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

KOHEI MATSUNO[1]*, ATSUSHI YAMAGUCHI[2], AMANE FUJIWARA[1], JONAOTARO ONODERA[3], EIJI WATANABE[3], ICHIRO IMAI[2], SANAE CHIBA[3], NAOMI HARADA[3] AND TAKASHI KIKUCHI[3]

[1]ARCTIC ENVIRONMENT RESEARCH CENTER, NATIONAL INSTITUTE OF POLAR RESEARCH, 10-3 MIDORI-CHO, TACHIKAWA, TOKYO 190-8518, JAPAN, [2]LABORATORY OF MARINE BIOLOGY, GRADUATE SCHOOL OF FISHERIES SCIENCES, HOKKAIDO UNIVERSITY, 3-1-1 MINATO-CHO, HAKODATE, HOKKAIDO 041-8611, JAPAN AND [3]JAPAN AGENCY FOR MARINE-EARTH SCIENCE AND TECHNOLOGY, NATSUSHIMA-CHO 2-15, YOKOSUKA, KANAGAWA 237-0061, JAPAN

*CORRESPONDING AUTHOR: matsuno.kohei@nipr.ac.jp, k.matsuno@fish.hokudai.ac.jp

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To examine seasonal changes in the mesozooplankton community, analyses were made on the swimmer samples (>1 mm) collected by a sediment trap mooring at 184 m depth on the Northwind Abyssal Plain in the western Arctic Ocean during October 2010–September 2011. The zooplankton swimmer flux ranged from 5 to 44 ind. m^{-2} day^{-1} and was greater during July to October; copepods were the dominant taxon. Based on the zooplankton swimmer flux, cluster analysis classified samples into three groups (A, B-1 and B-2). The occurrence of each group showed clear seasonality; group A was observed during July to October, group B-1 was seen in November to January and group B-2 during March to June. The seasonal variability in population structures of four dominant copepod swimmers was clearly different between the species. Most *Calanus hyperboreus* were copepodid stage 6 female (C6F) throughout the year. For *Metridia longa* and *Paraeuchaeta glacialis*, C6Fs dominated during January to May, and early copepodid stages increased during June to October. *Heterorhabdus norvegicus* was dominated by stage C5 during November to

February, and C6F/M during March to May. Since Pacific copepods (*Neocalanus cristatus*) occurred in significant number during August–September, possible causes are discussed.

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

INTRODUCTION

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

The zooplankton community in the western Arctic Ocean has been studied based on net samples (Springer *et al.*, 1989; Darnis *et al.*, 2008; Hopcroft *et al.*, 2010; Matsuno *et al.*, 2011, 2012). However, seasonal sea ice coverage in this area prevents collection of net samples in winter, and most of the studies were conducted only in summer. To evaluate seasonal changes in zooplankton community, analysis based on zooplankton swimmers (Knauer *et al.*, 1979) collected by moored sediment traps is a powerful tool (cf. Forbes *et al.*, 1992). According to Knauer *et al.* (1979), a swimmer is defined as zooplankton that actively swim into the trap and are killed by the preservation fluid filling the cups. Because of their importance, seasonal changes in the swimmer community collected by sediment traps have been studied in several areas of the Arctic Ocean, especially in the Beaufort Sea (Forbes *et al.*, 1992; Ota *et al.*, 2008; Makabe *et al.*, 2010). According to Makabe *et al.* (Makabe *et al.*, 2010), seasonal

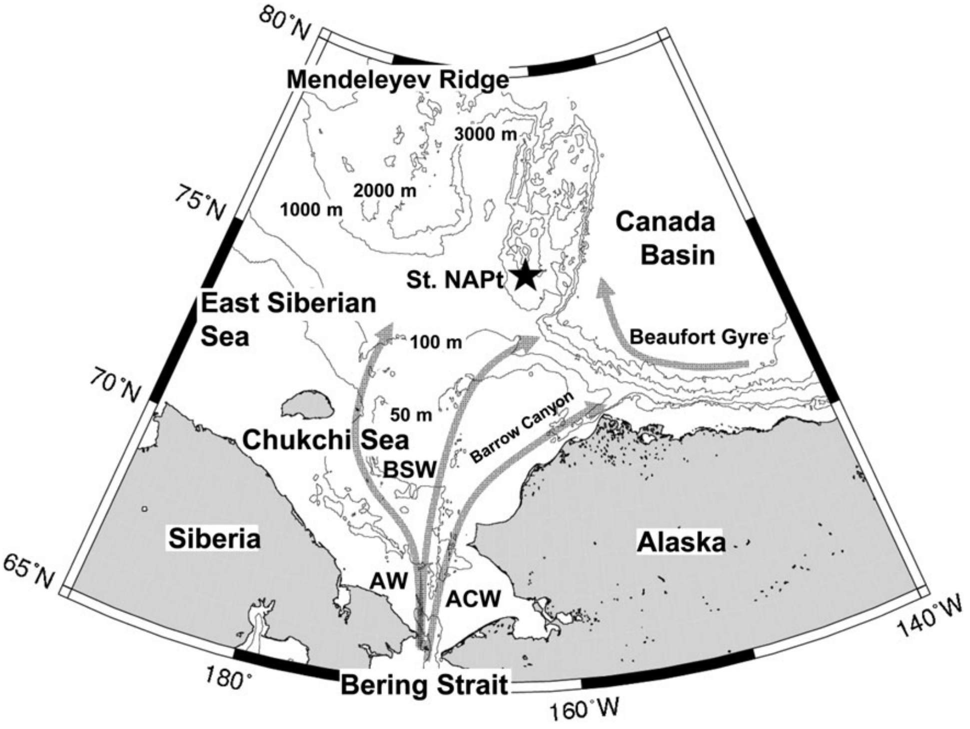

Fig. 1. Location of St NAPt (Northwind Abyssal Plain trap) in the western Arctic Ocean where the sediment trap was moored at 184 m during October 2010–September 2011. ACW, Alaskan Coastal Water; AW, Anadyr Water; BSW, Bering Shelf Water.

changes in the Arctic swimmer community are related to the sea ice concentration, temperature and salinity. This is partly because large copepods migrate to surface when the sea ice melts (Conover and Huntley, 1991), graze on phytoplankton in the ice-edge bloom (Springer and McRoy, 1993) and then reproduce. The reproduction seasons of dominant copepods vary with species and areas within the Arctic Ocean (Falk-Petersen *et al.*, 2009). Despite their importance, little information is available for copepod life cycles other than for dominant species. For dominant copepods, their species-specific lipid accumulation and gonad maturation have little studied in the western Arctic Ocean.

In the present study, we analyzed zooplankton swimmers collected by sediment trap sampling at 13–15-day intervals moored at 184 m on the Northwind Abyssal Plain during October 2010–September 2011. Through this analysis, seasonal changes in swimmer community structure and population structure of the four dominant copepods (*Calanus hyperboreus*, *Metridia longa*, *Paraeuchaeta glacialis* and *Heterorhabdus norvegicus*) were evaluated. Lipid accumulation and gonad maturation of adult females [copepodid stage 6 females (C6F)] of the dominant copepods were analyzed to evaluate their life cycle patterns. Seasonal occurrence of Pacific copepods (*Neocalanus cristatus*) was also noted and the possible cause is discussed.

METHOD

Field sampling

Samples were collected by sediment trap (SMD26 S-6000, open mouth area 0.5 m^2, Nichiyu Giken Kogyo, Co. Ltd.) rotated at 13–15-day intervals moored at 184 and 1300 m at St NAPt (Northwind Abyssal Plain trap, 75°00′N, 162°00′W, bottom depth 1975 m) during 4 October 2010–28 September 2011 (Fig. 1). This station is seasonally affected by inflow of Bering Shelf Water from the Bering Strait (Weingartner *et al.*, 2005; Woodgate *et al.*, 2005). The end of the trap rope was fixed to the sea bottom. Sea water for filling sample cups was taken from 1000 m water depth in the southern Canada Basin (salinity 34.89), and was membrane filtered (0.45 μm pore size) to make 5% buffered formalin seawater. The sample cups were filled with the 5% buffered formalin seawater before the sediment trap was deployed.

After the trap was retrieved, the 26 samples were each gently filtered with 1 mm mesh, and the remaining fraction (>1 mm size) on the mesh was treated as zooplankton swimmers. Since the number of zooplankton swimmers was low for the deeper trap (1300 m), we consider only the shallower trap (184 m) in this study. The fine size fraction (<1 mm) for each sample was evenly divided into 10 aliquots using the Wet Sample Divider (McLane^{TM} WSD-10). The one of divided aliquots for each sample was filtered on a weighed polycarbonate membrane filter, and was desalted with Milli-Q waters. The sample filters were dried with diphosphorus pentaoxide in a desiccator for 3 days. The dried sample filters were weighed with an analytical balance to calculate total mass flux (mg dry mass [DM] m^{-2} day^{-1}) of <1 mm size fraction for each sample period.

As supplemental environmental data, the moored trap depth and the water temperature (accuracy of ±0.2°C) were monitored every hour (sensor type: ST-26S-T). We estimated the current speed at St. NAPt in 2010 by a physical ocean general circulation model: Center for Climate System Research Ocean Component Model (COCO) version 4.9. The model performance in the western Arctic Ocean has been verified in previous decadal and seasonal experiments (Watanabe *et al.*, 2012; Watanabe and Ogi, 2013). Time-series data on weekly averaged percentage ice coverage around St NAPt (74.5–75.5°N, 161.5–162.5°W) during the mooring period were calculated from the sea ice concentration data set (http://iridl.ldeo.columbia.edu/SOURCES/.IGOS-S/.nmc/.Reyn_SmithOIv2/, cf. Reynolds *et al.*, 2002). For sea ice coverage data of the whole Arctic Ocean, data were downloaded from the AMSER-E data set (http://www.ijis.iarc.uaf.edu/seaice/-extent/plot.csv). The MODIS/Aqua Level 3 binned chlorophyll-*a* data (reprocessing version 2012.0) were downloaded from the Distributed Active Archive Center (DAAC) of the Goddard Space Flight Center (GSFC), NASA. We used daily data at 9 km resolution, and composited to 9 days running mean.

Analysis of zooplankton swimmers

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

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

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

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

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

Data analysis

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

RESULTS

Hydrography

The trap depth varied between 181 and 218 m (Fig. 2a), and was mostly stable around 184 m then temporally deepened (220 m) within a short period (6–7 days) in October, December 2010 and September 2011. Temperature at the sediment trap ranged from −1.6 to −0.6°C (Fig. 2b). Rapid decreases in temperature were paralleled with the changes in depth of the moored trap (Fig. 2a and b). The 5-day mean of current velocity simulated by the ocean circulation model showed a slow subsurface current ($<11.3\ \mathrm{cm\,s^{-1}}$ at 45 m and $<2.7\ \mathrm{cm\,s^{-1}}$ at 188 m water depths) at St NAPt (Fig. 2c). From repeated CTD casts at the station, four water masses were identified in 0–500 m of the water column: i.e. SML: Surface Mixed Layer (0–25 m), PSW (25–100 m), PWW: Pacific Winter Water (100–250 m), AW: Atlantic Water (>250 m) (Fig. 2d and e) (McLaughlin *et al.*, 2011).

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

Swimmer community

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

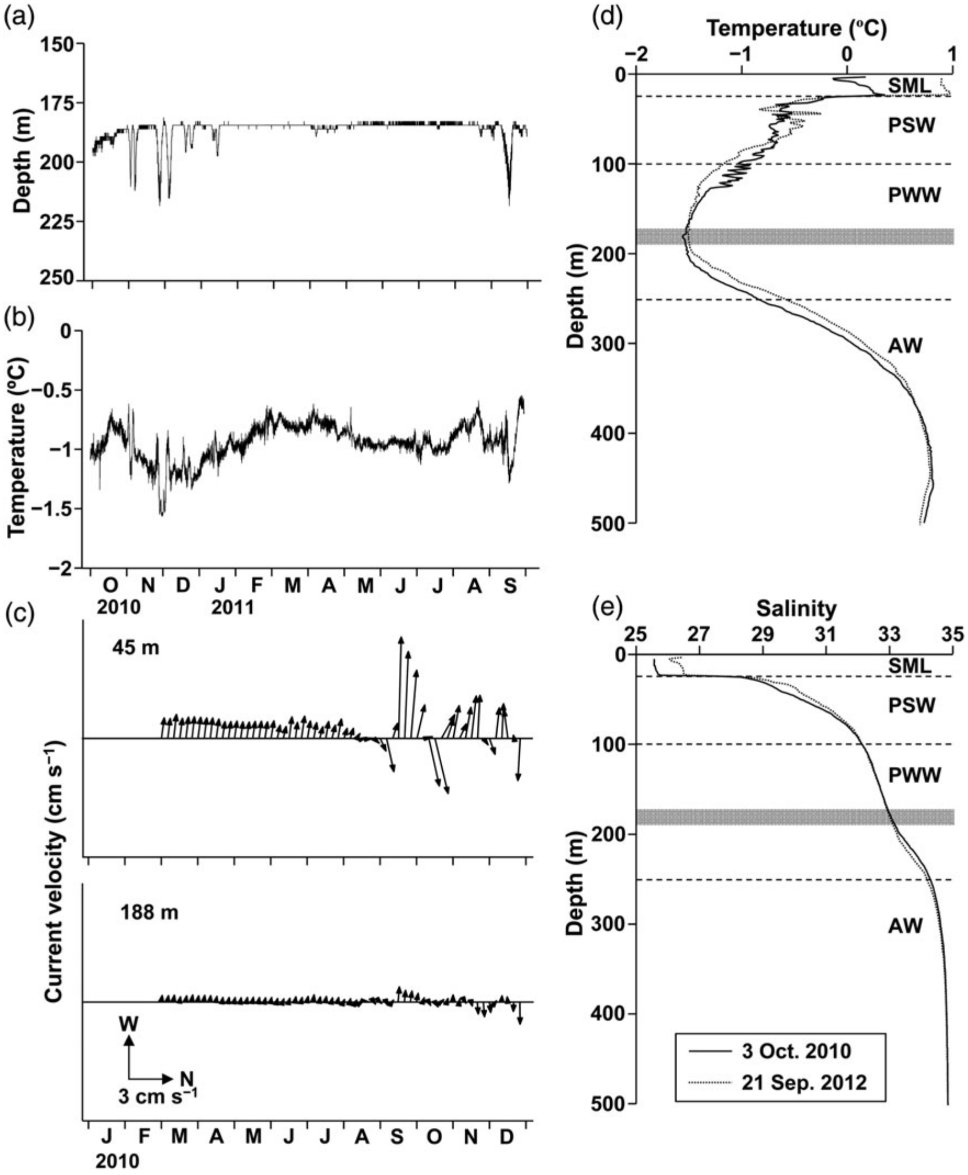

Fig. 2. Seasonal changes in depth (**a**) and temperature (**b**) monitored for the shallower trap at St NAPt during October 2010–September 2011. Current velocity at 45 and 188 m of St NAPt (**c**) estimated by a physical ocean general circulation model: Center for Climate System Research Ocean Component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

other groups analyzed by one-way ANOVA and Fisher's PLSD, $P < 0.05$) were as follows: A, the mesopelagic copepods *Paraeuchaeta glacialis*; B-2, the inter-zonal copepod *Calanus hyperboreus*. While group B-1 was dominated by *Metridia longa* and *Heterorhabdus norvegicus*, their flux showed no significant seasonal changes.

Copepod population structure

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

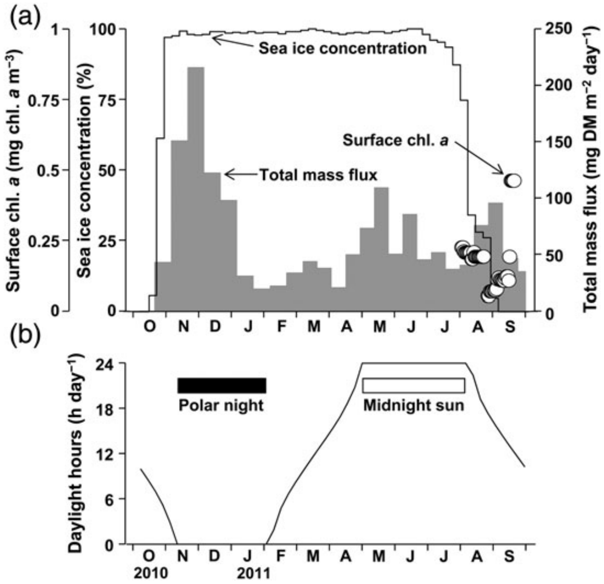

Fig. 3. Seasonal changes in sea ice concentration for the investigation area during the sampling period (http://iridl.ldeo.columbia.edu/SOURCES/.IGOSS/.nmc/.Reyn_SmithOIv2/, data from Reynolds *et al.*, 2002), total mass flux (<1 mm size fraction) collected by sediment trap, surface chl *a* from satellite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

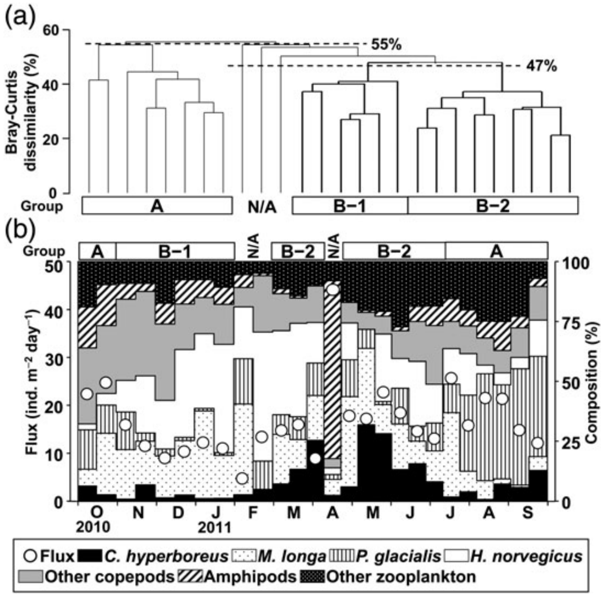

Fig. 4. Results of cluster analysis based on the flux of zooplankton swimmers. Twenty six samples were clustered into three groups from Bray–Curtis dissimilarity (**a**). Seasonal changes in zooplankton swimmer flux, species composition and clustered groups collected by sediment trap moored at 184 m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

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

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

Pacific copepods

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

DISCUSSION

Trap collection efficiency

In general, underestimation bias of sinking particle flux is due to low trap collection efficiency under water flow conditions especially shallower than 1000 m (Buesseler *et al.*, 2007). The time-series monitoring data for physical oceanography around St NAPt are limited. However, the directly measured current around St NAPt in winter was slower than 10 cm s^{-1} at 58 and 250 m depths (Sumata and Shimada, 2007). The current speed estimated by an ocean circulation model also confirmed that the speed of the subsurface current around the trap was slow (<2.7 cm s^{-1}) at St NAPt throughout the year (Fig. 2c). These slow current speeds are not expected to have a significant effect on sediment trap collection efficiency. The sediment trap temporarily deepened to 220 m with a short period (6–7 days) in October, December 2010 and September 2011 (Fig. 2a). Temporal changes in temperature also confirmed these changes (Fig. 2b). The tilt of the sediment trap was estimated to be within 15° during the deepening events. Except for these periods, the mooring depth of the sediment trap was kept between 180 and 190 m. Since the PWW occurred between 100 and 250 m (Fig. 2d and e), little change in water masses at the trap depth were expected. Although the sediment trap

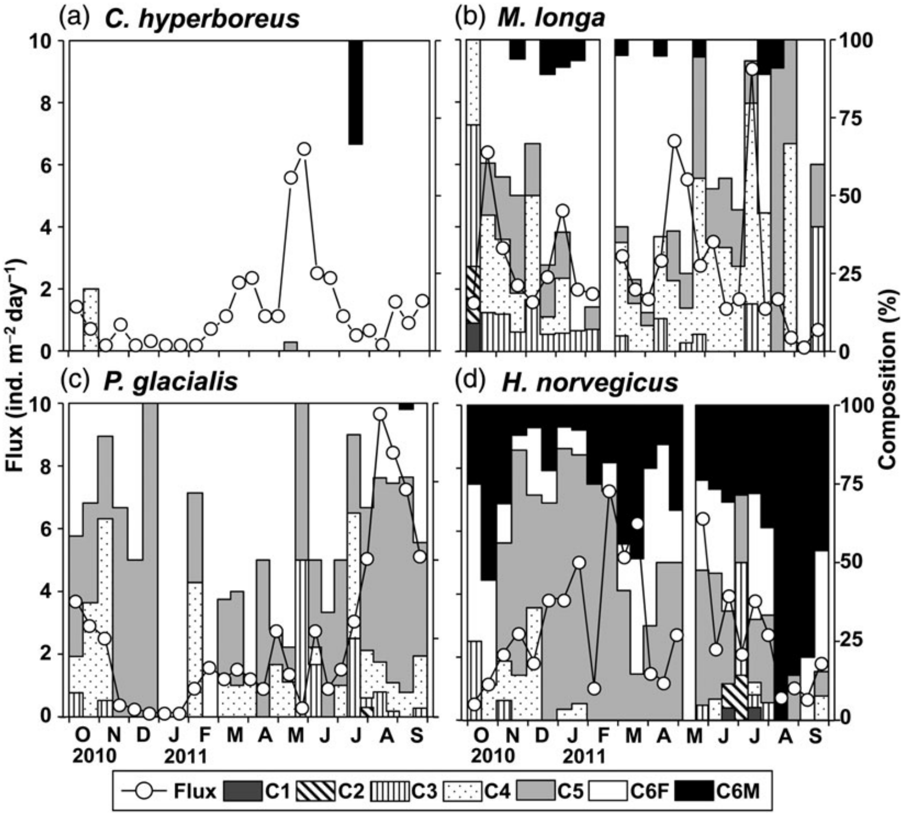

Fig. 5. Seasonal changes in flux and copepodid stage composition of the four dominant copepods: *Calanus hyperboreus* (**a**), *Metridia longa* (**b**), *Paraeuchaeta glacialis* (**c**), *Heterorhabdus norvegicus* (**d**), at 184 m at St NAPt during 4 October 2010–28 September 2011.

deployment depth was not completely constant throughout the study period, the seasonality of total mass fluxes at the 184 and 1300 m traps (Onodera *et al.*, pers. comm.) was essentially parallel ($r^2 = 0.621$, $P < 0.0001$). These results suggest that the influence of the trapping efficiency bias is relatively insignificant for the sediment trap samples studied.

Seasonal changes in swimmer community

Previously reported zooplankton swimmer communities collected by sediment trap in the Arctic Ocean are summarized in Table I. Throughout the studies, copepods are the most dominant taxa, followed by amphipods or pteropods consistent with the present study. Within the copepods, *C. finmarchicus* was reported to be dominant in the shallower trap (ca. 100 m) in a Norwegian fjord open to the North Atlantic Ocean (Willis *et al.*, 2006, 2008). While in the deep-layer (500 m) of the eastern Greenland Sea, *C. finmarchicus* was less abundant and the layer was dominated by *M. longa* (Seiler and Brandt, 1997). For the western Arctic Ocean (Amundsen Gulf and Beaufort Sea), not open to the Atlantic Ocean, *C. finmarchicus* did not occur and *M. longa* was dominant (Forbes *et al.*, 1992; Sampei *et al.*, 2012). For the northernmost station (81°N), diapausing *C. hyperboreus* dominated (Hargrave *et al.*, 1989). Thus, the dominant copepod species collected by sediment traps may vary with region and trap depths. The trap depth of this study (184 m) was relatively shallow, but because the NAPt is not open to the Atlantic Ocean, *C. finmarchicus* did not occur. Dominant copepods in this study were *H. norvegicus* followed by *M. longa*, unique because of the dominance of mesopelagic copepods (Yamaguchi and Ikeda, 2000). *Heterorhabdus norvegicus* is reported to be the second most dominant copepod in the zooplankton swimmer fauna of the eastern Greenland Sea (Seiler and Brandt, 1997); thus this species may be a dominant copepod throughout the mesopelagic layer of the Arctic Ocean. The copepod fauna evaluated by stratified net sampling has also shown the occurrence of *H. norvegicus* throughout the Arctic Ocean (Kosobokova and Hirche, 2000; Auel and Hagen, 2002; Kosobokova and Hopcroft, 2010; Dvoretsky and Dvoretsky, 2011). Additional to these copepods, the occurrence of a small number of Pacific copepods is a special feature of this study. Since the zooplankton swimmer community showed clear seasonal changes (groups A, B-1 and B-2), in the following we discuss the characteristics of each swimmer group.

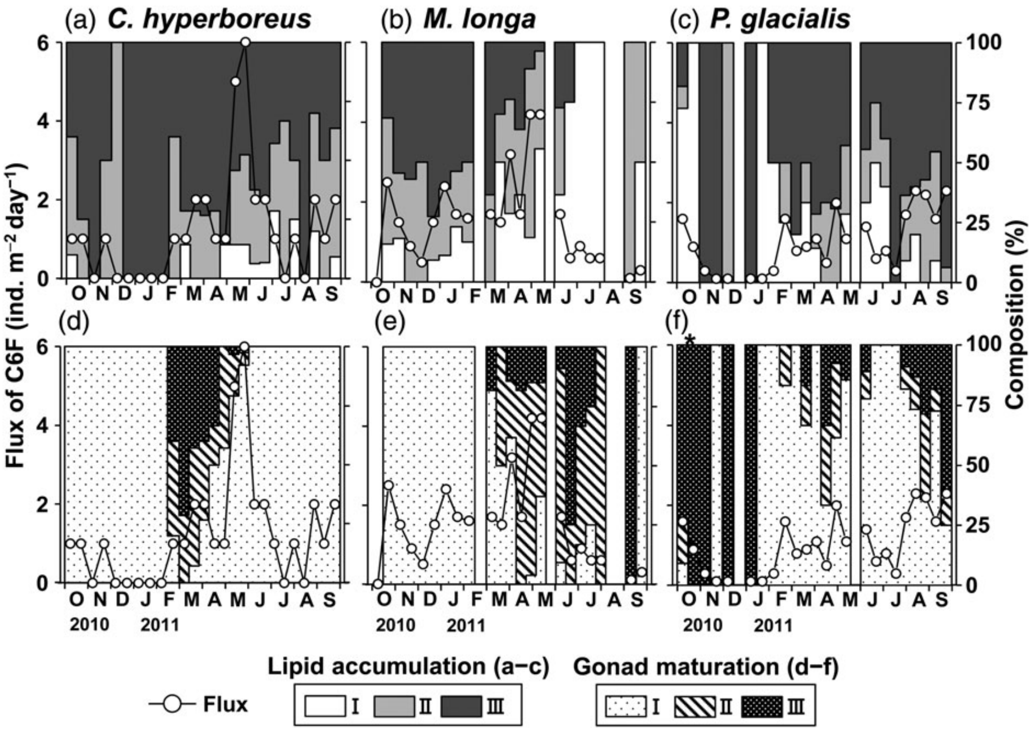

Fig. 6. Seasonal changes in flux, lipid accumulation (upper panels) and gonad maturation (lower panels) composition (stage I–III) of C6Fs of *Calanus hyperboreus* (whole $n = 232$) (**a** and **d**), *Metridia longa* ($n = 234$) (**b** and **e**) and *Paraeuchaeta glacialis* ($n = 166$) (**c** and **f**) at 184 m of St NAPt during 4 October 2010–28 September 2011. *Presence of female with egg sac attached.

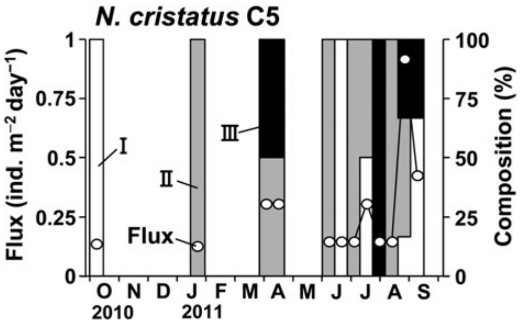

Fig. 7. Seasonal changes in flux and lipid accumulation composition (I–III) of the Pacific *Neocalanus cristatus* C5 collected by sediment trap moored at 184 m of St NAPt during 4 October 2010–28 September 2011.

The group A, corresponded with the open water period (July–October), dominated by the carnivorous *P. glacialis* (3.7–9.4 times greater flux than the other groups, one-way ANOVA, $P < 0.001$). For the numerical dominance of *P. glacialis* during July–October, two factors are considered: (i) the correspondence of growth to large copepodid stages (>1 mm in size), and (ii) correspondence of the presence of extensive diel vertical migration (DVM) during this period. For the former, dominance of stage C5 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 of *P. glacialis*, is known to perform DVM during autumn (Kaartvedt *et al.*, 2002), but ceases 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* exhibits similar DVM to *P. norvegica*, the dominance of *P. glacialis* in group A (July–October) was caused by *P. glacialis* DVM during this period.

Changes in the zooplankton swimmer community from groups A to B-1 corresponded to the timing of ice coverage and entry into polar night (Fig. 3c). The group B-1 was characterized by the dominance of mesopelagic *M. longa* and *H. norvegicus*. While their flux showed little seasonal change (Fig. 5b and 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 of mesopelagic copepods (*M. longa* and *H. norvegicus*) 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 governing the seasonal changes in the swimmer community.

Table I: *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)	October 2007 – July 2008	112	*M. longa* (50), *P. glacialis* (6), *C. hyperboreus*(2), *C. glacialis* (2)	Sampei *et al.* (2012)
Amundsen Gulf (70 – 72°N, 123 – 135°W)	October 2003 – August 2004	100, 200, 400	*Oncaea* spp. (34), *M. longa*(21), pteropods (11), *C. hyperboreus*(4)	Makabe *et al.* (2010)
Beaufort Sea Shelfbreak (69 – 72°N, 127 – 139°W)	September 1987 – March 1988	115, 128, 145	*M. longa* (49), amphipods (27), *P. glacialis*(15), *C. hyperboreus*(8)	Forbes *et al.* (1992)
East Greenland Sea (72°0′ – 30′N, 7°2′ – 43′W)	July 1989 – July 1992	500	*M. longa* (59), *H. norvegicus* (12), amphipods (9), ostracods (8)	Seiler and Brandt (1997)
Kongsfjorden (79°1.2′N, 11°46.4′E)	September 2005 – May 2006	115	*C. finmarchicus*, *C. glacialis*, *M. longa*, *P. norvegica*	Willis *et al.* (2008)
Kongsfjorden (79°3.2′N, 11°18.0′E)	April – June, July – September 2002	215	*C. finmarchicus*, *C. glacialis*, *C. hyperboreus*, *P. norvegica*	Willis *et al.* (2006)
Axel Heiberg Island (81°N, 96 – 98°W)	September 1986 – June 1987	100	*C. hyperboreus*(78), *M. longa* (9), *P. norvegica* (4), *C. glacialis* (2)	Hargrave *et al.* (1989)
Northwind Abbysal Plain (75°47′N, 126°30′W)	October 2010 – September 2011	180	*H. norvegicus* (17), *M. longa* (16), *P. glacialis* (15), *C. hyperbpreus* (8)	This study

During the ice coverage period (November–June), the swimmer community changed from groups 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 (500–1500 m) in winter and to make upward SVM to the surface layer in April (Hirche and Niehoff, 1996). In the present study, it was shown that the *C. hyperboreus* population comprised 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 the deep layer. Therefore, the change in swimmer community (from groups B-1 to B-2) during January–March might have been caused by the upward SVM of *C. hyperboreus*. As an arousal mechanism for resting copepods, the presence of an internal body timer has been discussed (Miller and Grigg, 1991; Miller *et al.*, 1991). Since daylight hours changed greatly from 0 (polar night) to 24 h (midnight sun) during February to April (Fig. 3c), this change in day–night cycle may affect the arousal from diapause for *C. hyperboreus*.

As a specialized seasonal event in this study, the occurrence of Pacific copepods was observed. The Pacific copepod *N. cristatus* C5 was abundant during August–September when sea ice coverage decreased (Fig. 8). This seasonal pattern suggests that the amount of Pacific Water inflow may increase when the sea ice coverage decreases. While *N. cristatus* C5 are known to perform SVM to deep layers to diapause during late summer (Miller *et al.*, 1984), the greater flux of *N. cristatus* C5 in August–September may also be caused by their SVM. Since their reproduction occurs >1000 m depth (Miller *et al.*, 1984), the possibility of their reproduction in the Arctic Ocean could not be evaluated in this study.

Population structure of dominant copepods

Calanus hyperboreus populations were composed mainly of C6F throughout the year (Fig. 5a). *Calanus hyperboreus* reproduces during November–April in the Amundsen Gulf (Ota *et al.*, 2008), November–March in the Greenland Sea (Hirche and Niehoff, 1996) and February–March in the Norwegian Sea (Østvedt, 1955). In the present study, mature C6F were seen only from February to April, which suggests this is the reproduction period (Fig. 8). This reproductive season (February–April) generally corresponds to the previous studies with slight seasonal variations. For the regional variability in reproduction timing of *C. hyperboreus*, timing of the phytoplankton bloom is reported to be a most important factor (Conover and Siferd, 1993; Hirche and Niehoff, 1996). Individuals in stage C6F with full lipid sacs dominated in December–January, and the lipid

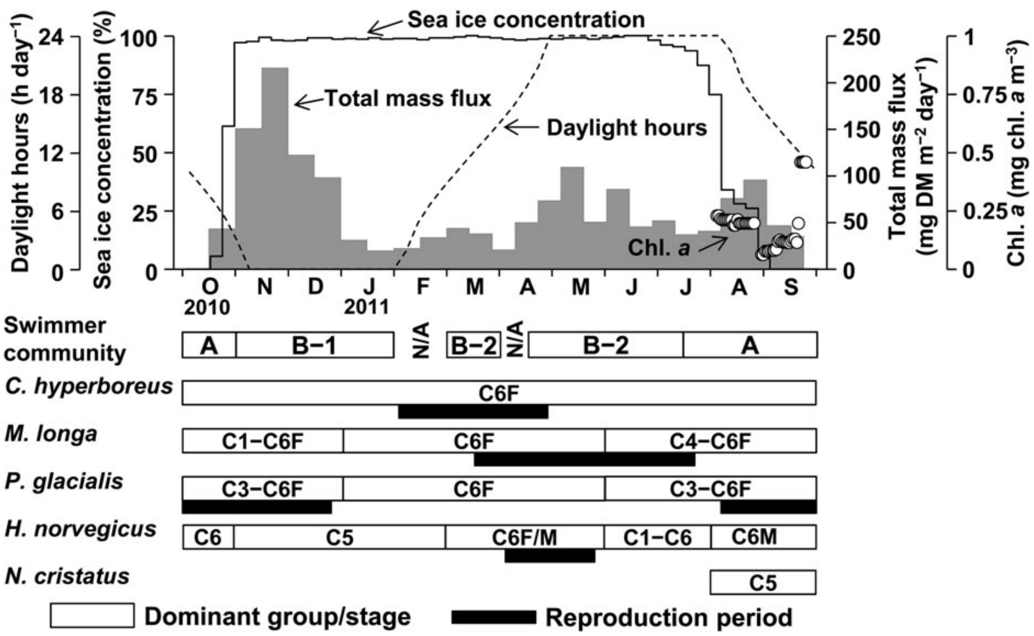

Fig. 8. Schematic diagram of seasonal changes in daylight hours, sea ice concentration, chl *a*, total mass flux (upper panel), swimmer community, population structure and reproduction period of copepods (*C. hyperboreus*, *M. longa*, *P. glacialis* and *H. norvegicus*), and occurrences of the Pacific *N. cristatus* collected by sediment trap at 184 m of St NAPt during 4 October 2010–28 September 2011 (lower panel). For *C. hyperboreus*, *M. longa* and *P. glacialis*, the 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).

accumulation decreased from February when reproduction started (Fig. 6a). This seasonal correspondence between the reproduction period and decrease of lipid accumulation would be caused by the utilization of the stored lipid during reproduction (Hirche and Niehoff, 1996; Vinogradov, 1997).

The *M. longa* population was dominated by C6F during January–May, and early copepodid stages (C1–C4) during June–October (Fig. 5b). *Metridia longa* is an omnivore and performs diel vertical migration (Conover and Huntley, 1991; Ashjian *et al.*, 1995), and has no diapause phase (Båmstedt and Ervik, 1984; Grønvik and Hopkins, 1984). The main reproduction season shows regional variability: during April–May in the Balsfjorden (Tande and Grønvik, 1983), in winter under the sea ice in the Barents Sea (Hirche and Kosobokova, 2011) and in autumn in a polynya in the Beaufort Sea (Makabe *et al.*, 2010). In this study, mature C6F occurred only during March–July (Fig. 6e), and early copepodid stages (C1–C4) dominated the population during June–October (Fig. 5b). These facts suggest that *M. longa* reproduces during March–July and the new population appears during June–October. This reproductive season (March–July) in the western Arctic Ocean is slightly longer than that in the Balsfjorden (April–May) (Tande and Grønvik, 1983). Individuals with lipid accumulation (stage III) dominated during October–December, decreased gradually over the winter and no specimens had oil sacs in July (Fig. 6b). This season of decreasing lipid (March–June) parallels the gonad maturation season (March–July). These facts suggest that stored lipids are used for gonad maturation by *M. longa* as has been seen in *C. hyperboreus*.

The *P. glacialis* population was dominated by C6F during January–May, and contained early copepodid stages (C2–C4) during June–October (Fig. 5c). Carnivorous *Paraeuchaeta* spp. performs raptorial feeding throughout the year, accumulates lipids and has no diapause phase (Båmstedt, 1979; Øresland, 1991). Since mature C6F *P. glacialis* dominated during August–January and egg carrying C6F also occurred during the same period (Fig. 6f), this species is assumed to reproduce in this period. This may be related to the ice-edge bloom at the surface. The ice-edge bloom is known to occur after ice melt (Springer and McRoy, 1993) (Fig. 3b). The bloom induces the upward migration of Arctic copepods (e.g. *C. glacialis*) and reproduction of small copepods (e.g. *Pseudocalanus* spp.) (Conover and Huntley, 1991), which would provide sufficient food condition for carnivorous *P. glacialis*. Since sufficient food (abundant small metazoan zooplankton) is a key to supporting growth and reproduction of *Paraeuchaeta* spp. (Yamaguchi and Ikeda, 2001; Abe *et al.*, 2012), *P. glacialis* may have reproduced in this season. This reproduction season of *P. glacialis* (August–January) differs from that of *C. hyperboreus* (February–April) and

M. longa (March–July). These differences may be related to differences in feeding modes, i.e. carnivory in *P. glacialis* and suspension feeding in *C. hyperboreus* and *M. longa*.

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

In summary, while the limitation of sampling design, through the analysis of zooplankton swimmers collected by the sediment trap, zooplankton communities were clearly separated into three seasons (Fig. 8). The season when each copepod dominated corresponded with the active vertical migration timing of each species. For the four dominant copepods, their reproduction timings varied with species, which may be related to the feeding modes. In addition, the occurrence of Pacific copepods was observed. Since their peak period (August–September) corresponded with timing of their SVM, they may have entered the sediment trap while performing descent SVM.

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