Spatial, seasonal and inter-annual variation in abundance and carbon turnover of small copepods in Young Sound, Northeast Greenland

Ane Bruun Middelbo¹, Eva Friis Møller^{1,3}, Kristine Engel Arendt², Jakob Thyrring^{1,4}, Mikael K. Sejr^{1,4*}

¹Arctic Research Centre, Aarhus University, Ny Munkegade 114, building 1540, 8000 Aarhus C, Denmark

²Greenland Climate Research Centre, Greenland Institute of Natural Resources, Kivioq 3, PO Box 570, 3900 Nuuk, Greenland

³Department of Bioscience, Aarhus University, Frederiksborgvej 399, 4000 Roskilde, Denmark

⁴Marine Ecology, Department of Bioscience, Aarhus University, Vejlsøvej 25, 8600 Silkeborg, Denmark

* Corresponding author: mse@bios.au.dk

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25 **Abstract**

26 We investigated the production and population dynamics of the small copepods *Oithona similis* and
27 *Pseudocalanus* spp. in Young Sound, Northeast Greenland, during the ice-free period from July to
28 October 2014 at four stations located along a freshwater gradient from the inner fjord to the
29 Greenland Sea. Additionally, inter-annual variation in copepod species composition over the past
30 decade was examined. Finally, egg hatching rate of *Pseudocalanus* spp. as a function of
31 temperature was measured in the laboratory. Small copepod species dominated total copepod
32 abundance throughout the season especially in the freshwater impacted inner fjord. The most
33 abundant species in the upper 100 m of the water column were *O. similis*, *Oncaea borealis* and
34 *Pseudocalanus* spp. Production of *Pseudocalanus* spp. was related to chlorophyll *a* concentration
35 while production of *O. similis* was less so. Egg production and stage composition indicated that *O.*
36 *similis* continued to reproduce throughout the year, while reproduction of *Pseudocalanus* spp. was
37 restricted to the spring and summer. Observed egg hatching rates of *Pseudocalanus* spp. were faster
38 at sub-zero temperatures than previously reported. The relative production of small species was
39 minor compared to *Calanus* spp. in July and August, but it accounted for a relatively large fraction
40 of the production in September and October (6-69%). On a decadal scale only *Pseudocalanus* spp.
41 showed an overall reduction in abundance, while the abundances of other genera were relatively
42 constant. Our study suggests that increasing freshwater runoff and a longer growth season, due to
43 later ice formation, may increase the proportion of primary production passing through the smaller
44 copepod species.

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50 **Introduction**

51 Arctic copepod species have several different life strategies for survival and reproduction under the
52 extreme light and sea ice regimes present in the Arctic (Darnis & Fortier 2014). Larger copepods of
53 the genus *Calanus* are often the most dominant species, in terms of biomass, during the productive
54 season and are therefore considered the most important grazers in Arctic and subarctic regions
55 (Hopcroft et al. 2005, Moller et al. 2006, Arendt et al. 2010, Dunweber et al. 2010). *Calanus* spp.
56 overwinter in deep waters in a diapause state with reduced metabolic activity. When the spring
57 phytoplankton bloom starts to develop, *Calanus* spp. ascend from the deep, feed, reproduce and
58 build up lipid stores (Madsen et al. 2001, Falk-Petersen et al. 2008, Darnis & Fortier 2014). In
59 contrast, smaller copepod species such as *Oithona similis* and *Oncaea borealis* are active
60 throughout the year (Zamora-Terol et al. 2013, Darnis & Fortier 2014, Zamora-Terol et al. 2014).
61 They are the most abundant copepods in surface waters year round and may dominate the copepod
62 biomass from late summer through winter (Madsen et al. 2001, Auel & Hagen 2002, Hopcroft et al.
63 2005, Moller et al. 2006, Madsen et al. 2008). Due to sustained reproduction and shorter generation
64 times (Ashjian et al. 2003, Lischka & Hagen 2005), the smaller copepods may be more important
65 contributors to secondary production than suggested by their biomass alone (Sabatini & Kiørboe
66 1994, Madsen et al. 2008).

67 The egg-carrying cyclopoid copepod *O. similis* feeds on motile phytoplankton and
68 protozooplankton (Paffenhofer 1993, Sabatini & Kiørboe 1994, Zamora-Terol et al. 2013), *Oncea*
69 *borealis* are omnivores or carnivores (Kattner et al. 2003, Martynova & Gordeeva 2010) whereas
70 the egg-carrying calanoid copepod *Pseudocalanus* spp. is a suspension feeder, mainly eating
71 phytoplankton (Eiane & Ohman 2004). Because of their size, small species only have limited ability
72 to store lipid reserves. This forces them to continue feeding even during winter (Madsen et al. 2008,
73 Narcy et al. 2009). However, *Pseudocalanus* spp. do go through the winter with considerably

74 reduced metabolism (Lischka & Hagen 2005). Assuming that mature females allocate most energy
75 for reproduction, the egg production rate can be used as a proxy for grazing and productivity
76 (Mclaren et al. 1989, Nielsen et al. 2002). Reproduction of small copepods is directly governed by
77 abiotic and biotic factors e.g. temperature, food availability and predator-prey interactions (Mclaren
78 et al. 1989, Nielsen et al. 2002), while reproduction of the larger *Calanus* species is additionally
79 determined by lipid content of the females (Henriksen et al. 2012, Kjellerup et al. 2012). This
80 introduces a potential time lag in the dependency of *Calanus* spp. on food. Due to differences
81 among copepod species in phenology and physiology, individual species respond differently to
82 changes in biotic and abiotic factors. To understand dynamics of productivity and potential changes
83 in the Arctic marine environment, it is essential to understand and identify the factors controlling
84 the productivity of ecologically distinctive copepod species.

85 Young Sound is a High Arctic fjord located in Northeast Greenland. Fjords constitute transition
86 zones between land or ice sheet and the ocean. They are under constant influence of both terrestrial
87 and marine processes. Young Sound is characterised by extended seasonal sea ice coverage and a
88 short open water period, though the tendency is toward a longer ice-free period (Glud et al. 2007).
89 During the summer several land terminating glaciers and melt-water rivers deliver fresh water into
90 the fjord. The freshwater input from land has major implications for stratification of the water
91 column and will therefore affect vertical distribution and production of primary and secondary
92 producers in the fjord (Arendt et al. 2016). Direct contact to the Greenland Sea at the mouth of the
93 fjord and freshwater input from the Greenland Ice Sheet in the inner fjord creates a freshwater
94 gradient along the fjord. Therefore, Young Sound is an ideal place to study how freshwater impacts
95 copepod production and species composition.

96 Our aim in the present study was to evaluate the importance of small copepod species in Young
97 Sound in relation to season and freshwater impact. We investigated the population dynamics and

98 production responses of *Pseudocalanus* spp., *O. similis* and *O. borealis* to differences in biotic and
99 abiotic factors in Young Sound from July to October.

100

101 **Materials and methods**

102 **Sampling and study site:** The study was conducted in Young Sound (Fig. 1), an Arctic fjord in
103 Northeast Greenland (74°18'N, 20°10'W) from July 11 to August 10 and from September 3 to
104 October 7, 2014. Young Sound is 90 km long, 2-7 km wide and covers 390 km². Maximum depth is
105 330 m, and two sills of about 50 meters depth separate the deeper parts of the fjord from the
106 Greenland Sea. The fjord receives melt water from the Greenland Ice Sheet and local ice caps.
107 There are no tide-water glaciers terminating directly into the fjord, but melt water reaches the fjord
108 through several rivers. Typically, the seasonal runoff of freshwater from land starts in early July,
109 peaks in early August and stops around September. Glacial melt water has been estimated to
110 contribute approximately 80% of the total freshwater runoff into the inner part of the fjord system
111 (Citterio et al. 2017). Sampling was conducted at four stations (Fig. 1) along the freshwater gradient
112 from the inner fjord to the ocean. Collecting was conducted between 09:00 and 16:00 h and
113 included samples from just before the sea-ice break-up in the middle of July to the end of the ice-
114 free period at the beginning of October. Station 1 was sampled five times, station 2 was sampled six
115 times, station 3 was sampled eight times and station 4 was sampled six times during the season.

116

117 **Hydrography and chlorophyll a:** Vertical profiles of temperature, salinity and fluorescence were
118 recorded on each sampling occasion using a Seabird SBE 19+ CTD (Seabird Electronics). All
119 profiles were conducted from the surface down to maximum possible depth. In addition to the 4 key
120 stations, we conducted CTD transects on approximately 25 stations along the fjord to describe in
121 detail the transition from the inner fjord to the coastal ocean. This transect was sampled four times

122 during the season. At the four key stations, water samples were taken at six depths (1, 10, 20, 30, 40
123 and 100 m) and in the chlorophyll *a* maximum (DCM) with a 12 bottle 1.2 l Niskin mini rosette. A
124 Satlantic Free-falling Optical Profiler was used to determine the DCM depth prior to every
125 sampling occasion. Water samples were kept in the dark in 10 l plastic containers and transported
126 back to the laboratory for further analysis. For chlorophyll *a* analysis, triplicate 250 ml aliquots
127 from each sampling depth were filtered through GF/F filters. At two depths (1 m and DCM)
128 additional triplicate 250 ml aliquots were filtered through 10 µm filters for size-fractionated
129 chlorophyll *a* concentrations. Chlorophyll *a* was extracted in 5 ml of 96% ethanol for 12-24 hours
130 and analysed on a Turner Design fluorometer before and after HCL addition (Jespersen &
131 Christoffersen 1987). Calibration was done against a chlorophyll *a* standard.

132

133 **Protozooplankton:** Ciliates and dinoflagellates were collected from 1 m depth and the DCM.
134 Samples were fixed in acid Lugol's solution (2% final concentration) and stored cold and dark until
135 analyses. In the laboratory, 50 ml were examined after 24 h sedimentation in Utermöhl chambers
136 (Utermöhl 1958). Ciliates and dinoflagellates were enumerated and identified to
137 species/morphotype level using an inverted microscope (magnification: 200–400 x).

138

139 **Copepod sampling:** On each sampling occasion at the 4 stations three vertical WP-2 net hauls from
140 0-100 m depth were made. Two hauls using a 45 µm net and one using a 200 µm. One of the 45
141 µm net sample was used to quantify copepod biomass and species composition and the other 45 µm
142 net sample was used to quantify egg hatching rate and egg:female ratio. The 200 µm sample was
143 used to estimate faecal pellet production rates as an indirect measure of *Calanus* production. These
144 experiments are reported in detail in a separate paper (Middelboe et al. submitted) but here we use

the integrated *Calanus spp.* production rates for comparison with production estimates for *Oithona spp.* and *Pseudocalanus spp.*

Each WP-2 net was equipped with a large, non-filtering cod-end. Filtered volumes were calculated as depth of the tow multiplied by the net opening area. Net clogging was not a problem in Young Sound, since chlorophyll *a* concentrations and zooplankton biomasses were low. Samples used for species identification were preserved in 5% buffered formalin. Individuals were counted, and species, stage and sex were identified. Prosome length was measured for 10 individuals of each species/stage group in all samples. Carbon contents of *O. similis*, *Pseudocalanus spp.* and *O. borealis* were calculated from length:C-weight regressions available in literature (Breteler et al. 1982, Sabatini & Kiørboe 1994), and depth integrated biomass was calculated.

Oithona similis and *O. borealis* were identified to species level. We found two species of *Pseudocalanus spp.* in Young Sound, *P. acuspes* and *P. minutus*. Due to difficulties in differentiating the two species, only adult females and males were identified to species level, and all copepodite stages and nauplii were identified to spp. Therefore, *Pseudocalanus* is represented by spp. in the following.

Egg hatching rate: To estimate the production of egg carrying copepods, information about egg hatching rate, eggs:female ratio and carbon contents of females and eggs were used. The egg hatching rate (HR, % d⁻¹) as a function of temperature (T, °C) for the cyclopoid copepod *O. similis* was available from the literature (Nielsen et al. 2002) and calculated from the following equation:

$$HR = 4.2176 + 1.7545T$$

where HR is egg hatching rate (% d⁻¹) and T is temperature (°C).

We measured egg hatching rate of the calanoid copepod *Pseudocalanus spp.* as a function of temperature. Female *Pseudocalanus spp.* for egg hatching experiments were collected from one of

168 the 45 μm WP-2 net hauls. Immediately after sampling, the content of the cod-end was diluted in
169 seawater from 20 m depth collected with a 5 l Niskin bottle and transported back to the laboratory
170 in a thermobox cooled with ice. Female *Pseudocalanus* spp. carrying egg sacs were sorted in petri
171 dishes in ice filled trays and placed individually in tissue culture trays (NUNCTM Multi wells) of 24
172 wells containing 3 ml GF/F filtered seawater and incubated at constant temperature. The experiment
173 was carried out at five different temperatures (-1.8, 1.1, 3.0, 4.7 and 6.6°C) representing the
174 seasonal temperature span in Young Sound. HOBO temperature data loggers recorded the
175 temperature every 20 min. Every ~8 hour, the wells were examined under a Leica stereomicroscope
176 and the number of females with eggs hatched from their sacs were noted. The experiments ran until
177 eggs in all sacs had hatched, except the -1.8° C experiments, which ran until 92% of the egg sacs
178 had hatched. Hatching time is the time required to reach 100% hatching. Hatching rate (% d⁻¹) at
179 each temperature was estimated by a linear regression between the incubation time and cumulative
180 hatching percentage. Hatching time for the -1.8°C experiment was predicted from the regression.
181 The above calculations were used to derive a general equation to estimate production of
182 *Pseudocalanus* spp. as a function of temperature.

183

184 **Estimation of egg production and secondary production:** Shortly after return to the laboratory,
185 the sample from one of 45 μm WP-2 net hauls was examined under a stereomicroscope and
186 *Pseudocalanus* spp. and *O. similis* females were collected. Number of females carrying egg sacs,
187 total number of egg sacs (including detached egg sacs), females without egg sacs and number of
188 eggs in each egg sac was noted. The sample was analysed until 50 females of each species were
189 collected. If fewer females were present, the whole sample was examined. The ratio of ovigerous
190 females was estimated by dividing the number of females with the number of egg sacs and the

191 abundance of eggs was calculated by multiplying the number of egg sacs with the average number
 192 of eggs per egg sac.

193 To estimate carbon content of females, the lengths of 10 *Pseudocalanus* spp. and *O. similis* females
 194 were measured from the biomass sample on each sampling date, and the average sizes were
 195 calculated. To estimate carbon content of eggs we used a mean egg diameter calculated from 10
 196 measured eggs from each species on each sampling date. Carbon content was calculated applying
 197 an egg carbon-content factor of $0.14 \cdot 10^{-6} \mu\text{g C } \mu\text{m}^{-3}$ to egg volume (Kiørboe et al. 1985, Sabatini &
 198 Kiørboe 1994).

199 The specific egg-production rate (SEP, % d⁻¹) of the egg carrying copepods was calculated by the
 200 following equation (Nielsen et al. 2002):

$$201 \quad SEP = \left(\frac{egg}{female} \right) HR \left(\frac{C_{egg}}{C_{female}} \right)$$

202 where egg/female is average ratio for the population, HR (% d⁻¹) is the hatching rate at the *in situ*
 203 temperature, C_{egg} and C_{female} are the carbon contents of eggs and females.

204 Assuming SEP to be equal to juvenile somatic growth rates (Corkett & McLaren 1978, Berggreen et
 205 al. 1988, Nielsen et al. 2002), secondary production (mg C m⁻³ d⁻¹) of each species was estimated as
 206 SEP multiplied by mean biomass of each species (mg C m⁻³) in the upper 100 m of the water
 207 column. We assumed that *Oncaea borealis* had the same SEP as *O. similis*.

208 The large copepods were mostly *Calanus* spp. To estimate their production we used the grazing
 209 rates estimated from faecal pellet production of copepods retained on a 200 µm net (Middelbo et al.
 210 submitted) and assumed a gross growth efficiency of 32% (ref).

211

212 **Time series data:** Data on copepod species abundance at station 3 from 2003-2014 were used to
 213 evaluate inter-annual variation in species composition over the past 10 years. Each year in late July
 214 to mid August, triplicate 45 µm WP-2 net hauls were collected on three separate sampling dates.

215 Net hauls were collected from the surface to 150 m depth. Sea ice data from the last 63 years were
216 used to evaluate the open-water period in Young Sound. Data were obtained from the Greenland
217 Ecosystem Monitoring program. (www.g-e-m.dk)

218

219 **Data analysis:** Prior to any analysis, data exploration was carried out following Zuur et al. (2010).
220 Homogeneity of variance was visually inspected using conditional boxplots, and normality of the
221 residuals was assessed using qqplots in R (Zuur et al. 2010). It was decided to use regression
222 analysis to test for relationships between egg hatching rates, production, temperature and food
223 availability. Two tailed *t*-tests were used for investigating the production of copepods among
224 seasons and a one-way ANOVA was applied to test differences in production among the four key
225 stations. To test for temporal changes in species composition we used linear regressions to test for
226 changes in the relative abundance of each individual species group in the period 2003-2014. Once
227 valid models were identified we re-examined the residuals to ensure model assumptions were
228 acceptable.

229

230

231 **Results**

232 **Hydrography, chlorophyll *a* and protozooplankton:** Sea ice in the central part of the fjord broke
233 up on July 15. Sea ice in the inner and outer fjord broke before that, and the spring phytoplankton
234 bloom had possibly initiated prior to our first sampling. Solar heating and freshening of the surface
235 water developed stratification of the water column that strengthened and deepened during the
236 summer. A thermocline with warmer surface water and colder water below 20 m was present in
237 July and August (Fig. 2). Freshwater runoff delivered to the inner fjord developed a halocline with a
238 thin (5-6 m) layer of low salinity water (< 20) in the surface (Fig. 3). The halocline was most

defined in the inner fjord and less so toward the Greenland Sea. We found a clear trend in surface salinity and turbidity in July and August, with low salinity and high turbidity in the inner fjord and higher salinity and lower turbidity towards the Greenland Sea. In September and October, the water column became mixed as convection of the freshwater in the upper 20 m of the water column even out the temperature difference (Fig. 2&3).

Mean chlorophyll *a* concentrations for the upper 100 m of the water column are shown in Figure 2. In July and August small (< 10 µm) phytoplankton cells were the most abundant at station 1 (77-92%), whereas station 2 was dominated by larger phytoplankton cells (73-94%) from mid July to mid August. Larger cells also dominated at stations 3 and 4 until the beginning of September (53-98%). Late in the season, small phytoplankton cells increased in abundance at all stations (Fig. 2). Protozooplankton was dominated by small ciliates (20-30 µm, relative abundance 32 %), *Gyrodinium spp.* (27%), *Protoperidinium spp.* (~25 µm, 23%) and *Strobidium spp.* (12 %) (Fig. 4).

Egg hatching of *Pseudocalanus* spp.: Egg hatching rate of *Pseudocalanus* spp. was related to temperature and increased from 8.0% d⁻¹ to 25.6% d⁻¹ across the temperature range from -1.8 °C to 6.6 °C (Fig. 5). Hatching rate (% d⁻¹) as a function of temperature was best described by an exponential model, while an exponential decay model provided a best fit for development time (days) (Fig. 6):

$$HR = 8.59 * e^{(0.164T)}, \quad (r^2 = 0.95, n = 5)$$

where HR is egg hatching rate (% d⁻¹), and T is temperature (°C). Hatching time is 1/HR. A comparison of egg hatching times of *Pseudocalanus* spp. (present study) to those of *P. minutus* and *P. acuspes* (McLaren et al. 1989) and *O. similis* (Nielsen et al. 2002) shows that the hatching time of *Pseudocalanus spp.* from this study was shorter at sub-zero temperatures compared to those reported by McLaren et al. (1989). Furthermore, *O. similis* has a longer hatching time at low

262 temperatures ($< 5^{\circ}\text{C}$) and shorter hatching time at higher temperatures compared to *Pseudocalanus*
263 *spp.* (Fig. 7).

264

265 **Copepod abundance:** Throughout the open water period in Young Sound small copepod species
266 dominated the copepod standing stock in terms of numerical abundance (Fig. 8). Dominance of
267 small taxa was lowest in July and August, the increasing toward the end of the season to account for
268 $>93\%$ of all individuals by the end of September and start of October. In terms of abundance, *O.*
269 *similis* was the most abundant copepod species followed by *O. borealis* and then *Pseudocalanus*
270 *spp.* (Fig 8). Together these three taxa constituted 55-98% of the total numerical abundance. The
271 mean abundance of *Calanus* spp. ranged between 120-1200 ind. m^{-3} during the sampling period,
272 and small non-*Calanus* species thus constituted 63-99% of copepod numbers during the open water
273 season. Overall, small species were most important at the freshwater impacted station 1 (mean
274 91.6% small species in July, August and early September) and least important at station 3 (mean
275 73.6% small species July, August and start September) (Fig. 8).

276

277 **Stage composition of *O. similis*, *Pseudocalanus* spp. and *O. borealis*:** For *O. similis*, nauplii were
278 most abundant at all stations. Abundances of larger copepodite stages (CII-CV) and females were
279 quite evenly distributed at all samplings, but their proportions increased toward the end of the
280 season at all stations (Fig. 9). Males were significantly less abundant than females but were present,
281 with a few individuals m^{-3} throughout the season at all stations.

282 For *Pseudocalanus* spp., all copepodite stages and nauplii were found during the sampling period.
283 However, no females were observed at station 4. Males were completely absent at all stations
284 throughout the sampling. Nauplii were most abundant early in the season, becoming less abundant
285 in September and October. Similarly, female abundance declined to ≤ 1 individual m^{-3} late in the

286 season. As naupliar abundance decreased, CIV and CV in particular became more abundant (Fig.
 287 9). For *O. borealis*, copepodites were most abundant in July and August, while males and females
 288 became more abundant in September and October (Fig. 9).
 289
 290 **Egg production and secondary production:** *Oithona similis* reproduced throughout the season,
 291 except at station 1 on September 27, where no egg sacs were found in the 45 μm net haul. However,
 292 egg sacs were observed in the 200 μm net tow used to estimate copepod biomass, suggesting that
 293 some *O. similis* were still reproducing at station 1 late in the season. *Oithona similis* reproduced at
 294 low rates (0.08 - 1% body C d^{-1}). The maximum SEP rate of $\sim 1\%$ body C d^{-1} was found at station 2
 295 in the middle of July (Fig. 10A). Only a few *Pseudocalanus* spp. females were caught for
 296 estimation of egg production in September and October at all stations and at station 4 throughout
 297 the sampling period consistent with low female abundance (Fig. 9). However, we calculated SEP
 298 based on few individuals (marked with * in figure 10).
 299 There were no significant relationships between total chlorophyll *a* and SEP for *Pseudocalanus* spp.
 300 ($r^2 = 0.03$, $P = 0.3378$, $n = 25$) or *O. similis* ($r^2 = 0.06$, $P = 0.2139$, $n = 24$). However, there was a
 301 significant linear relationship between large chlorophyll *a* fraction ($> 10 \mu\text{m}$) and SEP for
 302 *pseudocalanus* spp. ($r^2 = 0.11$, $P = 0.0492$, $n = 25$) but not for *O. similis*. In general *Pseudocalanus*
 303 spp. reproduced at low rates (0 – 0.9% body C d^{-1}) with the highest rates in July and August
 304 declining to zero toward the end of the open water period (Fig. 10A). The maximum SEP rate of
 305 $\sim 0.9\%$ body C d^{-1} was measured at station 3 in the middle of July (Fig. 10A). For *O. similis*,
 306 production ranged from 0.022 to 1.1 $\mu\text{g C m}^{-3} \text{d}^{-1}$, while production of *Pseudocalanus* spp. was
 307 lower ranging from 0 to 0.6 $\mu\text{g C m}^{-3} \text{d}^{-1}$. Production of *Pseudocalanus* spp. declined to zero in the
 308 end of the sampling period at all sites, while production of *O. similis* fluctuated more over the
 309 season (Fig. 10B). A comparison of the relative production by large and small copepod species

310 showed that *Calanus* spp. accounted for 89-99% of the copepod production in July and August (Fig
311 11). In contrast, small species accounted for 6-69% of the production in September and October
312 (Fig. 11). Season (July/August vs. September/October) had a significant effect on the relative
313 production of small (Two-tailed *t*-test; $t_{23} = 5.719$, $P < 0.0001$) and large copepods (Two-tailed *t*-
314 test; $t_{23} = 5.801$, $P < 0.0001$). Station had no effect on production of either small or large copepods
315 (One-way ANOVA; $F_{3,25} = 315.3$ $P = 0.6594$).

316

317 **Open-water duration and inter-annual variation in species composition:** 63 years of data for
318 sea ice break-up and ice formation dates show that the ice-free period in Young Sound is
319 increasing. This is primarily due to later ice formation (Fig. 12A). The duration of the open water
320 period has increased from 82 ± 9 (SD) to 100 ± 5 days from 1950-1955 to 2009-2013. A time series
321 of species composition in August (2003-2014) revealed that *Pseudocalanus* spp. showed a
322 significant reduction in relative abundance ($r^2 = 0.15$, $P < 0.0001$, $n = 96$) (Fig 12B), while other
323 species have non-significantly fluctuated during the last decade (all linear regressions; $P > 0.05$)
324 (Fig. 12B). Total copepod abundance has been fluctuating from ~ 70 to 350 individuals m^{-3} .

325

326 Discussion

327 **Copepod species composition:** Along the freshwater gradient in Young Sound, small copepod
328 species were most important at the freshwater impacted station 1 and least important in the outer
329 region of the fjord in terms of abundance (Fig. 8). In July, August and the beginning of September,
330 when glaciers and meltwater rivers deliver fresh water to the fjord, small species accounted for
331 91.6% of the total copepod abundance at station 1. In contrast, only 73.9% of the copepod
332 abundance at station 3 consisted of small species. Similarly, the freshwater impacted site was
333 dominated by small phytoplankton cells throughout the sampling period, while larger cells

334 dominated the outer fjord in July and August (Fig. 2). Thus, our findings agree with observations
 335 from other areas that small phytoplankton species are favoured as the upper ocean freshens
 336 (Daufresne et al. 2009, Li et al. 2009, Gardner et al. 2011), and could subsequently influence
 337 zooplankton community composition. The large *Calanus* species are generally not able to graze on
 338 the small phytoplankton cells (Campbell et al. 2009) whereas the smaller cyclopoid copepods,
 339 *Oithona* spp. and *Oncaea* spp., are omnivores feeding on motile items mainly protozooplankton
 340 (Paffenhofer 1993, Sabatini & Kiørboe 1994), and their nauplii feed on the small phytoplankton
 341 (Böttjer et al. 2010). This may explain the high percentage of smaller copepod species at the
 342 freshwater impacted site.

343 Total copepod abundance in Young Sound was low compared to other Arctic and Sub- Arctic fjord
 344 systems. The copepod abundance in Young Sound ranged from between ~100 to 1200 individuals
 345 m⁻³ (including nauplii) from July to October (Fig. 8). In contrast, Madsen et al. (2008) found up to
 346 3400 individuals m⁻³ in September in Disko Bay, and Arendt et al. 2013 reported >200.000
 347 individuals m⁻³ in July in Godthaabsfjorden (primarily *Microsetella norvergica*). From the central
 348 Arctic Ocean, Auel & Hagen (2002) reported a total mesozooplankton abundance of 160 to 460
 349 individuals m⁻³ in August and September and Hopcroft et al. (2005) found a concentration of 1447
 350 copepods m⁻³ (including nauplii) in August in the Canada Basin. Thus, abundance in Young Sound
 351 is comparable to these low productive High Arctic sites. The most abundant species were *O. similis*,
 352 *O. borealis* and *Pseudocalanus* spp., which agrees with other observations from open-water high-
 353 latitude areas (Auel & Hagen 2002, Hopcroft et al. 2005, Moller et al. 2006, Madsen et al. 2008,
 354 Svensen et al. 2011). A previous study conducted in Young Sound through ice-cover in June 1999
 355 (Nielsen et al. 2007) showed the total copepod community to be evenly divided between large
 356 *Calanus* spp. and small species, suggesting that their study was conducted at the onset of the spring
 357 phytoplankton bloom, when *Calanus* spp. are present in the surface waters to feed on the

358 phytoplankton bloom and reproduce (Madsen et al. 2001, Falk-Petersen et al. 2008). Low
359 abundance of *Calanus* spp. in our study indicates that *Calanus* had already started to leave the
360 surface waters. However, due to shallow depths and cold temperatures ($< -1,7^{\circ}\text{C}$) in Young Sound,
361 it is questionable whether *Calanus* are capable of overwintering in the fjord (Nielsen et al. 2007).
362 Both the copepod abundance and the community composition at the genus level seem to have been
363 relatively constant during the last decade (Fig. 12B), despite the open water period varying between
364 72 and 140 days in the same period (Fig 12A). Only *Pseudocalanus* spp. showed a reduction in
365 abundance over time probably due to decrease in retention time of their habitat in the freshwater
366 layer in the inner fjord (Arendt et al. 2016, Bendtsen et al. 2014). Our data are consistent with
367 annual monitoring measurements in August from 2003 to 2013 at station 3, were 195 ± 16 (S.E)
368 individuals m^{-3} (excluding nauplii) were reported, compared to an average abundance at station 3 of
369 172 individuals m^{-3} (also excluding nauplii) at the beginning of August and start of September in
370 2014 (Fig. 12B).

371

372 **Temperature dependence of egg production:** Copepods of the genus *Pseudocalanus* are often,
373 numerically, amongst the most important copepods and important in the copepod biomass from late
374 summer to the spring when *Calanus* are absent from the surface waters (Madsen et al. 2008,
375 Hopcroft et al. 2010, Arendt et al. 2013, Zamora-Terol et al. 2014). We found two *Pseudocalanus*
376 species in Young Sound, *P. minutus* and *P. acuspes*, and the egg-hatching rate equation is therefore
377 based on data from these two species. Despite differences in the number of eggs produced between
378 the two species, their mass specific egg production is similar (Hopcroft & Kosobokova 2010). A
379 comparison of hatching times for *P. minutus* and *P. acuspes* from McLaren et al. (1989) and for
380 *Pseudocalanus* spp. from the present study reveals a shorter hatching time at sub-zero temperatures
381 and a slightly longer hatching time at $> 2.2^{\circ}\text{C}$ (Fig. 7). From their equations, McLaren et al. (1989)

382 estimated hatching times of 15.6 and 15.4 days for *P. minutus* and *P. acuspes*, respectively, at -2
383 °C. Our result was 13.4 days. This suggests that hatching rates at low temperatures in Young Sound
384 are higher than previously reported. From our egg hatching experiment and previous experiments
385 (Mclaren et al. 1989, Nielsen et al. 2002), we know the temperature dependency of hatching time of
386 *O. similis* and *Pseudocalanus* spp.. The relatively fast hatching time of *Pseudocalanus* spp. at sub-
387 zero temperatures may be related to feeding and reproductive behaviour. When melting of sea ice is
388 initiated in the spring, *Pseudocalanus* spp. migrates to the surface to feed on algae under the ice to
389 complete gonad maturation and to reproduce (Runge & Ingram 1988, 1991, Weydmann et al.
390 2013). Thus, *Pseudocalanus* spp. seem well adapted to reproduce in the cold water just below the
391 ice (Runge et al. 1991).

392

393 **Production of *Oithona similis* and *Pseudocalanus* spp.:** In general, production of *O. similis*
394 seemed to be uncoupled from the chlorophyll *a* concentrations, whereas we found a significant
395 linear relationship between SEP of *Pseudocalanus* spp. and availability of larger phytoplankton
396 cells (chl *a* > 10 µm). This corresponds well to the feeding biology of the two species.
397 *Pseudocalanus* spp. are suspension feeders, explaining the relationship between large
398 phytoplankton and their egg production (Eiane & Ohman 2004) whereas *Oithona* spp. feed on the
399 microbial food web, mainly eating protozooplankton (Lischka & Hagen 2007, Zamora-Terol et al.
400 2013), and we should expect a link between concentration of protozooplankton and production of
401 *O. similis*. The SEP estimate ranges were 0.08-1% and 0-0.9% body C d⁻¹ for *O. similis* and
402 *Pseudocalanus* spp., respectively. These rates are comparable to SEP values reported by Madsen et
403 al. (2008) in Disko Bay, by Zamora-Terol et al. (2013) from both Disko Bay and Godthaabsfjorden
404 and by Castellani et al. (2007) from the Irminger Sea. Seasonal patterns in production seemed to be
405 more pronounced for *Pseudocalanus* spp. than for *O. similis* (Lischka & Hagen 2007: cf. our Fig.

10), suggesting that *Pseudocalanus* spp. overwinters with reduced metabolic activity, low feeding rates and no reproduction during winter (Lischka & Hagen 2005). Similar to our results, Lischka & Hagen (2005) reported continuous reproduction by *O. similis* in Kongsfjorden on Svalbard, with two generations per year, while reproduction of *P. minutes* was restricted to spring and summer with a 1-year life cycle. This suggests that production of *Pseudocalanus* spp. had peaked in early spring before our first sampling.

Stage compositions of *Pseudocalanus* spp. and *O. similis* match their observed egg production; for *O. similis*, all stages were present during the season, and the relative distribution was more or less constant, consistent with continuous reproduction year round (Fig. 9) (Madsen et al. 2008, Dvoretsky & Dvoretsky 2009). For *Pseudocalanus* spp., nauplii dominated in terms of abundance in July and August while CIII, CIV and CV became more abundant in September and October (Fig. 9). Low abundance of nauplii late in the season corresponds to the low egg production observed then (Fig. 10B). Stage composition of *O. borealis*, with few nauplii and younger copepodite stages early in the season, but higher abundance of nauplii, males and females late in the season indicates that *O. borealis* reproduces late in the open water period (Fig. 9). In contrast, Nishibe and Ikeda (2007) reported that Oncaeid copepods in the western subarctic Pacific reproduce throughout the year. Production of *Calanus* was 89-90% of the total copepod production in July and August. However, the small copepods were more important in September and October, when they accounted for 6-68% (mean 38%) of the production (Fig. 11).

Conclusion: The ice-free period in Young Sound has been slowly increasing since observations began in the 1960s, primarily due to later sea ice formation in the fall (Fig. 12A). During fall is where the small copepods contribute most to the carbon cycling and where the phytoplankton standing stock consists of small cells (Fig. 2) favouring the smaller copepod species and the

430 microbial food web. The changing sea ice conditions and increased influence of freshwater in
431 Young Sound (Sejr et al. submitted) will likely influence carbon cycling in the future. We suggest
432 that later ice formation and increasing freshwater runoff may increase the fraction of primary
433 production turned over by the small copepods and the microbial food web, in contrast to earlier
434 break up of ice which potentially favours the relatively large size-fraction of the zooplankton
435 community, which is dominated by *Calanus* spp.

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Station	1	2	3	4
Depth, m	128	229	163	229
Position	74°30.15'N 21°53.28'W	74°26.12'N 20°46.31'W	74°18.58'N 20°18.00'W	74°10.35'N 19°41.98'W
Surface salinity (Jul-Aug)	21.9	24.1	26.8	29.0
Sampling dates	Jul-21	Jul-17	Jul-11	Jul-24
	Aug-1	Jul-27	Jul-19	Aug-3
	Aug-9	Aug-5	Jul-30	Aug-10
	Sep-20	Sep-6	Aug-7	Sep-11
	Sep-27	Sep-13	Sep-9	Sep-19
		Sep-27	Sep-16	Oct-4
			Sep-28	
			Oct-4	

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598
599 Table 1. Sampling dates, position, surface salinity (0-5 m) and depth of the 4 stations sampled for
600 copepods in Young Sound, NE Greenland 2014.
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609 **Figure 1.** A) Study site and (B) Location of the four sampling stations in Young Sound, NE

610 Greenland.

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 617 **Figure 2.** Integrated chlorophyll *a* concentrations in the upper 100 m $>$ and $<$ than $10 \mu\text{m}$, mean
 618 surface temperature (0-5 m) and temperature at 20 m depth at stations 1, 2, 3 and 4.

Figure 3. Salinity in Young Sound along transects from the inner fjord (left) to the Greenland Sea in (A) July, (B) August, (C) September and (D) October.

Figure 4. Abundance of protozooplankton at stations 1, 2, 3 and 4. Abundance is the mean value from 1 m depth and the depth of the chlorophyll a maximum.

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635 **Figure 5.** Egg hatching experiments for *Pseudocalanus* spp. at 5 different temperatures. For each
636 experiment, temperature, hatching rate (HR, % d⁻¹), r² and n (number of females in the experiment)
637 are shown.

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Figure 6. Egg hatching rate for *Pseudocalanus* spp (% d⁻¹) ($HR = 8.59 * e^{(0.164T)}$, $r^2 = 0.95$, $n = 5$)

Figure 7. Comparison of egg hatching time (d) for *Pseudocalanus* spp. (present study), *P. minutus* (Mclaren et al. 1989), *P. acuspes* (Mclaren et al. 1989), and *O. similis* (Nielsen et al. 2002).

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683 **Figure 8.** Abundance of copepods in the upper 100 m of the water column at station 1, 2, 3 and 4.

684 The curve indicates the percentage of small species of the total copepod abundance.

Figure 9. Relative abundance (%) of copepodit stages and nauplii in the upper 100 m of the water column at station 1, 2, 3 and 4. *O. similis*, *Pseudocalanus* spp. and *O. borealis*. For *O. borealis* copepodit stages CI to CV are presented as pooled value.

Figure 10. (A) Carbon specific egg production (d⁻¹) for *Pseudocalanus* spp. and *O. similis* at station 1, 2, 3 and 4. Grey shaded area: depth integrated (0-100 m) total chlorophyll a concentration. Dark shaded area: depth integrated (0-100 m) chlorophyll a > 10 μm. (B) Secondary production of *Oithona similis* and *Pseudocalanus* spp. in Young Sound at station 1, 2, 3 and 4. * Indicates that SEP is calculated based on less than ten individuals of *Pseudocalanus* spp.

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Figure 11. Relative production (%) of *Calanus* spp., *O. borealis*, *O. similis* and *Pseudocalanus* spp. at station 1, 2, 3 and 4.

Figure 12. (A) Development in the ice-free period in Young Sound from year 1950-2013. Ice melts: $Y = -0.1488x + 494$, $r^2 = 0.1692$. Ice forms: $Y = 0.2091x - 127.4$, $r^2 = 0.1265$. (B) Relative copepod abundance in late July and early August from 2003-2014. The curve indicates individuals m^{-3}