ind  $m^{-2}$ ) of *Microsetella norvegica* females  
 521 (#F), females to males (F:M), egg sacs (#ES total, i.e. the sum of detached egg sacs and egg sacs  
 522 attached to females), percentage detached egg sacs (%ES detached) and the ratio of total (attached  
 523 and detached) egg sacs to total females (ES:F) for each sampling date. All data were obtained from  
 524 samples collected with the Go-Flo. Temperature ( $^{\circ}C$ ) is presented as average for the 0-50 depth  
 525 interval.

526

527 Table IV: *Microsetella norvegica* mean  $\pm$  SD body length (N=30), number of eggs per egg sac (N=  
 528 30), egg volume (N= 150) and egg sac volume (N=30) in June 2014.

529

530 Table V: Maximum abundances (individuals  $m^{-3}$ ) of *Microsetella norvegica* reported from different  
 531 regions. Abundances of copepodites (C) and nauplii (N) are given separately when possible;  
 532 otherwise the abundances represent total abundance of individuals, as reported in the respective  
 533 studies. Mesh sizes ( $\mu m$ ) of sampling devices are provided.

534



535 **FIGURE LEGENDS**

536

537 Fig. 1. Map of the Tromsø area, showing the location of sampling station Svartnes in Balsfjord,  
538 northern Norway.

539

540 Fig. 2. A) Temperature (°C), B) salinity (g kg<sup>-1</sup>) and C) fluorescence at station Svartnes from August  
541 2013 to June 2014. The black vertical lines indicate dates of sampling, ND implies no data.

542

543 Fig. 3. *Microsetella norvegica* seasonal body length (mean ± SD).

544

545 Fig. 4. Vertical distribution of the sum of *Microsetella norvegica* females and males from May 2013  
546 to June 2014 as sampled with a WP-2 net (90 μm mesh) and integrated in the surface (50-0 m) and in  
547 the deep layer (175-50 m). Data are presented in terms of abundance (10<sup>3</sup> ind. m<sup>-2</sup>). For months with  
548 more than one sampling, the mean is given.

549

550 Fig. 5. Integrated (0-50 m) abundance (ind m<sup>-2</sup>) of *Microsetella norvegica* developmental stages  
551 sampled with Go-Flo from May 2013 to June 2014. Note the logarithmic y-axes.

552

553 Fig. 6. Integrated (0-50 m) biomass (mg C m<sup>-2</sup>) and relative stage composition (% contribution) of  
554 *Microsetella norvegica* sampled with Go-Flo from May 2013 to June 2014. ND implies no data, for  
555 months with more than one sampling, the mean is given.

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559 **TABLES**

560

561 **Table I.**

Date	Nauplii*		CI*		CII*		CIII*		CIV-CV*		Females <sup>ns</sup>		Males <sup>ns</sup>		Total*	
	G	W	G	W	G	W	G	W	G	W	G	W	G	W	G	W
27.05.13	1235	9	234	21	70	178	23	53	0	20	125	398	36	49	1723	629
28.06.13	2165	0	552	10	785	15	657	26	26	0	994	1102	276	385	5455	1538
23.08.13	121	0	46	10	221	15	237	26	253	0	828	1102	922	385	2519	1538
19.09.13	0	0	3	0	31	0	21	8	61	86	768	904	876	1004	1759	2002
15.10.13	0	0	0	0	0	0	0	0	26	10	514	248	1253	567	1792	826
19.11.13	0	0	0	0	0	0	0	0	23	10	163	205	358	383	543	599
08.01.14	0	0	0	0	0	0	0	0	39	0	167	322	588	387	794	709
30.01.14	0	0	0	0	0	0	0	0	12	2	116	108	289	143	418	254
04.03.14	0	0	0	0	0	0	0	0	9	11	190	214	278	227	477	452
25.03.14	0	0	0	0	0	0	0	0	43	8	579	395	459	476	1081	878
29.04.14	213	0	0	0	0	0	0	0	51	31	916	897	445	604	1626	1532
06.05.14	678	0	0	0	0	0	0	0	239	96	1083	1169	801	705	2801	1971
16.06.14	6372	870	517	24	229	0	97	0	24	5	1616	290	494	86	9349	1276
Mean	821	68	104	5	103	8	80	9	62	22	620	566	544	415	2334	1093

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571 **Table II.**

	October	January	March	May
Body length, $\mu\text{m}$	$464 \pm 37$	$438 \pm 36$	$457 \pm 41$	$486 \pm 45$
$\mu\text{g C female}^{-1}$	$0.39 \pm 0.01$	$0.30 \pm 0.04$	$0.18 \pm 0.04$	$0.26 \pm 0.01$
$\mu\text{g N female}^{-1}$	$0.04 \pm 0.00$	$0.04 \pm 0.01$	$0.03 \pm 0.01$	$0.05 \pm 0.00$
C/N female <sup>-1</sup>	$11.2 \pm 0.5$	$9.8 \pm 1.2$	$8.2 \pm 1.6$	$6.0 \pm 0.3$

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575 **Table III.**

Month	Dates (D/M/Y)	Temp, °C (0-50 m)	# F	F:M	# ES total	% ES detached	ES:F
Jan	08/01/14	4.5	166	0.3	0	-	-
	30/01/14	3.2	116	0.4	0	-	-
March	04/03/14	2.6	190	0.7	0	-	-
	25/03/14	2.4	579	1.3	0	-	-
April	29/04/14	3.2	916	2.1	979	49	1.1
May	27/05/13	nd	125	3.5	124	49	1
	06/05/14	3.5	1083	1.4	1225	98	1.6
June	28/06/13	5.6	994	3.6	940	73	0.9
	16/06/14	6.7	1616	3.3	1367	36	0.8
Aug	23/08/13	8.0	828	0.9	82	96	0.1
Sept	19/09/13	8.6	768	0.9	20	100	<0.1
Oct	15/10/13	8.4	514	0.4	5	100	<0.1
Nov	19/11/13	6.4	163	0.5	0	-	-

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580 **Table IV.**

Body length ( $\mu\text{m}$ )	# Eggs egg sac <sup>-1</sup>	Volume egg <sup>-1</sup> (mm <sup>3</sup> )	Volume egg sac <sup>-1</sup> (mm <sup>3</sup> )
542 $\pm$ 38	11 $\pm$ 2	152 $\pm$ 45	8463 $\pm$ 2711

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584 **Table V.**

Region	Latitude	Max abund. (Ind. m <sup>-3</sup> )	Mesh size ( $\mu$ m)	Reference
Balsfjord, Norway	69 °N	156 800 (C) 127 440 (N)	20*	This study
White Sea, Russia	66 °N	20 000	93	Demchuk et al. (2015)
Godthåpsfjord, Greenland	64 °N	91 995 (C) 408 125 (N)	45	Arendt et al. (2013)
Storfjorden, Norway	62 °N	20 000	53	Halliday et al. (2001)
Sandsfjorden, Norway	59 °N	3990	45*	Nielsen and Andersen (2002)
Central North Sea	56 °N	1100 (C) 500 (N)	50*	Koski et al. (2007)
Scotian Shelf, Canada	42-43 °N	3940	80	Dugas & Koslow (1984)
Inland Sea of Japan	34 °N	73 200 (C) 25 000 (N)	94 40*	Uye et al. (2002)
Patagonian Shelf, Argentina	47-66 °S	917	66	Antacli et al. (2014)
Patagonian Shelf, Argentina	43-45 °S	256	67	Temperoni et al. (2014)

585 \*Sampled with water-bottles, mesh size at which sample was concentrated is given

18°

20°

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Tromsø

Ullsfjord

Balsfjord

Svartnes

Malangen

Målselv

10°

20°

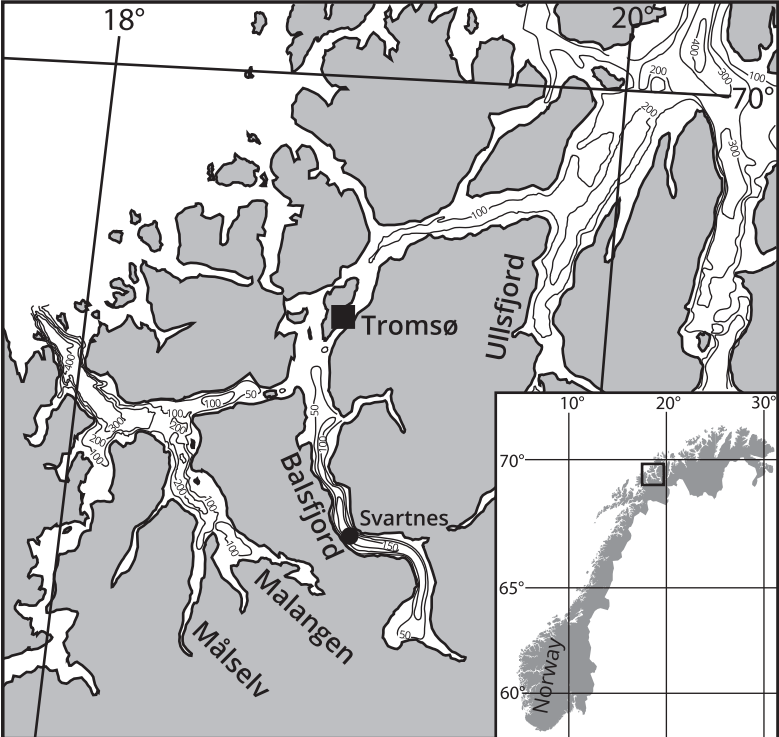
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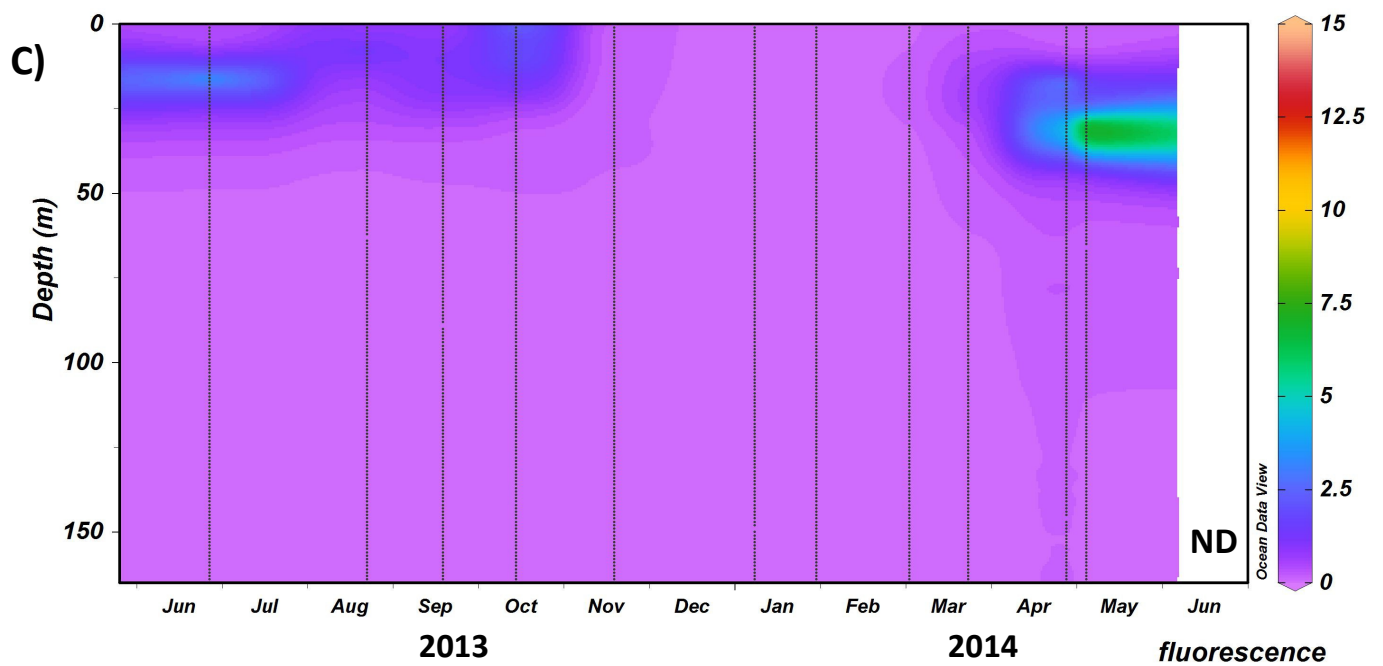
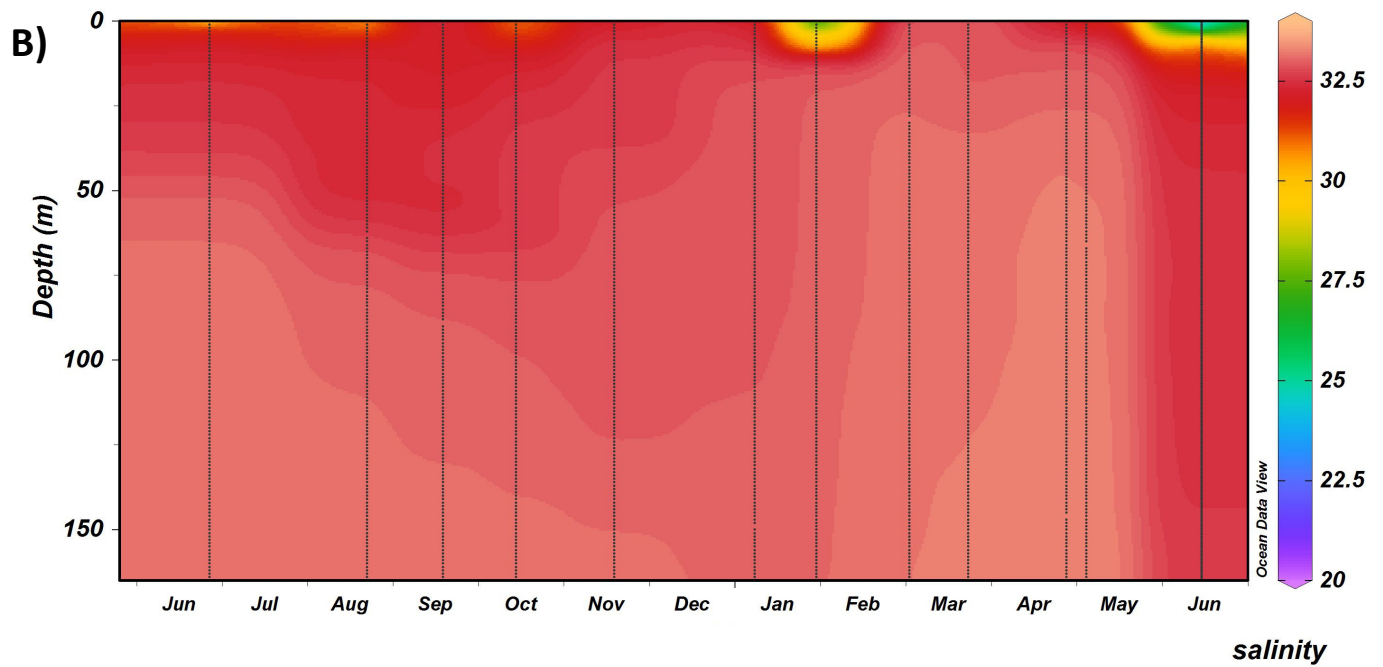
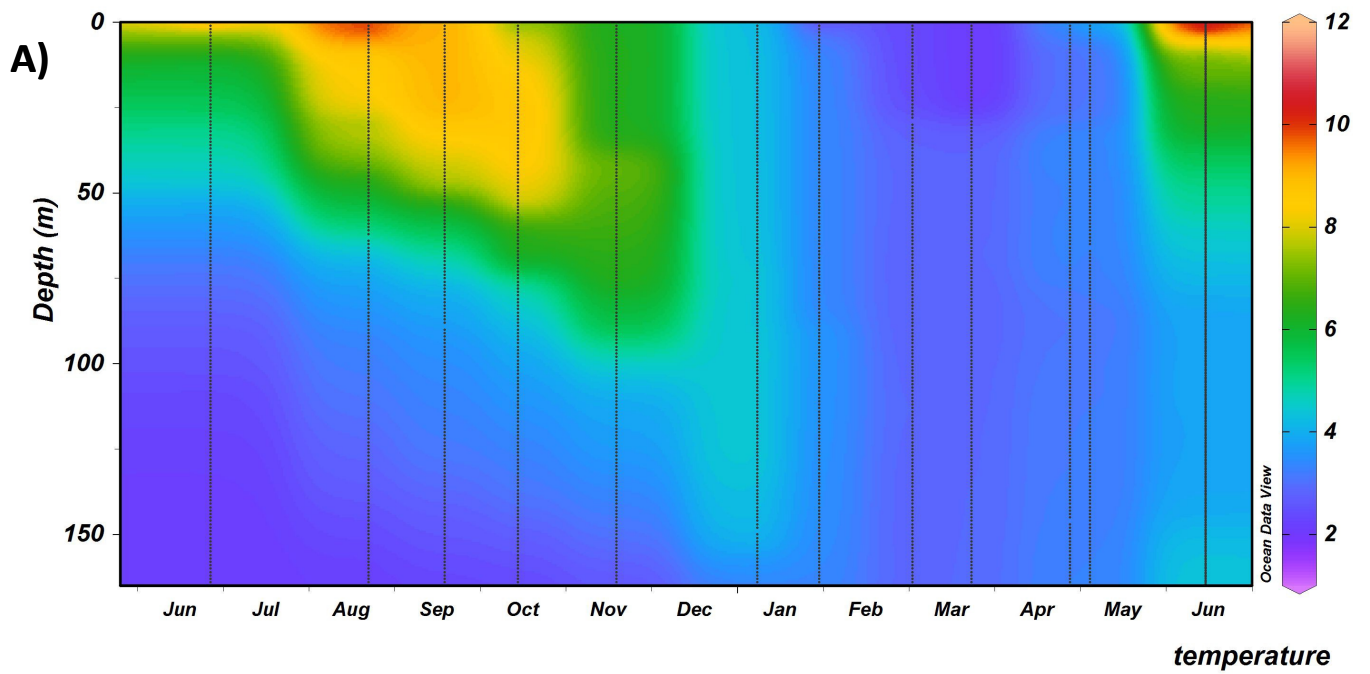
70°

65°

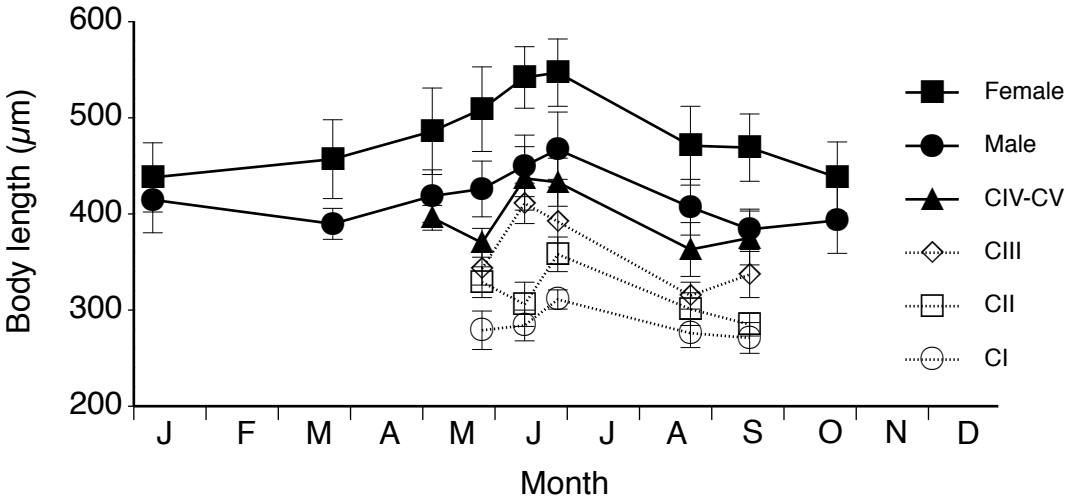
60°

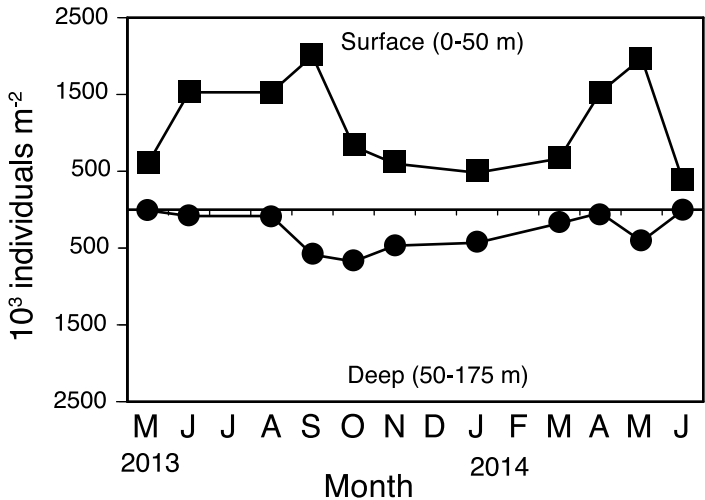
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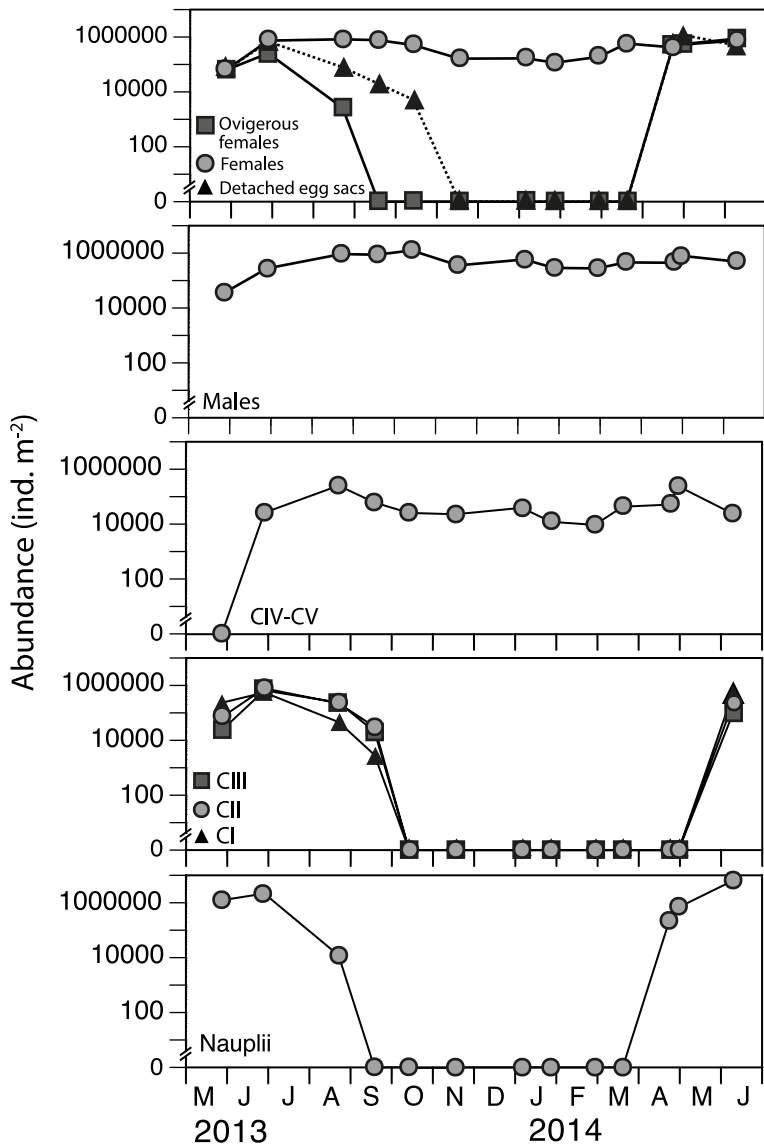


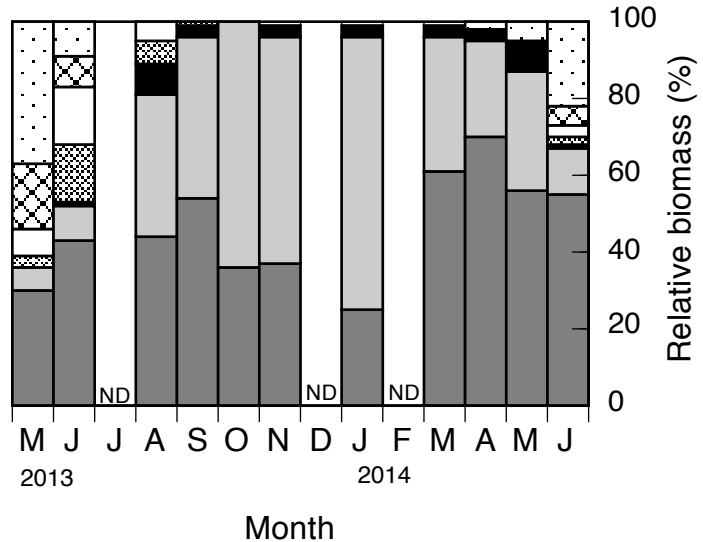
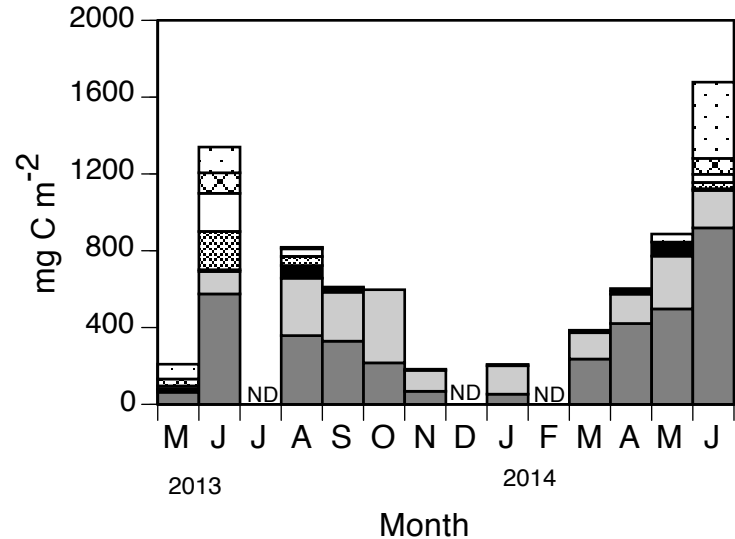












Nauplii
  C I
  C II
  C III
  C IV-CV
  Males
  Females