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1 Seasonal changes in mesozooplankton swimmers collected by sediment trap moored at a single
2 station of Northwind Abyssal Plain in the western Arctic Ocean

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13 KEYWORDS: copepods; life cycle; Pacific water; sea ice; sediment trap

14 RUNNING HEAD: Seasonal changes of mesozooplankton in Arctic Ocean

15 **Abstract**

16 To examine seasonal changes in mesozooplankton community, analyses were made on the swimmer
17 samples (>1 mm) collected by a sediment trap mooring at 184 m depth of Northwind Abyssal Plain
18 in the western Arctic Ocean during October 2010 to September 2011. The zooplankton swimmer
19 flux ranged 5–44 ind. m⁻² day⁻¹ and was greater during July to October; copepods were the
20 dominant taxon. Based on the zooplankton swimmer flux, cluster analysis classified samples into
21 three groups (A, B-1 and B-2). The occurrence of each group showed clear seasonality; group A
22 was observed during July to October, group B-1 was seen in November to January, and group B-2
23 was seen during March to June. The seasonal variability in population structures of four dominant
24 copepod swimmers were clearly different among the species. Most *Calanus hyperboreus* were
25 C6F throughout the year. For *Metridia longa* and *Paraeuchaeta glacialis*, C6Fs dominated during
26 January to May, and early copepodid stages increased during June to October. *Heterorhabdus*
27 *norvegicus* was dominated by C5 during November to February, and C6F/M during March to May.
28 Since Pacific copepods (*Neocalanus cristatus*) occurred with significant number during
29 August–September, possible causes are discussed.

30 **INTRODUCTION**

31 After 1990's, a drastic reduction of sea ice cover area has been observed in the Arctic Ocean during
32 summer (July–October). This reduction is considered to have been caused by an increased flow of
33 warm Pacific Summer Water (PSW) from the Bering Sea Strait into the Arctic Ocean (Shimada *et*
34 *al.*, 2006; Woodgate *et al.*, 2010). The Pacific sector of the Arctic Ocean comprises both shallow
35 (Chukchi Sea and East Siberian Sea) and deep (Canada Basin and Mendeleyev Ridge) areas (Fig. 1).
36 Sea ice reduction in this region has been the greatest in the Arctic Ocean (Shimada *et al.*, 2001,
37 2006; Stroeve *et al.*, 2007; Comiso *et al.*, 2008; Markus *et al.*, 2009), and this reduction of sea ice is
38 expected to alter the marine ecosystem structure in the Arctic Ocean (Grebmeier *et al.*, 2006; Hunt
39 and Drinkwater, 2007; Grebmeier, 2012).

40 The zooplankton community in the western Arctic Ocean has been studied based on net

41 samples (Springer *et al.*, 1989; Darnis *et al.*, 2008; Hopcroft *et al.*, 2010; Matsuno *et al.*, 2011,
42 2012). However, seasonal sea ice coverage in this area prevents collection of net samples in
43 winter, and most of the studies were conducted only in summer. To evaluate seasonal changes in
44 zooplankton community, analysis on zooplankton swimmers (Knauer *et al.*, 1979) collected by
45 moored sediment trap is a powerful tool (cf. Forbes *et al.*, 1992). According to Knauer *et al.* 1979,
46 swimmer is defined that zooplankton actively swam into the trap and was killed by the preservation
47 fluid filled with the cups. Because of their importance, seasonal changes in swimmer community
48 collected by sediment trap have been studied in several areas of the Arctic Ocean, especially in the
49 Beaufort Sea (Forbes *et al.*, 1992; Ota *et al.*, 2008; Makabe *et al.*, 2010). According to Makabe *et*
50 *al.* (2010), seasonal changes in Arctic swimmer community are related to the sea ice concentration,
51 temperature and salinity. This is partly because large copepods migrate to surface when the sea ice
52 melts (Conover and Huntley, 1991), graze on phytoplankton in the ice-edge bloom (Springer and
53 McRoy, 1993), and then reproduce. The reproduction seasons of dominant copepods vary with
54 species and areas within the Arctic Ocean (Falk-Petersen *et al.*, 2009). Despite their importance,
55 little information is available for life cycle of copepods other than dominant species. For dominant
56 copepods, their species-specific lipid accumulation and gonad maturation have little evaluated in
57 the western Arctic Ocean.

58 In the present study, we analyzed zooplankton swimmers collected by sediment trap
59 sampling at 13–15 day intervals moored at 184 m in Northwind Abyssal Plain during October 2010
60 to September 2011. Through this analysis, seasonal changes in swimmer community structure and
61 population structure of the four dominant copepods (*Calanus hyperboreus*, *Metridia longa*,
62 *Paraeuchaeta glacialis* and *Heterorhabdus norvegicus*) were evaluated. Lipid accumulation and
63 gonad maturation of adult females (C6F) from the dominant copepods were analyzed to evaluate
64 their life cycle patterns. Seasonal occurrence of the Pacific copepods (*Neocalanus cristatus*) was
65 also noted and the possible cause was discussed.

66 **METHOD**

67 **Field sampling**

68 Samples were collected by sediment trap (SMD26 S-6000, open mouth area 0.5 m², Nichiyu Giken
69 Kogyo, Co. Ltd.) rotated at 13–15 day intervals moored at 184 m and 1,300 m at St. NAPt
70 (Northwind Abyssal Plain trap, 75°00′N, 162°00′W, bottom depth 1975 m) during 4 October 2010
71 to 28 September 2011 (Fig. 1). This station is seasonally affected by inflow of Bering Shelf Water
72 (BSW) from Bering Strait (Weingartner *et al.*, 2005; Woodgate *et al.*, 2005). The end of the trap
73 rope was fixed to the sea bottom. Sea water for filling sample cups was taken from 1,000 m water
74 depth in the southern Canada Basin (salinity 34.89), and was filtered with membrane filter (0.45 µm
75 pore size) to make 5% buffered formalin seawater. The sample cups were filled with the 5%
76 buffered formalin seawater before the sediment trap was deployed.

77 After the trap was retrieved, the 26 samples each were gently filtered with 1 mm mesh, and
78 the remaining fraction (>1 mm size) on the mesh was treated as zooplankton swimmers. Since the
79 number of zooplankton swimmer was low for deeper trap (1,300 m), we treated only shallower trap
80 (184 m) in this study. The fine size fraction (<1 mm) for each sample was evenly divided to 10
81 aliquots using the Wet Sample Divider (McLaneTM WSD-10). The one of divided aliquots for
82 each sample was filtered on weighed polycarbonate membrane filter, and was desalted with Milli-Q
83 waters. The sample filters were dried with diphosphorus pentaoxide in desiccator for three days.
84 The dried sample filters were weighed with analytical balance to calculate total mass flux (mg dry
85 mass [DM] m⁻² day⁻¹) of < 1 mm size fraction for each sample period.

86 As the supplemental environmental data, the moored trap depth and the water temperature
87 (accuracy of ±0.2°C) were monitored every hour (sensor type: ST-26S-T). We estimated the
88 current speed at St. NAPt in 2010 by a physical ocean general circulation model: Center for Climate
89 System Research Ocean Component Model (COCO) version 4.9. The model performance in the
90 western Arctic Ocean has been verified in previous decadal and seasonal experiments (Watanabe *et*
91 *al.*, 2012; Watanabe and Ogi, 2013). Time-series data on weekly averaged percentage ice
92 coverage around St. NAPt (74.5–75.5°N, 161.5–162.5°W) during the mooring period were
93 calculated from the sea ice concentration data set (<http://iridl.ldeo.columbia.edu/SOURCES/.IGOS->

94 S/.nmc/.Reyn_SmithOlv2/, cf. Reynolds *et al.*, 2002). For sea ice coverage data of whole Arctic
95 Ocean, the data were downloaded from the AMSER-E data set (<http://www.ijis.iarc.uaf.edu/seaice/->
96 extent/plot.csv). The MODIS/Aqua Level 3 binned chlorophyll-*a* data (reprocessing version
97 2012.0) were downloaded from the Distributed Active Archive Center (DAAC) of Goddard Space
98 Flight Center (GSFC), NASA. We used daily data at 9-km resolution, and composited to 9 days
99 running mean.

100 **Analysis of zooplankton swimmer**

101 For zooplankton swimmer samples (>1 mm), identification and enumeration of zooplankton were
102 made under a dissecting microscope. In this study, swimmer defined that zooplankton in >1 mm
103 samples swam actively into the trap (cf. Knauer *et al.*, 1979). Specimens damaged before
104 collection were distinguished based on the description of Sampei *et al.* (2009), while their
105 contribution was small (<0.65% in total count) and excluded from following analysis. Species
106 identification of copepods followed mainly Brodsky (1967) and Frost (1989) for *Pseudocalanus* spp.
107 (*P. minutus* and *P. newmani*), Frost (1974) for *Calanus* spp. (*C. glacialis* and *Calanus marshallae*),
108 and Miller (1988) for *Neocalanus* spp. Identification of the four dominant calanoid copepods
109 (*Calanus hyperboreus*, *Metridia longa*, *Paraeuchaeta glacialis* and *Heterorhabdus norvegicus*) was
110 made to the copepodid stage level.

111 For *C. hyperboreus*, *M. longa* and *P. glacialis*, the copepodid stage 6 females (C6Fs)
112 contain a large oil sac in the prosome. To analyze the amount of oil, oil length relative to prosome
113 length (PL) was scored into three groups: I (the lipid length is 0–4% of PL), II (4–40% of PL) and
114 III (>40% of PL). For the same three species, gonad maturation of the C6F was also scored into
115 three groups: I (immature), II (small oocytes in ovary or oviduct) and III (large eggs or distended
116 opaque in oviduct). For this gonad maturation index, we referred to those used previously for *C.*
117 *hyperboreus* (Hirche and Niehoff, 1996) and *M. longa* (Tande and Grønvik, 1983). Of the four
118 dominant copepods, only *H. norvegicus* was not analyzed for lipid accumulation and gonad
119 maturation, because of the difficulty in observation. *Heterorhabdus norvegicus* accumulate lipids

120 in many small oil droplets, and the low transparency of the prosome prevents observation of their
121 gonad.

122 The flux (F , ind. $\text{m}^{-2} \text{day}^{-1}$) of zooplankton swimmers was calculated from the following
123 equation:

$$124 \quad F = N \times \frac{1}{0.5} \times \frac{1}{d}$$

125 where N is the number of individuals (ind.), 0.5 is the mouth area (m^2) of the sediment trap, and d is
126 the sampling interval (days). We counted total zooplankton swimmers 37–288 individuals per
127 sample. Since the sampling interval is similar (13–15 days) throughout the sampling period,
128 conversion factor between count and flux was similar (one individual sample $^{-1}$ corresponded to
129 0.133–0.154 ind. $\text{m}^{-2} \text{day}^{-1}$ [=1/0.5/13–15]).

130 **Data analysis**

131 Zooplankton swimmer flux data (F : ind. $\text{m}^{-2} \text{day}^{-1}$) for each species was log transformed
132 ($\log_{10}[X+1]$) prior to analysis to reduce the bias of flux. Similarities between samples were
133 examined using the Bray-Curtis index (Bray and Curtis, 1957). To group samples, the similarity
134 indices were coupled with hierarchical agglomerative clustering using a complete linkage method
135 (Unweighted Pair Group Method using Arithmetic mean: UPGMA) (Field *et al.*, 1982). All of
136 these analyses were carried out using PRIMER v6 software (PRIMER-E Ltd.). Inter-group
137 differences in flux of all zooplankton swimmers were tested by one-way ANOVA and an ex post
138 facto test by Fisher's Protected Least Significant Difference test (PLSD). These statistical
139 analyses were carried out using StatView v5 software (SAS Institute Inc.).

140 **RESULTS**

141 **Hydrography**

142 The trap depth varied between 181 and 218 m (Fig. 2a), and was stable around 184 m most of the
143 date then temporally deepened (220 m) within short period (6–7 days) in October, December 2010

144 and September 2011. Temperature at sediment trap ranged from -1.6 to -0.6°C (Fig. 2b). Rapid
145 decreases in temperature were paralleled with the deepening changes in the moored trap depth (Fig
146 2a, b). The five days mean of current velocity simulated by ocean circulation model showed slow
147 subsurface current ($<11.3\text{ cm s}^{-1}$ at 45 m and $<2.7\text{ cm s}^{-1}$ at 188 m water depths) at St. NAPt (Fig.
148 2c). From two times CTD casts at the station, four water masses were identified at 0–500 m water
149 column: i.e. SML: Surface Mixed Layer (0–25 m), PSW: Pacific Summer Water (25–100 m),
150 PWW: Pacific Winter Water (100–250 m), AW: Atlantic Water (>250 m) (Fig. 2d, e) (McLaughlin
151 *et al.*, 2011).

152 Sea ice around the sediment-trap site showed clear seasonal changes, with a decrease from
153 early July, complete melting (sea ice concentration: 0%) in September, a rapid increase during
154 October, and 100% coverage during November to June (Fig. 3a). The total mass flux (<1 mm size
155 range) ranged $19.3\text{--}215.9\text{ mg DM m}^{-2}\text{ day}^{-1}$ and peaked during November–December (Fig. 3a).
156 High chl. *a* was observed during August–September (Fig. 3a). At St. NAPt, the midnight sun
157 occurred during early May to early August, and polar night was from early November to early
158 February (Fig. 3b).

159 **Swimmer community**

160 Based on the zooplankton swimmer flux, cluster analysis classified the zooplankton swimmer
161 communities largely (A and B) at 55% dissimilarity level, then group B subdivided (B-1 and B-2) at
162 47% dissimilarity level (Fig. 4a). Occurrence of each group showed distinct seasonality. Group
163 A ($n = 8$) was observed from July to October, group B-1 ($n = 6$) from November to January, and
164 group B-2 ($n = 9$) from March to June (Fig. 4b). Zooplankton swimmer flux ranged from 5 to 44
165 ind. $\text{m}^{-2}\text{ day}^{-1}$. While except extremely high peak of amphipods (*Themisto libellula*) in April,
166 zooplankton swimmer flux was highest during July to October (Fig. 4b). The averaged
167 zooplankton swimmer flux was highest in A ($20.0\pm 4.9\text{ ind. m}^{-2}\text{ day}^{-1}$), lower in B-2 (16.1 ± 3.9), and
168 lowest in B-1 (11.9 ± 2.4). Copepods comprised 18 to 94% of the zooplankton swimmer flux and
169 were the dominant taxon; amphipods the second most dominant group (0–74%) (Fig. 4b). The

170 characterized species of each group (significantly abundant than the other groups analyzed by
171 one-way ANOVA and Fisher's PLSD, $p < 0.05$) were as follows: A, the mesopelagic copepods
172 *Paraeuchaeta glacialis*; and B-2, the inter-zonal copepod *Calanus hyperboreus*. While group B-1
173 dominated by *Metridia longa* and *Heterorhabdus norvegicus*, their flux showed no significant
174 seasonal changes.

175 **Copepod population structure**

176 The population structures of the four dominant copepods (*C. hyperboreus*, *M. longa*, *P. glacialis*
177 and *H. norvegicus*) varied with species. Throughout the year, *C. hyperboreus* was predominated
178 by C6F (Fig. 5a). The population structure of *M. longa* and *P. glacialis* showed seasonal change;
179 both were dominated by C6F from January to May, and early copepodid stages (C1–C4) occurred
180 during June–October (Fig. 5b, c). *Heterorhabdus norvegicus* showed a different seasonal pattern;
181 it was dominated by C5 during November–February, the contribution of C6F/M increased during
182 March–October, and C1 and C2 stages occurred in June–July (Fig. 5d).

183 Lipid accumulation in C6Fs of the dominant copepods (excluding *H. norvegicus*) also
184 showed species-specific seasonal patterns. Most *C. hyperboreus* contained more lipids (stage III)
185 during December–January (83%) than during February–October (56%) (Fig. 6a). For *M. longa*,
186 stage III individuals dominated during October–December, their composition gradually decreased
187 during March to June, and all specimens had no oil sacs in July (Fig. 6b). The lipid accumulation
188 of *P. glacialis* showed fluctuated seasonal change (Fig. 6c).

189 Gonad maturation of C6Fs of the dominant copepods (excluding *H. norvegicus*) showed
190 more distinct seasonality. For *C. hyperboreus*, mature individuals were observed only during
191 February–April (Fig. 6d). Mature *M. longa* were seen during March–July, note that in September
192 was based on only one specimen (Fig. 6e), with the lipid accumulation decreased (Fig. 6b). Most
193 *P. glacialis* (47%) matured during August–January (Fig. 6f), when egg carrying *P. glacialis* C6Fs
194 were also seen.

195 **Pacific copepods**

196 The Pacific copepod *Neocalanus cristatus* occurred ($0\text{--}0.92\text{ ind. m}^{-2}\text{ day}^{-1}$) throughout the year,
197 and was higher during August–September when the sea ice was reduced (Fig. 7). All *N. cristatus*
198 were stage C5, and lipid accumulation varied.

199 **DISCUSSION**

200 **Trap collection efficiency**

201 In general, underestimate bias in sinking particle flux is concerned due to low trap collection
202 efficiency under flowing water condition especially shallower than 1,000 m (Buesseler *et al.*, 2007).
203 The time-series monitoring data for physical oceanography around St. NAPt are limited. However,
204 the directly measured water current around St. NAPt in winter was slower than 10 cm s^{-1} at 58 and
205 250 m water depths (Sumata and Shimada, 2007). The current speed estimated by ocean
206 circulation model also confirmed that the speed of the subsurface current around trap was slow
207 ($<2.7\text{ cm s}^{-1}$) at St. NAPt throughout the year (Fig. 2c). These slow current speeds were not
208 expected to have a significant effect on sediment trap collection efficiency. The sediment trap
209 temporarily deepened to 220 m with short period (6–7 days) in October, December 2010 and
210 September 2011 (Fig. 2a). Temporal changes in temperature also confirmed these changes (Fig.
211 2b). The tilt of sediment trap was estimated within 15° in the deepening events. Except for these
212 periods, mooring depth of sediment trap was kept 180–190 m. Since the PWW were occurred
213 between 100–250 m (Fig. 2d, e), there expected little changes in water masses at the trap depth.
214 Although the deployment depth of sediment trap was not completely constant throughout the
215 studied period, the seasonality of total mass fluxes at 184 m trap and at 1,300 m trap (Onodera *et al.*,
216 pers. comm.) was well paralleled ($r^2 = 0.621$, $p < 0.0001$). These results suggest that the influence
217 of the trapping efficiency bias is usually insignificant for the studied sediment trap samples.

218 **Seasonal changes in swimmer community**

219 Previously reported zooplankton swimmer communities collected by sediment trap in the Arctic

220 Ocean are summarized in Table 1. Throughout the studies, copepods are the most dominant taxa,
221 followed by amphipods or pteropods similar with this study. Within the copepods, *C.*
222 *finmarchicus* is reported to be dominated for the shallower trap (ca. 100 m) in the Norwegian fjord
223 faced to the North Atlantic Ocean (Willis *et al.*, 2006, 2008). While in the deep-layer (500 m) of
224 the eastern Greenland Sea, *C. finmarchicus* was lesser and dominated by *M. longa* (Seiler and
225 Brandt, 1997). For the western Arctic Ocean (Amundsen Gulf and Beaufort Sea), not faced to the
226 Atlantic Ocean, *C. finmarchicus* did not occur and *M. longa* was dominated (Forbes *et al.*, 1992;
227 Sampei *et al.*, 2012). For the northernmost station (81°N), diapausing *C. hyperboreus* was
228 predominated (Hargrave *et al.*, 1989). Thus, the dominant copepod species collected by sediment
229 trap may vary with region and trap depths. The trap depth of this study (184 m) was relatively
230 shallow, but because the NAPt is not faced to the Atlantic Ocean, *C. finmarchicus* did not occur.
231 Dominant copepods of this study, *H. norvegicus* followed with *M. longa*, were a unique, because of
232 the dominance of the mesopelagic copepods (Yamaguchi and Ikeda, 2000). *Heterorhabdus*
233 *norvegicus* is reported to be the second dominant copepods in the zooplankton swimmer fauna of
234 the eastern Greenland Sea (Seiler and Brandt, 1997), thus this species may be dominant copepods
235 throughout the mesopelagic layer of the Arctic Ocean. Copepod fauna evaluated by stratified net
236 samplings also noted the occurrence of *H. norvegicus* throughout the Arctic Ocean (Kosobokova
237 and Hirche, 2000; Auel and Hagen, 2002; Kosobokova and Hopcroft, 2010; Dvoretzky and
238 Dvoretzky 2011). Add to these copepods, occurrence of small number of the Pacific copepods is a
239 special feature of this study. Since the zooplankton swimmer community of this study showed
240 clear seasonal changes (groups A, B-1 and B-2), following, we discuss the characteristics of each
241 swimmer group.

242 The group A, corresponded with open water period (July–October), dominated by the
243 carnivorous *P. glacialis* (3.7–9.4 times greater flux than the other groups, one-way ANOVA,
244 $p < 0.001$). For the numerical dominance of *P. glacialis* during July–October, two factors are
245 considered: i) correspondence of growth to large copepodid stages (>1 mm in size), ii)
246 correspondence of presence of massive diel vertical migration (DVM) at that period. For the

former, dominance of C5 stage during the period (Fig. 5c) suggests that the major population grew up this season. For the latter, *P. norvegica*, which is an Atlantic congener species for *P. glacialis*, is known to perform DVM during autumn (Kaartvedt *et al.*, 2002), but cease DVM during midnight sun and polar night (Fleddum *et al.*, 2001). At St. NAPt, the midnight sun occurred during early May to early August, and polar night was from early November to early February (Fig. 3c). Thus, if *P. glacialis* had similar DVM of *P. norvegica*, the dominance of *P. glacialis* in group A (July–October) was caused by the presence of DVM for *P. glacialis* during that period.

Changes in zooplankton swimmer community from group A to B-1 was corresponded with the timing of ice coverage and entered polar night (Fig. 3c). The group B-1 was characterized with the dominance of mesopelagic *M. longa* and *H. norvegicus*. While their flux showed little seasonal changes (Fig. 5b, d), the other two species showed clear seasonality: peaked in May–June for *C. hyperboreus* (Fig. 5a) and July–October for *P. glacialis* (Fig. 5c). Thus, group B-1 was composed mainly by mesopelagic copepods (*M. longa* and *H. norvegicus*) stable occurred in the mesopelagic layer. For the other two species (*C. hyperboreus* and *P. glacialis*), seasonal vertical migration (SVM) and presence/absence of DVM is considered to be a key mechanism to govern the seasonal changes in swimmer community.

During the ice coverage period (November–June), the swimmer community changed from group B-1 to B-2 in February due to the drastic increase (ca. 10 times) of *C. hyperboreus* (one-way ANOVA, $p < 0.01$). *Calanus hyperboreus* is known to perform SVM (Hirche, 1997; Vinogradov, 1997), diapause at depth (500–1,500 m) in winter, and make upward SVM to the surface layer in April (Hirche and Niehoff, 1996). In the present study, it was shown that *C. hyperboreus* included only C6Fs and their flux increased from February and peaked in May (Fig. 5a). This increase in flux during February to May was presumably due to their upward SVM from deep layer. Therefore, the change in swimmer community (from group B-1 to B-2) during January–March might have been caused by the upward SVM of *C. hyperboreus*. For arousal mechanism of resting copepods, presence of an internal body timer is discussed (Miller and Grigg, 1991; Miller *et al.*, 1991). Since daylight hours changed greatly from zero (polar night) to 24h (midnight sun) during

274 February to April (Fig. 3c), this change in day-night cycle may affect the arousal of diapause for *C.*
275 *hyperboreus*.

276 As specialized seasonal event of this study, the occurrence of Pacific copepods was
277 observed. The Pacific copepod *N. cristatus* C5 was abundant during August–September when sea
278 ice coverage decreased (Fig. 8). This seasonal pattern suggests that the amount of the inflow
279 Pacific Water may increase when the sea ice coverage decreases. While *N. cristatus* C5 is known
280 to perform SVM to deep layer to diapause during late summer (Miller *et al.*, 1984), the greater flux
281 of *N. cristatus* C5 in August–September may also be caused by their SVM. Since their
282 reproduction occurs >1,000 m depth (Miller *et al.*, 1984), the possibility of their reproduction in the
283 Arctic Ocean could not be evaluated from this study.

284 **Population structure of dominant copepods**

285 *Calanus hyperboreus* populations were composed much of C6F throughout the year (Fig. 5a).
286 *Calanus hyperboreus* reproduces during November–April in Amundsen Gulf (Ota *et al.*, 2008),
287 November–March in the Greenland Sea (Hirche and Niehoff, 1996), and February–March in the
288 Norwegian Sea (Østvedt, 1955). In the present study, mature C6F were seen only from February
289 to April, which suggests this is the reproduction period (Fig. 8). This reproduction season
290 (February–April) generally corresponds to the previous studies with slight seasonal variances. For
291 the regional variability in reproduction timing of *C. hyperboreus*, timing of the phytoplankton
292 bloom is reported to be a most important factor (Conover and Siferd, 1993; Hirche and Niehoff,
293 1996). Full-lipid individuals in stage C6F dominated in December–January, and the lipid
294 accumulation decreased from February when the reproduction started (Fig. 6a). This seasonal
295 correspondence between reproduction period and decrease of lipid accumulation would be caused
296 by the utilization of the stored lipid to reproduction (Hirche and Niehoff, 1996; Vinogradov, 1997).

297 The *M. longa* population was dominated by C6F during January–May, and early copepodid
298 stages (C1–C4) during June–October (Fig. 5b). *Metridia longa* is omnivore and performs diel
299 vertical migration (Conover and Huntley, 1991; Ashjian *et al.*, 1995), and has no diapause phase

300 (Båmstedt and Ervik, 1984; Grønvik and Hopkins, 1984). The main reproduction season shows
301 regional variability: during April–May in the Balsfjorden (Tande and Grønvik, 1983), in winter
302 under the sea ice in the Barents Sea (Hirche and Kosobokova, 2011), and in autumn in a polynya in
303 the Beaufort Sea (Makabe *et al.*, 2010). In this study, mature C6F occurred only during
304 March–July (Fig. 6e), and early copepodid stages (C1–C4) dominated the population during
305 June–October (Fig. 5b). These facts suggest that *M. longa* reproduces during March–July and the
306 new population appear during June–October. This reproduction season (March–July) in the
307 western Arctic Ocean is slightly longer than that in the Balsfjorden (April–May) (Tande and
308 Grønvik, 1983). Lipid accumulated (stage III) individuals dominated during October–December,
309 decreased gradually over winter and no specimens had oil sacs in July (Fig. 6b). This season of
310 decreasing lipids (March–June) parallels the gonad maturation season (March–July). These facts
311 suggest that the stored lipids are used for gonad maturation of *M. longa* as was seen in *C.*
312 *hyperboreus*.

313 The *P. glacialis* population was dominated by C6F during January–May, and contained
314 early copepodid stages (C2–C4) during June–October (Fig. 5c). Carnivorous *Paraeuchaeta* spp.
315 performs raptorial feeding throughout the year, accumulate much lipids, and have no diapause phase
316 (Båmstedt, 1979; Øresland, 1991). Since mature C6F *P. glacialis* dominated during
317 August–January and egg carrying C6F also occurred during the same period (Fig. 6f), this species is
318 assumed to reproduce in this period. This may be related to the ice-edge bloom at the surface.
319 Ice-edge bloom is known to be occurred after ice melting (Springer and McRoy, 1993) (Fig. 3b).
320 Ice-edge bloom induces the upward migration of Arctic copepods (e.g., *C. glacialis*) and
321 reproduction of small copepods (e.g., *Pseudocalanus* spp.) (Conover and Huntley, 1991), which
322 would provide sufficient food condition for carnivorous *P. glacialis*. Since sufficient food
323 condition (abundant small metazoan zooplankton) is a key to make growth and reproduction of
324 *Paraeuchaeta* spp. (Yamaguchi and Ikeda, 2001; Abe *et al.*, 2012), *P. glacialis* may have performed
325 reproduction in this season. This reproduction season of *P. glacialis* (August–January) differs
326 with those of *C. hyperboreus* (February–April) and *M. longa* (March–July). These differences

327 may be related to differences in feeding modes, i.e., carnivory in *P. glacialis* and suspension feeding
328 in *C. hyperboreus* and *M. longa*.

329 The *H. norvegicus* population was dominated by C5 during November–February and
330 C6F/M during March–October, and C1 and C2 were collected in June and July (Fig. 5d). Since
331 lipid accumulation and gonad maturation could not be analyzed for *H. norvegicus*, the reproduction
332 season was estimated from the population structure data. Combining dominance of early
333 copepodid stage (June and July) and assuming development time of *Heterorhabdus* spp. nauplii
334 (1–2 months) (Yamaguchi and Ikeda, 2000), the reproduction season is thought to be during April
335 and May. Little comparable information is available for the life cycle of *H. norvegicus*. Thus,
336 the reproduction seasons of the dominant four copepods differed (Fig. 8), and possible causes of
337 these differences include species-specific feeding modes, seasonal changes in food availability, and
338 the presence/absence of ontogenetic vertical migration.

339 In summary, while the limitation of sampling design (data based on single sediment trap at
340 a single station and depth), through the analyses on zooplankton swimmers collected by a sediment
341 trap, zooplankton communities were clearly separated into three seasons (Fig. 8). The season
342 when each copepod dominated corresponded with the reproduction timing of each species. For the
343 four dominant copepods, their reproduction timings varied with species, which may be related to the
344 feeding modes. In addition, the occurrence of the Pacific copepods was observed. Since their
345 peak period (August–September) corresponded with timing of their SVM, they may enter sediment
346 trap to perform descent SVM.

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524 **Figure legends**

525 **Fig. 1.** Location of St. NAPt (Northwind Abyssal Plain trap) in the western Arctic Ocean where
526 the sediment trap was moored at 184 m during October 2010 to September 2011. ACW:
527 Alaskan Coastal Water, AW: Anadyr Water, BSW: Bering Shelf Water.

528 **Fig. 2.** Seasonal changes in depth (a) and temperature (b) monitored for shallower trap at St.
529 NAPt during October 2010 to September 2011. Current velocity at 45 m and 188 m of St.
530 NAPt (c) estimated by a physical ocean general circulation model: Center for Climate
531 System Research Ocean Component Model (COCO) version 4.9. Temperature (d) and
532 salinity (e) observed from CTD casts at St. NAPt in 30 October 2010 and 21 September
533 2012. Shades indicate the trap depths (180–190 m). SML: Surface Mixed Layer (0–25
534 m), PSW: Pacific Summer Water (25–100 m), PWW: Pacific Winter Water (100–250 m),
535 AW: Atlantic Water (>250 m).

536 **Fig. 3.** Seasonal changes in sea ice concentration for the investigation area during the sampling
537 period (http://iridl.ldeo.columbia.edu/SOURCES/.IGOSS/.nmc/.Reyn_SmithOIv2/, data
538 from Reynolds *et al.*, 2002), total mass flux (<1 mm size fraction) collected by sediment
539 trap, surface chl. *a* from satellite (a) and daylight hours (b) at St. NAPt during 4 October
540 2010 to 28 September 2011.

541 **Fig. 4.** Results of cluster analysis based on the flux of zooplankton swimmers. Twenty six
542 samples were clustered into three groups from Bray-Curtis dissimilarity (a). Seasonal
543 changes in zooplankton swimmer flux, species composition and clustered groups collected
544 by sediment trap moored at 184 m of St. NAPt during 4 October 2010 to 28 September
545 2011 (b).

546 **Fig. 5.** Seasonal changes in flux and copepodid stage composition of the four dominant copepods:
547 *Calanus hyperboreus* (a), *Metridia longa* (b), *Paraeuchaeta glacialis* (c), *Heterorhabdus*
548 *norvegicus* (d), at 184 m of St. NAPt during 4 October 2010 to 28 September 2011.

549 **Fig. 6.** Seasonal changes in flux, lipid accumulation (upper panels) and gonad maturation (lower
550 panels) compositions (stage I–III) of C6Fs of *Calanus hyperboreus* (whole $n = 232$) (a, d),

Metridia longa ($n = 234$) (b, e) and *Paraeuchaeta glacialis* ($n = 166$) (c, f) at 184 m of St. NAPt during 4 October 2010 to 28 September 2011. *: Egg sac attached individual was occurred.

Fig. 7. Seasonal changes in flux and lipid accumulation composition (I–III) of the Pacific *Neocalanus cristatus* C5 collected by sediment trap moored at 184 m of St. NAPt during 4 October 2010 to 28 September 2011.

Fig. 8. Schematic diagram on seasonal changes in daylight hours, sea ice concentration, chl. *a*, total mass flux (upper panel), swimmer community, population structure and reproduction period of copepods (*C. hyperboreus*, *M. longa*, *P. glacialis* and *H. norvegicus*), and occurrences of the Pacific *N. cristatus* collected by sediment trap at 184 m of St. NAPt during 4 October 2010 to 28 September 2011 (lower panel). For *C. hyperboreus*, *M. longa* and *P. glacialis*, reproduction period was evaluated by C6F gonad maturation (Fig. 6d–f). For *H. norvegicus*, their reproduction period was estimated by the occurrence of early copepodid stages (Fig. 5d).

Table 1. Comparison of zooplankton swimmer community collected by sediment trap in the Arctic Ocean.

Region (position)	Period	Depth (m)	Dominant taxa/species (percentage to total zooplankton flux in number)	References
Amundsen Gulf (71°47'N, 126°30'W)	Oct. 2007–July 2008	112	<i>M. longa</i> (50), <i>P. glacialis</i> (6), <i>C. hyperboreus</i> (2), <i>C. glacialis</i> (2)	Sampei <i>et al.</i> (2012)
Amundsen Gulf (70°–72°N, 123°–135°W)	Oct. 2003–Aug. 2004	100, 200, 400	<i>Oncaea</i> spp. (34), <i>M. longa</i> (21), pteropods (11), <i>C. hyperboreus</i> (4)	Makabe <i>et al.</i> (2010)
Beaufort Sea Shelfbreak (69°–72°N, 127°–139°W)	Sep. 1987–Mar. 1988	115, 128, 145	<i>M. longa</i> (49), amphipods (27), <i>P. glacialis</i> (15), <i>C. hyperboreus</i> (8)	Forbes <i>et al.</i> (1992)
East Greenland Sea (72°0'–30°N, 7°2'–43°W)	July 1989–July 1992	500	<i>M. longa</i> (59), <i>H. norvegicus</i> (12), amphipods (9), ostracods (8)	Seiler and Brandt (1997)
Kongsfjorden (79°1.2'N, 11°46.4'E)	Sep. 2005–May 2006	115	<i>C. finmarchicus</i> , <i>C. glacialis</i> , <i>M. longa</i> , <i>P. norvegica</i>	Willis <i>et al.</i> (2008)
Kongsfjorden (79°3.2'N, 11°18.0'E)	Apr.–June, July–Sep. 2002	215	<i>C. finmarchicus</i> , <i>C. glacialis</i> , <i>C. hyperboreus</i> , <i>P. norvegica</i>	Willis <i>et al.</i> (2006)
Axel Heiberg Island (81°N, 96°–98°W)	Sep. 1986–June 1987	100	<i>C. hyperboreus</i> (78), <i>M. longa</i> (9), <i>P. norvegica</i> (4), <i>C. glacialis</i> (2)	Hargrave <i>et al.</i> (1989)
Northwind Abyssal Plain (75°47'N, 126°30'W)	Oct. 2010–Sep. 2011	180	<i>H. norvegicus</i> (17), <i>M. longa</i> (16), <i>P. glacialis</i> (15), <i>C. hyperboreus</i> (8)	This study

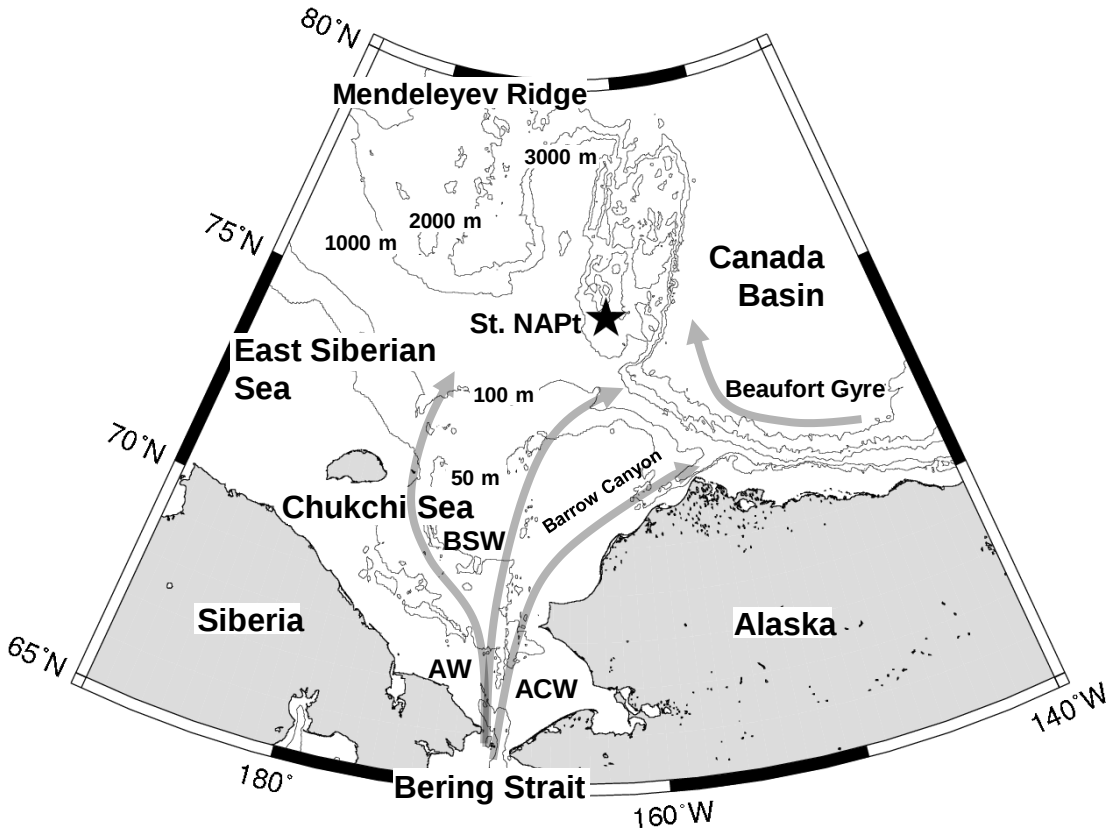


Fig. 1 (Matsuno et al.)

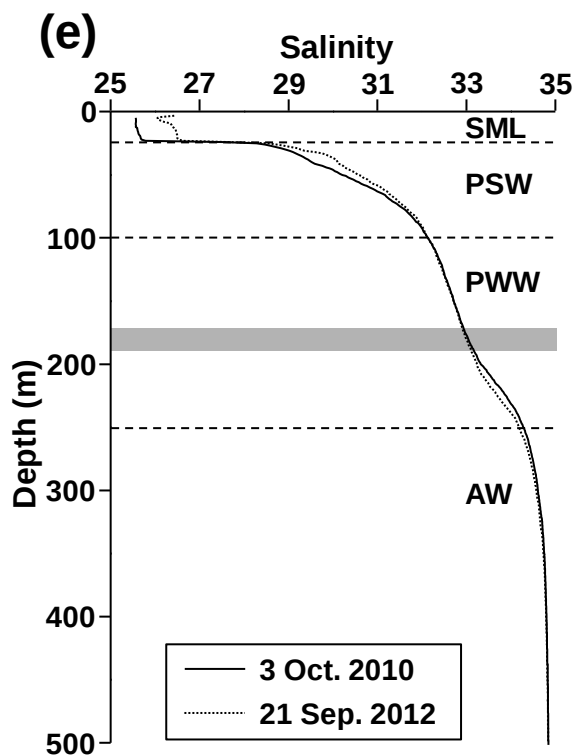
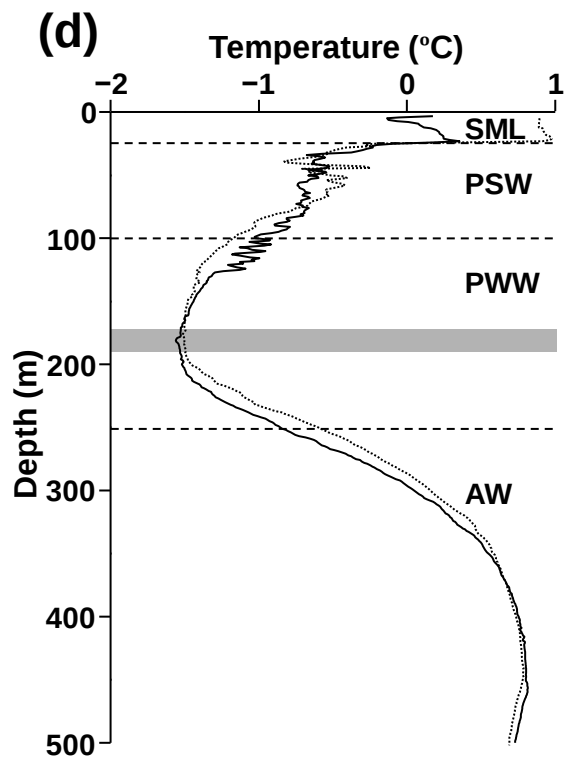
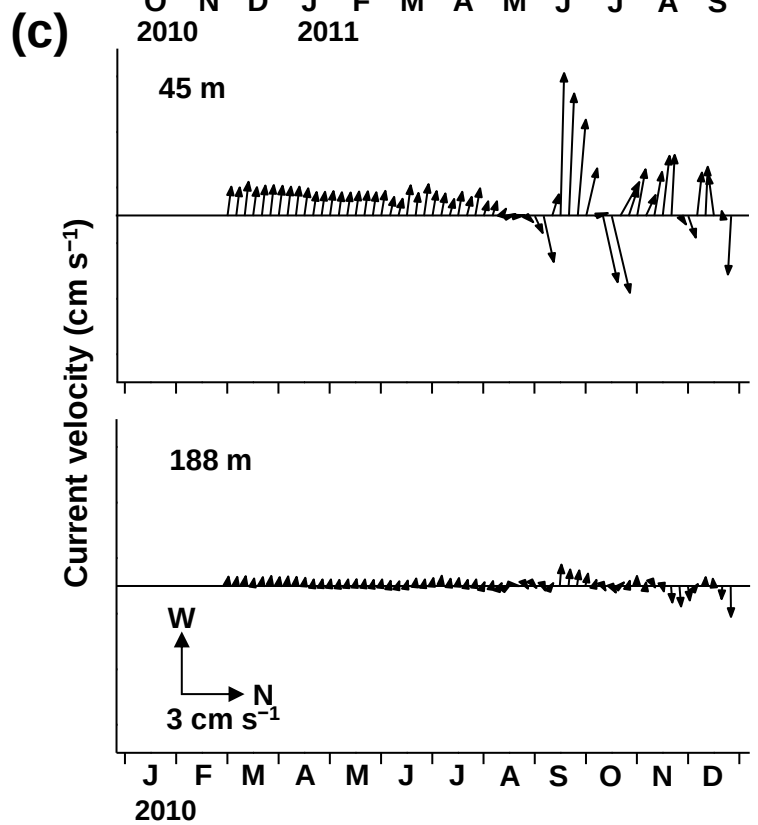
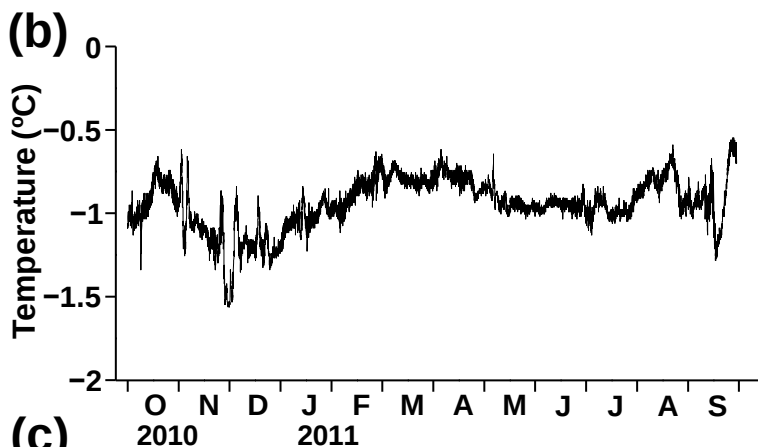
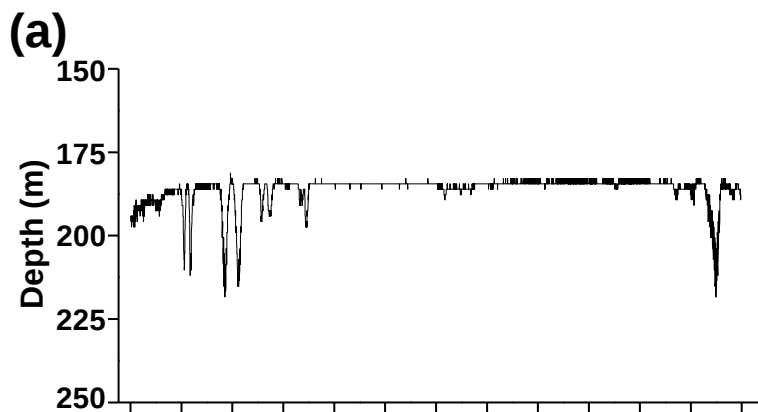


Fig. 2 (Matsuno et al.)

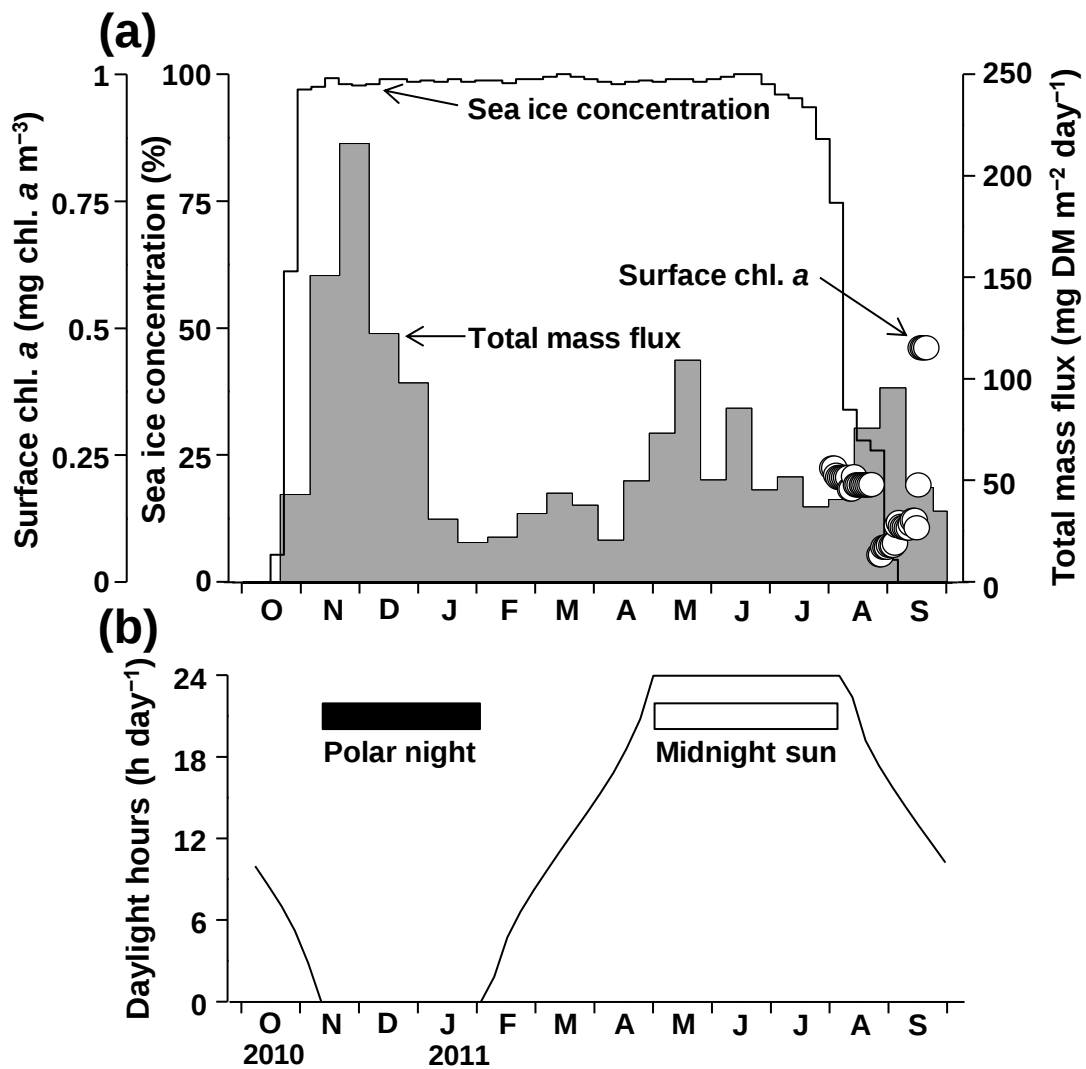


Fig. 3 (Matsuno et al.)

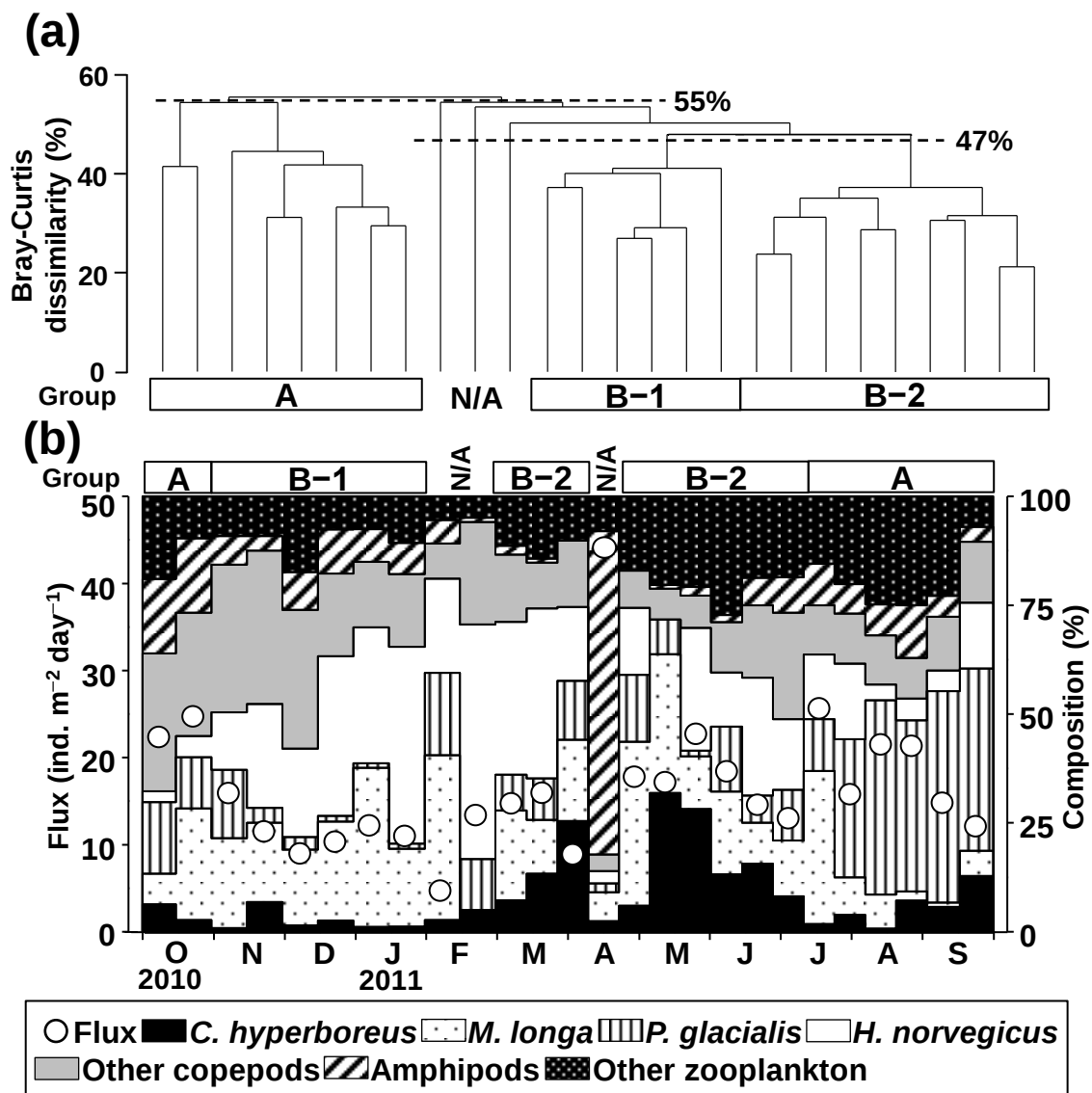


Fig. 4 (Matsuno et al.)

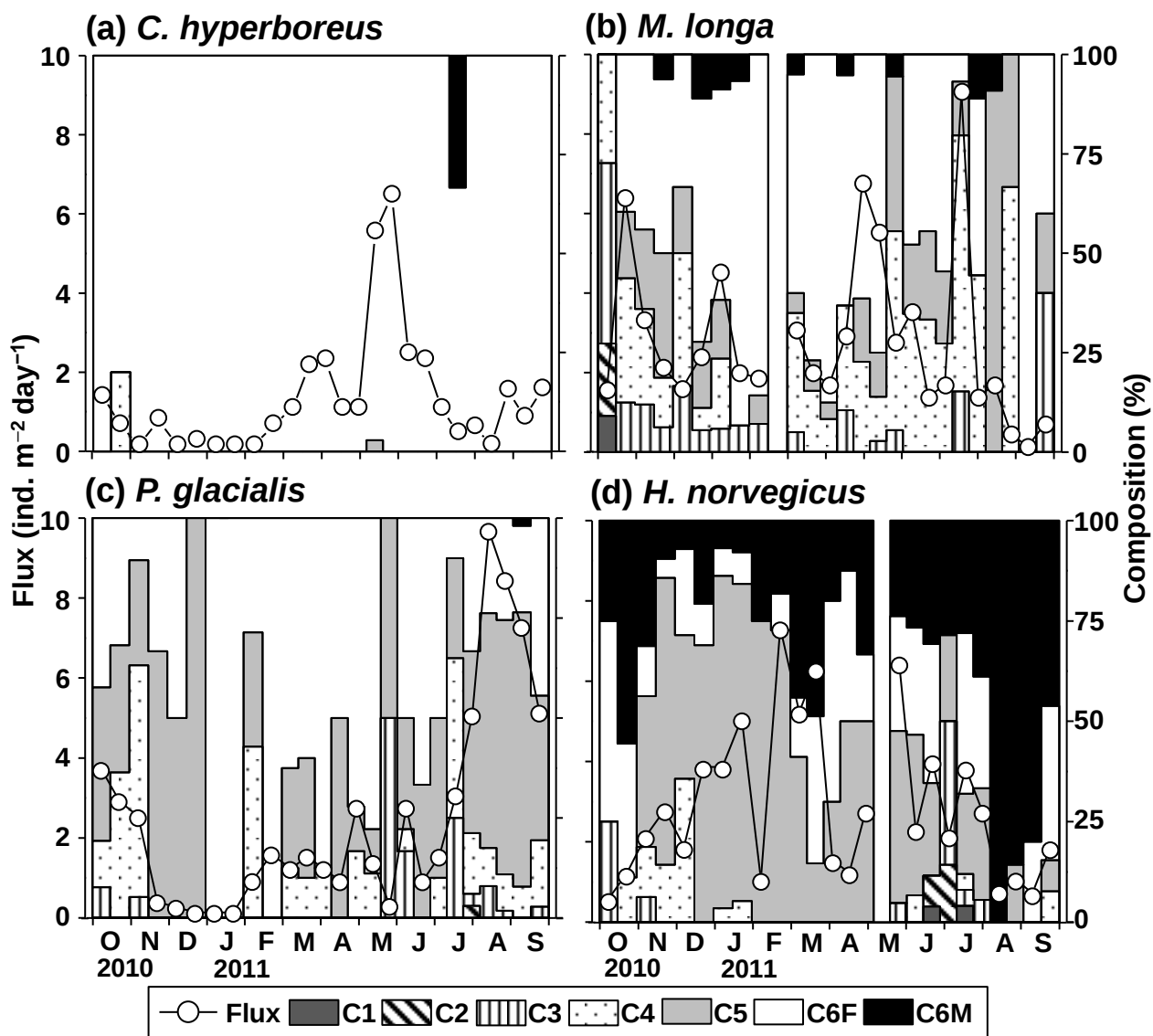


Fig. 5 (Matsuno et al.)

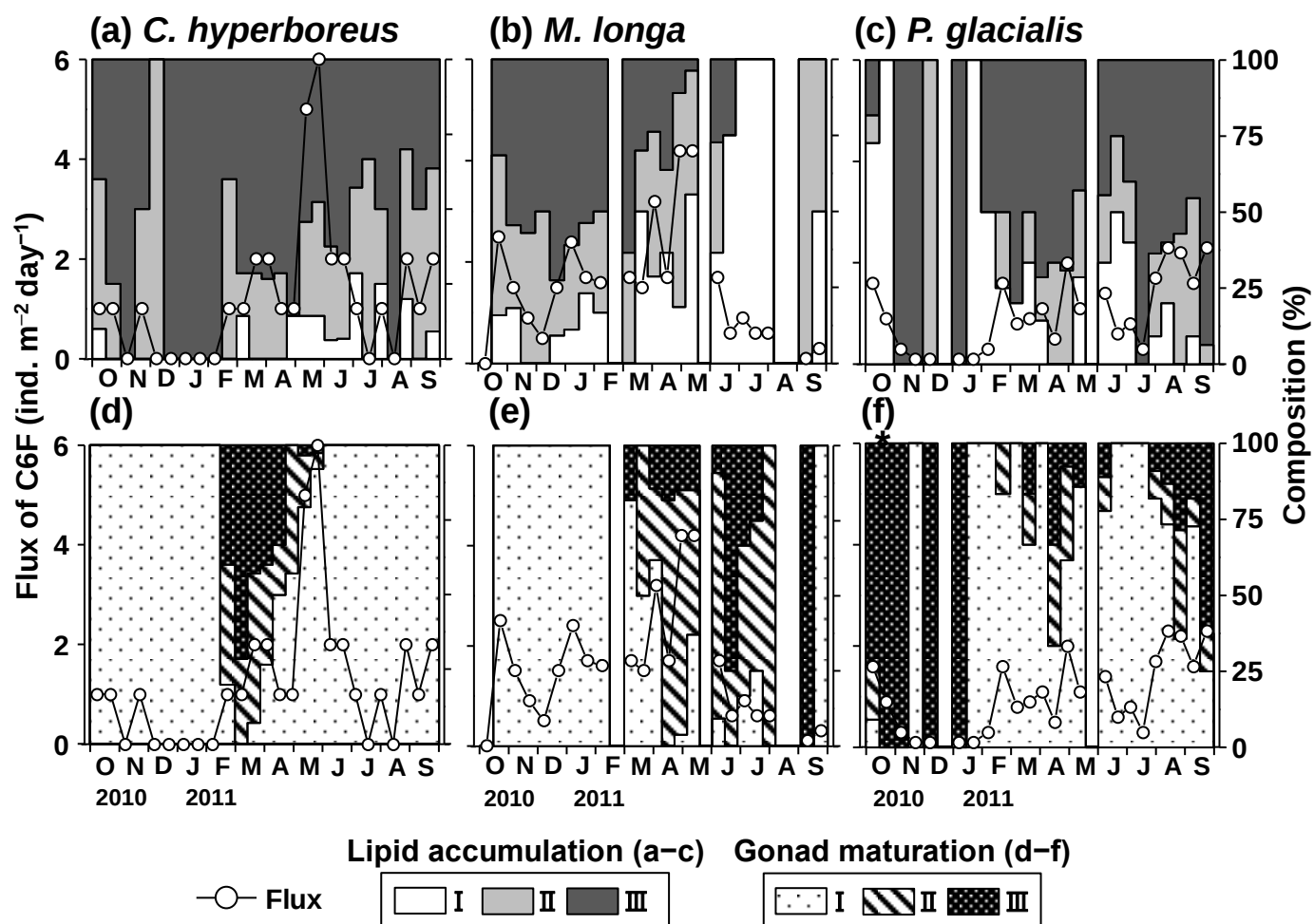


Fig. 6 (Matsuno et al.)

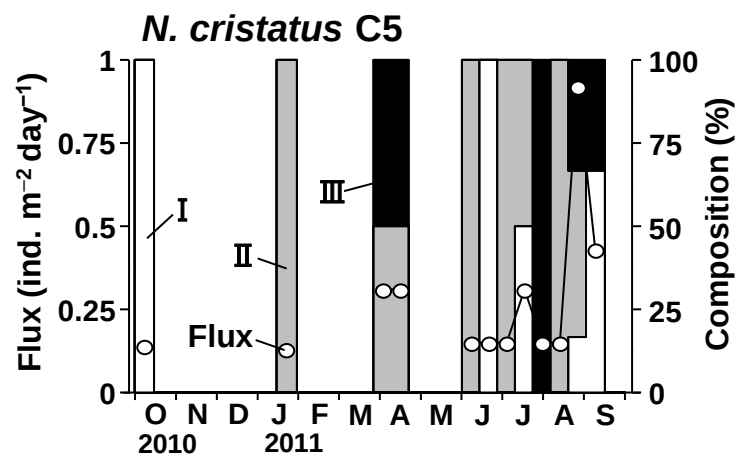


Fig. 7 (Matsuno et al.)

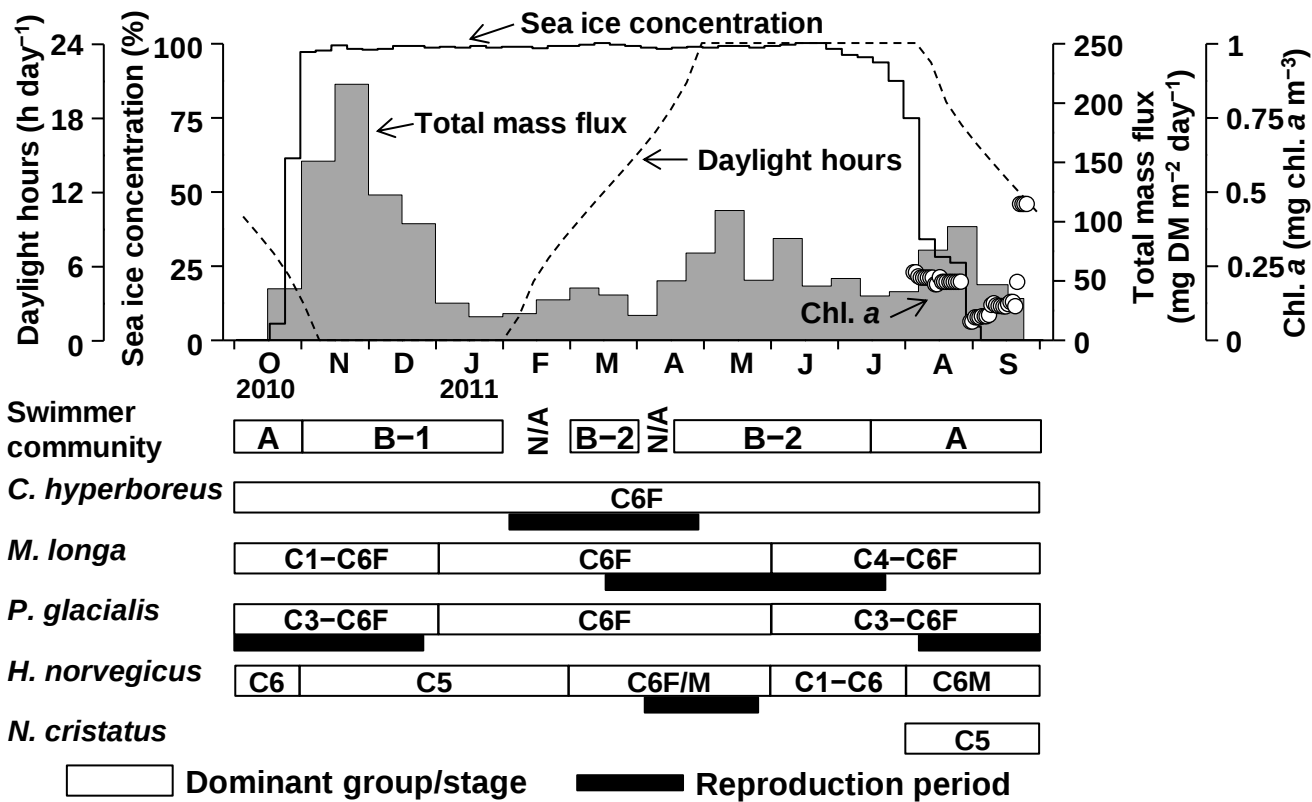


Fig. 8 (Matsuno et al.)