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Regional comparison of seasonal changes on copepod community structure in the Arctic Ocean

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Abstract: The Arctic Ocean is characterized as the greatly variable oceanic environment both seasonality and regionally. Such environmental variability would affect regional differences in the respective copepod community structures, though it has not been reported so far. In this study, we analyzed time-series zooplankton samples with focus on large copepods collected by sediment traps moored in three different regions of the Arctic Ocean at approximately 72-260 m water depth, and seasonality of copepod community structures were compared. Remarkable seasonality in the copepod community structure around Molloy deep in the eastern Fram Strait were due to the influence of endemic species transported by the West Spitsbergen Current. In contrast, in the southern Canada Basin (Northwind Abyssal Plain, Hanna Canyon and Barrow Canyon), the community structure of predominant large copepods showed less seasonality due to low primary production. In the MacKenzie Trough, the number of copepod swimmers were greater than those in all other regions investigated, which cooccur with much higher primary production in that area. These spatial differences in seasonality of copepod swimmer community structure were thought to be caused by various factors, not only sea ice seasonality but also differences in current patterns, endemic species and the magnitude of primary production.

Keywords: sediment trap; zooplankton swimmer; Arctic copepods seasonality

1. Introduction

In the Arctic Ocean, increase of air and sea water temperatures due to global warming induce rapid sea-ice reduction during summer (Markus et al., 2009). The concurrent drastic change of the marine environment is thought to critically affect marine ecosystems in the Arctic Ocean (Wassmann et al., 2011; Grebmeier, 2012). In the pelagic system, zooplankton organisms represent the most important prey of various higher trophic levels (Lowry et al., 2004; Wassmann et al., 2006). For instance, they are the main food source for polar cod (*Boreogadus saida*), which is an important commercial species in the Arctic Ocean (Bradstreet and Cross, 1982). Copepods can also be regarded as important indicators of currents, water mass and marine environments because of their low swimming ability and short life cycle compared to other organisms (e.g., fish) (Wassmann et al., 2006). Because of their dominance in the marine pelagic realm, it is an important topic to clarify the phenology of copepods. However, year-round ship-board observation is difficult in the deep Arctic Ocean because of the seasonal ice coverage lasting for eight months minimum. Due to this restriction, almost all studies investigating copepods in the Arctic Ocean have been carried out mainly during summertime when sea ice is very thin or melted (e.g., Springer et al., 1989). Thus, knowledge about seasonal changes within copepod community structures is still scarce.

Automatic sediment traps programmable to collect samples are a marine observation equipment to collect sinking particles in the water column over a certain time period when mooring at fixed depths. Since automatic sediment traps can collect one-year-round or even longer, they were used in the open ocean and the Arctic Ocean where it is difficult to collect year-round samples by ship-board expeditions (Matsuno et al., 2015; Makabe et al., 2016).

It has been reported that zooplankton actively swim into the trap and are killed by the preservation fluid filled in the cups (Knauer et al., 1979; Ota et al., 2008). Zooplankton species composition in sediment trap samples have usually been excluded from analysis. They were picked out of the samples to avoid an overestimation of sinking particles in water column. No attention had been drawn to the picked-out swimmers in most cases. Additionally, the zooplankton collected by sediment traps is thought to be semiquantitative because they are deployed at fixed depths (Seiler and Brandt, 1997). However, in recent years that attitude has changed, seasonal changes of the zooplankton community structure have been reported after having analyzed zooplankton that swam or sunk into the collecting jars of sediment traps (Makabe et al., 2010; Kraft et al., 2012; Bauerfeind et al., 2014; Matsuno et al., 2014).

Studies evaluating seasonal changes on zooplankton community structures by means of sediment traps have been conducted in the Fram Strait located at the entrance of the Atlantic sector to the Arctic Ocean (Kraft et al., 2012; Bauerfeind et al., 2014). In the Fram Strait, seasonal changes in the community structures of pelagic amphipods (*Themisto libellula*, *T. abyssorum* and *T. compressa*) were reported (e.g. Kraft et al., 2012, Schröter et al., 2019). The long-term seasonal changes of community structures of pteropods (*Limacina helicina* and *L. retroversa*) were revealed (Bauerfeind et al., 2014). Several studies have reported about seasonal changes of copepod community structures also for the Pacific sector of the Arctic such as for the Beaufort Sea (Makabe et al., 2010, 2016) and the Canada Basin (Matsuno et al., 2014, 2015, 2016). However, those investigations were limited to only a specific region of the Arctic Ocean and thus it is still unclear how the seasonality of copepod community structures differs among various regions pan-Arctic Ocean (e.g., Fram Strait, MacKenzie Trough and Canada Basin). Periods of sea-ice coverage, amount and timing of primary production, daytime hours and the feeding environment affecting copepod community structure. Seasonal changes of these environmental factors are different between Arctic regions (Conover, 1988; Harada, 2016), eventually resulting in different copepod communities in each region. Until now, there is no comparative study describing differences of seasonal changes in copepod community structures in high Arctic marine environments.

In this study, we compared seasonal changes of the community structures of dominant large copepods collected with time-series sediment traps moored in three different Arctic regions: Fram Strait, MacKenzie Trough and Canada Basin in order to understand the community compositions as well as to clarify what environmental factors can affect the observed differences in seasonal changes of the dominating copepod community structures.

2. Material and Methods

2.1. Field sampling

Time-series sediment traps were moored at seven stations in three Arctic regions (eastern Fram Strait, Canada Basin and MacKenzie Trough) collecting samples throughout several seasons between 2010 and 2016 (Fig. 1, Table 1).

Fram Strait: Two time-series sediment traps (K/MT 234, open mouth area 0.5 m^2, Kiel) were moored at St. N-4 (79.7°N, 4.5°E, 2670 m bottom depth) and St. HG-IV (79.0°N, 4.3°E, 2600 m bottom depth) in eastern Fram Strait from 15 July 2010 to 15 June 2014 and from 10 July 2010 to 15 June 2014, respectively (Fig. 1, Table 1). Range of the sediment trap depths were 190−205 m at St. N-4 and 200−205 m at St. HG-IV, respectively. The cups of sediment traps were automatically rotated and replaced at 5−59 days (St. N-4) and 7−59 days (St. HG-IV), respectively. Twenty collection cups were used to collect samples per year. However, 13−19 samples per year in N-4 and 17−20 samples per year in HG-IV were used for analysis because of sediment trap funnel clogging during few summer sampling intervals.

Canada Basin: In total three trap arrays were moored. A time-series sediment trap (SMD26S-6000, open mouth area 0.5 m^2, Nichiyu Giken Kogyo, Co. Ltd.) was moored at St. NAPt (75.0°N, 162.0°W, 1910 m bottom depth) of Northwind Abyssal Plain of Canada Basin from 4 October 2010 to 10 September 2014 (Fig. 1 and Table 1). Range of the sediment trap depths were 186−260 m. The cups of sediment traps were replaced at 10−15 days, and twenty-six collection cups were used per year. Another time-series sediment trap (SMD26S-6000, open mouth area 0.5 m^2, Nichiyu Giken Kogyo, Co. Ltd.) was moored at a different location within the Canada Basin during 1-year at St. NHC (73.3°N, 160.8°W, 426 m bottom depth) of North of Hanna Canyon in Canada Basin from 28 September 2015 to 10 September 2016 (Fig. 1, Table 1). The sediment trap depth was deployed at 170 m. Collection interval were 7−14 days and twenty-six collection cups were used. But twenty-four samples were used for analysis because of sediment trap funnel clogging during few summer sampling intervals. A third time-series sediment trap (SMD26S-6000, open mouth area 0.5 m^2, Nichiyu Giken Kogyo, Co. Ltd.) was moored at St. NBC (72.5°N, 155.4°W, 2000 m bottom depth) of North of Barrow Canyon in Canada Basin from 21 September 2015 to 9 September 2016 (Fig. 1, Table 1). The deployed trap depth was approximately 250 m. Collection interval were 12−14 days and twenty-six collection cups were used. Again, only twenty samples were used for analysis because of sediment trap funnel clogging during few summer sampling intervals.

MacKenzie Trough: In total two moorings were deployed over a time interval of one year only. At St. MG (71.0°N, 135.3°W, 700 m bottom depth) of the MacKenzie Trough off the coast in Beaufort Sea, a time-series sediment trap (PPS. 6/2, open mouth area 0.5 m^2, Technicap) was moored at 125 m depth from 20 September 2011 to 2 September 2012 (Fig. 1, Table 1). Collection interval days were 8−16 days and twenty-four collection cups were used. In addition, at St. MA (70.5°N, 136.0°W, 680 m bottom depth) of the MacKenzie Trough, two time-series sediment traps (PPS. 3/3, open mouth area 0.125 m^2, Technicap) were moored at 72 and 172 m depths from 14 September 2011 to 2 September 2012 (Fig. 1, Table 1). Collection interval days were 8−17 days and twenty-four collection cups were used each depth.

Fixation of collected material was different: The sample cups of the sediment traps at St. N-4 and St. HG-IV were filled with mercuric chloride (0.14% final solution) and 5% buffered formalin seawater was used all the other stations to preserving sinking particle and zooplankton swimmer.

2.2. Environmental data from satellite

The weekly average of sea-ice coverage near each station during the mooring periods were calculated at 25-km resolution from the sea-ice concentration dataset (National Snow and Ice Data Center). MODIS/Aqua Level 3 binned chlorophyll *a* data was downloaded from the Distributed Active Archive Center (DAAC) of the Goddard Space Flight Center (GSFC) of NASA and a running mean of 9 days were calculated by 9-km resolution. Daytime hours at each station were calculated according to Brock (1981).

2.3. Sample analysis

The zooplankton samples from eastern Fram Strait (St. N-4 and HG-IV) were gently filtered with a 0.5-mm mesh net, and the organisms retained on the mesh net (> 0.5 mm size) were treated as zooplankton swimmers. Large copepods (prosome width >1.41 mm) were identified to species level according to Brodsky (1967) and counted under a stereo microscope. Because species identification using morphological features between three *Calanus* developmental stages (*Calanus hyperboreus*, *Calanus glacialis* and *Calanus finmarchicus*) was difficult, we identified them using prosome length of each copepodite stage (Hirche et al., 1994; Kosobokova and Hirche, 2016; Table 2). In addition, species identification for the younger than copepodite stage 5 of *Paraeuchaeta glacialis* and *Paraeuchaeta norvegica* was not possible (Auel, 1999), we treated these species as *Paraeuchaeta* spp.

The samples from the other station (St. NAPt, NHC, NBC, MG and MA) were gently filtered through a 1-mm mesh net, and the organisms retained on the mesh net (>1 mm size) were treated as zooplankton swimmers. Large copepods fraction of the zooplankton swimmers was identified at species level and counted according to Brodsky (1967).

The flux (F, individuals m^{-2} day^{-1}) of zooplankton swimmers was calculated using the following equation:

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

where N is the number of individuals, O is the mouth area (m^2) of the sediment trap and *d* is the collection interval (days).

2.4. Data analysis

Flux data (ind. m^{-2} day^{-1}) of large copepods (prosome width >1.41 mm) for each station were forth root transformed. Similarities between samples were examined using a Bray-Curtis similarity index and dendrogram created using Unweighted Pair Group Methods using Arithmetic mean (UPGMA) were punctuated arbitrary similarity to group samples (Field et al., 1982). According to these groups, average flux (ind. m^{-2} day^{-1}) and contribution percentage (%) of the dominant large copepods of each group were calculated by similarity percentages (SIMPER). Besides, nonmetric multidimensional scaling analysis (NMDS) was carried out using same similarity to confirm relationship between groups and environmental factor (sea ice concentration, surface chlorophyll *a* and daytime) . All these analyses were carried out using PRIMER 7 software (PRIMER-E Ltd.).

3. Results

3.1. Hydrography

In the Fram Strait, polar night occurred from mid-October to mid-February, and midnight sun was observed from mid-April to mid-August. The sea ice concentration (SIC) around St. N-4 of eastern Fram Strait showed no clear seasonal changes related with seasonality of sun and low coverage (4 years average 8.79%) throughout the year (Fig. 2a). SIC increased during October and March of 1st, 3rd and 4th year, but during September and March of 2nd year was very low. Surface chlorophyll *a* (Chl. *a*) concentration ranged between 0.05−3.87 mg m^{-3} and showed peaks from May to June. The SIC around St. HG-IV of eastern Fram Strait was even lower than St. N4 and reached about 40% in spring (Fig. 2b). Also, SIC was increasing in October and June of 3rd year. Surface Chl. *a* concentration ranged between 0.02 and 16.7 mg m^{-3}, which was 4 times higher than these of St. N-4, but the timing of the peaks was similar at the both stations.

The SIC around St. NAPt of Canada Basin showed clear seasonal changes (4 years average 76.2%), and sea ice completely melted from August to October and rapidly increased from October to November (Fig. 2c). Surface Chl. *a* concentration increased when sea ice melting, and the values were much lower than at all the other stations (0.02−0.35 mg m^{-3}). Midnight sun occurred from late April to early August, and polar night was observed from late October to early February. Sea ice concentration at St. NHC (1-year average 72.6%) was increasing rapidly from mid-October and melted mid-June, and completely sea-ice melting period was observed in August (Fig. 2d). Only 7 valid surface Chl. *a* was detected during open ocean period because of a lot of clouds. Polar night was observed from early November to early February, and midnight sun occurred from early May to early August. Rapid freezing was observed from mid-October to mid-November, and gradual melting occurred from mid-May at St. NBC (1-year average

68.4%) (Fig. 2e). Surface Chl. *a* could be detected only 1 time in September because of a lot of clouds. Polar night and midnight sun period were almost same as St. NHC.

The SIC of St. MG and St. MA of the MacKenzie Trough increased rapidly from late October to mid-November and it was more than 90% from mid-September to mid-May, and sea ice rapidly decreased from mid-May to mid-June (Fig. 2f, g). 1-year average of SIC is 59.3% at St. MG and 58.3 % at St. MA, respectively. Surface Chl. *a* concentration was increased during open water period (from July to August), and the values were higher than at all other stations (0.03–38.9 mg m^{-3}). Polar night and midnight sun occurred from mid-November to mid-January and early May to late July, respectively.

3.2. Community structure

In the eastern Fram Strait, *C. finmarchicus*, *C. glacialis*, *C. hyperboreus*, *Metridia longa*, *Paraeuchaeta* spp. and *Heterorhabdus norvegicus* dominated. Flux of these dominant large copepods changed from 1.25 to 164 ind. m^{-2} day^{-1} (mean ± sd: 25.9 ± 28.3 ind. m^{-2} day^{-1}) at St. N-4 and 0.93 to 128 ind. m^{-2} day^{-1} (36.4 ± 35.0 ind. m^{-2} day^{-1}) at St. HG-IV (Fig. 3a, b). The flux of the large copepods in St. N-4 showed two peaks every year, first peak was from March to May and second peak was from August to October. The flux of the second peak was higher than that of the first peak. The flux at St. HG-IV showed two peaks every year, first peak was from March to May and second peak was from August to October. The flux of the first peak and the second peak were almost equal, but the species composition changed: the composition of *C. finmarchicus* was high in the first peak despite 1st year, while *M. longa* and *Paraeuchaeta* spp. were dominant in the second peak.

In the Canada Basin, *C. glacialis*, *C. hyperboreus*, *M. longa*, *Paraeuchaeta* spp., *H. norvegicus* and *Gaetanus tenuispinus* were observed at St. NAPt (Fig. 3c). The flux of these large copepods changed from 1.29 to 36.9 ind. m^{-2} day^{-1} (10.8 ± 5.93 ind. m^{-2} day^{-1}). Seasonal fluctuation of the flux throughout year was smaller than those in the Fram Strait, but the flux showed two small peaks in March-August and September-October with increasing share of the composition by *C. hyperboreus*. At St. NHC, *C. glacialis*, *C. hyperboreus*, *M. longa*, *Paraeuchaeta* spp., *H. norvegicus* and *Chiridius obtusifrons* were abundant and the flux of these large copepods ranged between 2.15 and 42.7 ind. m^{-2} day^{-1} (9.05 ± 8.72 ind. m^{-2} day^{-1}) (Fig. 3d). Two peaks of the flux were observed from April to June and October with dominance of *Paraeuchaeta* spp. and *M. longa*. At St. NBC, *C. hyperboreus*, *M. longa*, *Paraeuchaeta* spp., *H. norvegicus*, *G. tenuispinus* and *Aetideopsis* spp. occurred (Fig. 3e). The flux of these large copepods changed from 0.71 to 21.4 ind. m^{-2} day^{-1} (8.23 ± 4.86 ind. m^{-2} day^{-1}). The peaks on the flux were observed in March-May and September-November, and composition of *C. hyperboreus* was high at the spring peak. In addition, share of *H. norvegicus* on the flux was higher than that of at St. NHC.

In the MacKenzie Trough, *C. glacialis*, *C. hyperboreus*, *M. longa*, *Paraeuchaeta* spp, *G. tenuispinus* and *C. obtusifrons* dominated at St. MG (shallow) (Fig. 3f). The flux of these copepods ranged from 0.30 to 268 ind. m^{-2} day^{-1} (45.8 ± 63.1 ind. m^{-2} day^{-1}) and showed a peak in September-October with dominance of *Paraeuchaeta* spp. and *M. longa*. At St. MA (shallow and deep traps), *C. glacialis*, *C. hyperboreus*, *M. longa*, *Paraeuchaeta* spp., *H. norvegicus* and *G. tenuispinus* were abundant (Fig. 3g, h). The flux of the copepods at St. MA (shallow) changed from 38.7 to 1440 ind. m^{-2} day^{-1} (295 ± 290 ind. m^{-2} day^{-1}) and maximum flux was the highest comparing to all other stations. The flux showed a peak in September-October and low in November-January and no clear seasonal change from February to August. With the seasonal change of the flux, dominant species changed: *Paraeuchaeta* spp. dominated in the peak of September-October, *C. glacialis* occurred in January-April and *M. longa* were abundant from May to July. The flux of the copepods at St. MA (deep) ranged from 3.23 to 126 ind. m^{-2} day^{-1} (25.6 ± 23.7 ind. m^{-2} day^{-1}). Similarity was observed in seasonal change on flux between shallow and deep traps at St. MA, but *C. hyperboreus* and *H. norvegicus* were higher in deep trap than these of shallow.

To clarify seasonal change and comparison between stations of copepod community structure, copepod communities were divided into 10 groups (A-J) with 74% similarity using cluster analysis based on flux (Fig. 4a). Then, we classified groups including less than 2 samples as not-available group (NA) and did not use it for later analysis. Average fluxes in the order of group A to J were 250, 22.5, 10.9, 5.88, 7.28, 9.96, 19.3, 39.8, 61.1 and 39.3 ind. m^{-2} day^{-1} (Fig. 4b). The average flux of group A was the highest, and group D had the lowest in all groups. As results of SIMPER (Table 3), *Paraeuchaeta* spp. (contribution percentage: 58.5%), *M. longa* (19.8%) and *C. glacialis* (13.2%) dominated in group A, and the share of *C. glacialis* was higher than those of the other groups. *M. longa* (52.7%), *H. norvegicus* (26.8%) and *Pseudocalanus* spp. (12.0%) dominated in group B, and *Pseudocalanus* spp. was only found in the group B as dominant species. In group C, *M. longa* (30.4%), *H. norvegicus* (26.8%) and *Paraeuchaeta* spp. (11.9%) were dominant. Similar to group C, *M. longa* (40.8%), *Paraeuchaeta* spp. (27.5%) and *H. norvegicus* (18.8%) dominated in group D. Dominant species of group E were *M. longa* (60.1%), *Paraeuchaeta* spp. (17.0%) and *H. norvegicus* (11.4%), and *M. longa* occupied more than half on total of flux. *Paraeuchaeta* spp. (70.1%) dominated, and *M. longa* (24.7%) and *C. hyperboreus* (3.4%) predominated in group F. *M. longa* (50.7%), *Paraeuchaeta* spp. (28.1%) and *C. hyperboreus* (9.6%) occurred in group G. In the group H, dominant species were *Paraeuchaeta* spp. (52.2%), *C. finmarchicus* (33.7%), *M. longa* (6.1%) and many *C. finmarchicus* were observed comparing to the other groups. *Paraeuchaeta* spp. (55.5%), *M. longa* (29.9%) and *C. glacialis* (5.0%) occurred in group I. *Paraeuchaeta* spp. (43.5%), *M. longa* (34.3%) and *C. hyperboreus* (16.0%) dominated in group J. To analyze relationship between copepods assemblage and environmental factor, NMDS was carried out. But this result wasn't used according to Clarke and Warwick (2001) because stress value was 0.22.

Seasonal changes on copepod groups identified by cluster analysis on flux at each station were shown in Fig. 5. Seasonal changes were clearly observed in the eastern Fram Strait (St. N-4 and St. HG-IV). Groups E, F and H occurred in winter (January-March), groups E, F and J were shown in spring (April-June), group I was observed in summer (July-September) and group I and E occurred in autumn (October-December). Groups E, H, I and J were observed only in eastern Fram Strait. In the St. NAPt, copepods community showed no clear seasonal change and group C was mainly dominant. At St. NHC, occurrences of the groups C, D, F and G changed within short periods (monthly or every two weeks). Seasonal change of community structure in NBC was similar to that of St. NAPt. In the MacKenzie Trough, groups A, B, C, E, F and G were observed at St. MG and the copepods community exchanged in the short periods (monthly or every two weeks). At St. MA (shallow), group B occurred only in winter, and the other seasons were occupied by group A. In the St. MA (deep), group A and B occurred from autumn, but the occurrences of groups C, D, F and G were exchanged complexly from winter to summer. The groups A and B were observed only in the stations of the MacKenzie Trough (St. MA and St. MG).

4. Discussion

4.1. Zooplankton sampling by sediment trap

For quantitative evaluation of abundance, biomass and distribution of zooplankton species, plankton net sampling is the common method (e.g., Darnis and

Fortier, 2014), although it is known that some large zooplankton may avoid the net. While zooplankton collected by net reflect most of the zooplankton in the towed water layers, sediment trap sampling of zooplankton is believed to reflect only the organisms occurring around the sediment trap depth layer because the sediment trap depth is fixed at a certain depth (Seiler and Brandt, 1997). This is regarded as a disadvantage and it is argued that sediment trap sampling therefore does not reflect the zooplankton community as a whole. In addition, zooplankton seems to be attracted by the trap's abundances and by the respective preservatives so that collecting zooplankton with traps can only be regarded as a semi-quantitative method (see also Lee et al., 1992). However, since high-frequency investigations using research vessels are very difficult and expensive in the Arctic Ocean because of sea-ice coverage, very low temperatures and the Polar Night samples collected by sediment trap is an effective method to clarify seasonal changes on zooplankton communities in certain depth and allow to explain ecological phenology like life cycles of copepods in the Arctic Ocean (Tokuhiro et al., 2019). The few studies of zooplankton collected by means of sediment traps in the Arctic Ocean, reveal reproducible seasonal changes on community structure of, for instance pelagic amphipods, like *Themisto* spp. and pteropods *Limacina* spp. in the eastern Fram Strait (Kraft et al., 2012; Bauerfeind et al., 2014) and seasonal changes on copepod community structure in the Chukchi Sea and the Beaufort Sea (Makabe et al., 2010; Matsuno et al., 2014, 2015, 2016; Tokuhiro et al., 2019). Thus, despite the disadvantages, the sampling of zooplankton swimmers with sediment traps have been gradually recognized as an approach for evaluating seasonal change of copepod community in recent years. In this study, seasonal changes in the copepod community clearly showed different patterns in each region.

4.2. Fram Strait

In the eastern Fram Strait, the copepod community changed clearly during the season. The group H was observed during spring only in eastern Fram Strait and was characterized by a dominance of *C. finmarchicus*. *C. finmarchicus* is known to be distributed in the Atlantic sector (e.g., Barents Sea) of the Arctic Ocean, but does not occur in the Pacific sector (Conover, 1988). However, only a few populations were found near St. N-4 and St. HG-IV (Conover, 1988; Hirche and Kosobokova, 2007) originally. In addition, copepodite stage 6 male (C6M) was dominant (maximum 76%) when the peak of this species was observed (data not shown). In the Barents Sea, C6M in *C. finmarchicus* occur from February to March, but they did not dominate the population and they disappeared quickly (Tande, 1982). This may show that adult males have a short life-period. Fram Strait is affected by inflow of the East Greenland Current (EGC) from the north, the West Spitzbergen Current (WSC) from the south and the Return Atlantic Current (RAC) from the East, and these currents (WSC and RAC) were most intense during spring (Beszczynska-Möller et al., 2012; Armitage et al., 2017). From these facts, C6M of *C. finmarchicus* is thought to be transported from coastal areas of Greenland

and/or Svalbard archipelago by WSC and RAC during spring, and they eventually reached the end of their life-period, and weakened individuals finally sunk and were collected by the traps. *Paraeuchaeta* spp. and *M. longa* always appeared in the trap samples because the distribution depth of *P. norvegica* and *P. glacialis* in eastern Fram Strait is between 0-200 m depth (Laakmann et al., 2009) and *M. longa* mainly occurs at 100-500 m water depth (Conover and Huntley, 1991; Ashjian et al. 2003). *C. hyperboreus* appeared in spring and autumn. It is known that this species conducts seasonal vertical migration (Hirche, 1997), therefore, this movement seems to affect their appearance in the trap samples. In contrast, *C. glacialis* was mainly observed during autumn. This species usually occurs over continental shelves (Darnis et al., 2008) but few individuals of the population appear in this study area during sampling (Conover, 1988; Hirche et al., 1991). Whereas many *C. glacialis* were observed at a 1500 m depth layer in late autumn in southern Greenland Sea (Hirche, 1991). Thus, this species may have been transported by currents from coastal areas (e.g. Svalbard archipelago) and must also perform vertical migration in late autumn. Therefore, movement and distribution depth of respective species may cause clearly seasonality of copepods community.

In the Fram Strait, a strong seasonality of sea ice concentration wasn't observed, thus Chl. *a* was detected for a long time only interrupted by short sea ice coverage periods. It is reported that sea ice in the Fram Strait is affected by the Atlantic Water (Beszczynska-Möller et al., 2012). Although a relationship between environmental factors (SIC and Chl.

a) and copepod community structure wasn't analyzed statistically due to lack of environmental data in this study, obvious relationships were not observed by comparing with figures except for current. This means that there are several steps in the process until copepod communities get effected by sea ice melting and freezing. Thus, since only relationship between current and copepods community structure was thought to be observed in this study, seasonality as well as variability of current patterns may have affected the variability of copepod communities in the Fram Strait the most.

4.3. Canada Basin

Seasonal changes of community structure in St. NAPt and NBC were not observed, and group C occupied the water column close to the trap during almost during all periods. Average flux of group C was low and percentages of *M. longa* and *H. norvegicus* were high. Also, share of *Paraeuchaeta* spp. in St. NAPt and St. NBC were lower than those in the Fram Strait and the MacKenzie Trough. *M. longa* is omnivore, *H. norvegicus* and *Paraeuchaeta* spp. are carnivore (Conover and Huntley, 1991; Nishida and Ohtsuka, 1996; Dvoretsky and Dvoretsky, 2015). *Paraeuchaeta* spp. have a large body mass and thus need much more energy for growth compared with *M. longa* and *H. norvegicus* (Ashijian et al., 2003; Kosobokova et al., 2007; Dvoretsky and Dvoretsky, 2015). In this region, seasonality of sea ice concentration was like observed in the MacKenzie Trough, but surface Chl. *a* concentration was much lower than that of the

Fram Strait and the MacKenzie Trough, as primary production is also thought to be low in the Canada Basin (Arrigo et al., 2008; Pabi et al., 2008). Therefore, *Paraeuchaeta* spp. could eventually not obtain enough food for completing their life cycle because of too few small copepods as a prey due to low primary production. This might be the reason why flux and abundance of *Paraeuchaeta* spp. was low in the copepod community.

Short-term seasonal change was observed only at St. NHC in the Canada Basin. Mooring condition (bottom depth and sediment trap mooring depth) and seasonal change of copepod communities of St. NHC was like St. MA and St. MG in the MacKenzie Trough rather than St. NAPt and St. NBC. Moreover, surface zooplankton is transported by an eddy from the continental shelf to the Canada Basin during summer (Llinás et al., 2009) and the continental species *C. glacialis* appeared at St. NHC in this study. Lane et al. (2008) also reported that high abundances of zooplankton around St. NHC was observed due to horizontal inflow from the continental shelf. Therefore, the observed complex changes in community structures within the large copepods may be caused by these transport mechanisms of zooplankton from the continental area. In summary, due to influence of bottom depth, sediment trap depth and transportation from the continental area, the copepod community structure of St. NHC exhibits the most complex resembling short-term changes of the here investigated Arctic regions.

4.4. MacKenzie Trough

In the MacKenzie Trough, group A occurred frequently, and group B was observed only during winter. Average flux of group A was higher than those of the other groups. *Paraeuchaeta* spp., *M. longa* and *C. glacialis* were characteristically dominated in group A. Because *C. glacialis* is a continental shelf species (Darnis et al., 2008), they were thought to be observed in St. MA and St. MG where are shallow bottom depth and locate near continental shelf. According to Darnis et al. (2008), large copepods composed in order to *C. glacialis*, *C. hyperboreus*, *M. longa* and *P. glacialis* using plankton net samples in continental shelf of the Beaufort Sea, and *P. glacialis* showed low abundance and *H. norvegicus* did not occur. In the slope area, however, the large copepods were abundant in order to *M. longa*, *C. hyperboreus*, *C. glacialis*, *P. glacialis* and *H. norvegicus*, and the numbers of *P. glacialis* and *H. norvegicus* were low. in contrast, during this study, *Paraeuchaeta* spp. and *C. glacialis* were dominant in group A and *M. longa* was abundant in group B, and composition of *Paraeuchaeta* spp. was much greater than that of net sampling (Darnis et al., 2008). This species is known to be a cruising feeder swimming actively when they feed on small copepods (Almeda et al., 2017), and this behavior may be a positive factor to be collected by sediment traps.

Moreover, we compared samples among St. MA (shallow, 72 m), St. MG (shallow, 125 m) and St. MA (deep, 172 m) to analyze effect of trap depth because St. MA and St. MG deployed near and mooring period were same. Group A occurred when the sediment trap depth was shallower, and the other groups (e.g., group G and group F) were observed as the sediment trap depth was deeper. Also, *Paraeuchaeta* spp. and *C. glacialis* showed higher abundances at shallow depth and that of *M. longa* and *C. hyperboreus* increased with deeper sediment trap depth. These facts mean that vertical distribution of the various species overlapped at deep sediment trap depth. Thus, community structure in shallow depth of the MacKenzie Trough showed no seasonal changes in the dominance of *Paraeuchaeta* spp. and *C. glacialis* because all the other large species (*C. hyperboreus* and *M. longa*) didn't overlap in the shallower layer. Flux of *Paraeuchaeta* spp. and *C. glacialis* decreased with increasing depth and distribution depth of the other species overlapped. Hence complex seasonal changes of copepod community structures were observed at deeper layers.

In the MacKenzie Trough, sea ice concentration changed like in the Canada Basin and surface Chl. *a* was higher than the other regions. Neither remarkable (St. MA shallow) nor short-term (St. MG and St. MA deep) seasonality of community structure was observed in this region. Especially, high-flux group A was observed throughout the year, which wasn't observed in the other regions. This may be induced by small sediment trap open area (0.125 m^2).

Since only one-year observation was performed in the MacKenzie Trough, we cannot consider the observed species compositions found in the trap samples as the usually occurring structure. Based on same the sampling program in 2009-2010, maximum flux of *Paraeuchaeta* spp. was 971 ind. m^{-2} day^{-1} at St. MA (shallow) and 701 ind. m^{-2} day^{-1} St. MG (shallow), and *Paraeuchaeta* spp. dominated (data not shown) similar to results of this study. In addition, Dezutter et al. (2019) reported that high flux of *C. glacialis* was observed in sediment trap samples at the MacKenzie Trough, although interannual variability was observed. Thus, the tendency we found is thought to be a common feature of sediment trap samples over the MacKenzie Trough eventually caused by high concentrations of surface chl. *a* across the MacKenzie Trough compared to all other regions investigated in this study.

4.5. Regional comparison

Seasonal changes of copepods community structure obtained with sediment trap samples showed large variations among the investigated regions, and in summary, three patterns of seasonal changes were observed in this study: clear seasonal changes (eastern Fram Strait), no seasonal change (Canada Basin) and changes within short periods (MacKenzie Trough). The following three points could be mentioned as factor of these differences. First point is the influence of the sediment trap depth. With or without seasonal change we found differences only due to the chosen sediment trap depth in the MacKenzie Trough samples, and group A which showed a high flux rate, was observed mainly at shallow depths. Therefore, effects of sediment trap depth should not be ignored for evaluating zooplankton community by sediment traps. Second point is horizontal transportation of copepods by currents. Ocean-specific community (e.g., group H) characterized by *C. finmarchicus* was observed only in the Fram Strait due to the inflow of the Atlantic water. Also, transportation from shelf areas led to specific short-term changes in community structures at St. NHC even in Canada Basin where usually little seasonality is reported. Third point is the hydrographic environment and related to this as biological factor, especially primary production here expressed as surface Chl. *a* concentration. The latter was quite high over the MacKenzie Trough, but low in the eastern Fram Strait and the Canada Basin (Arrigo et al., 2008; Pabi et al., 2008; in this study), and copepod fluxes showed the same patterns. In addition, dominant species of group A, which had the highest flux of all samples examined, were observed in the eastern Fram Strait and Canada Basin, but they were especially abundant in group A. If this fact is true, not only flux but also dominant species of copepods would be driven rather by the feeding environment (primary production) than by anything else between regions in the Arctic Ocean. However, in this study, relationship between seasonal change of sea ice concentration and copepods community structure was complex. In the Fram Strait, sea ice concentration showed diffuse seasonal changes, but the copepods community structure exhibited a clear seasonality. In the Canada Basin, seasonal change of sea ice concentration was evident and copepods community structure didn’t show any variation. In the MacKenzie Trough, remarkable seasonal changes of sea ice concentration and short-term seasonal change of copepods communities were observed. Thus, seasonality of sea ice concentration may not affect directly large copepods community structures in all region.

Seasonal changes of copepod community structures within Arctic Ocean was shown to be quite different between the three regions in this study. It was additionally discussed that these differences were influenced by several environmental factors (sea ice concentration, current patterns, endemic species occurrence and the amount of primary production). These discussions couldn't be obtained when only using plankton net sample collected during the short Arctic summer. However, also variations of mooring situations (e.g. mooring periods, depth and site) between regions seemed to affect the seasonal change of large copepods community structure in this study. Therefore, for more robust comparison, exhaustive observation webs of sediment traps and comparison of seasonal changes within same deployment depths and same sampling periods are required for different regions in the Arctic Ocean.

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Figure/table captions

Fig. 1. Location of the 3 mooring sites: Fram Strait, Canada Basin, MacKenzie Trough. Fram Strait was sampled at two stations (St. N-4 and St. HG-IV) from 15 July 2010 to 15 June 2014. Canada Basin was sampled at three stations (St. NAPt, St. NHC and St. NBC) from 04 October 2010 to 10 September 2016. MacKenzie Trough was sampled two stations (St. MG and St. MA) from 14 September 2011 to 01 September 2012. West Spitzbergen Current, WSC; Return Atlantic Current, RAC; East Greenland Current; EGC.

Fig. 2. Seasonal changes in sea ice concentration and surface Chl. *a* at each mooring station. Open and solid bars indicate the period of the midnight sun and polar night, respectively. (Pay attention to the different scales on y-axis).

Fig. 3. Seasonal changes on copepods abundance and community structure in the Arctic Ocean. (Pay attention to the different scales on y-axis).

Fig. 4. Dendrogram showing the Bray-Curtis similarity results based on zooplankton flux (a). Ten groups (A-J) were identified at 74% similarity. Numbers in parentheses indicate the number of stations included in each group. NA: not available. The mean flux and species composition of each group (b).

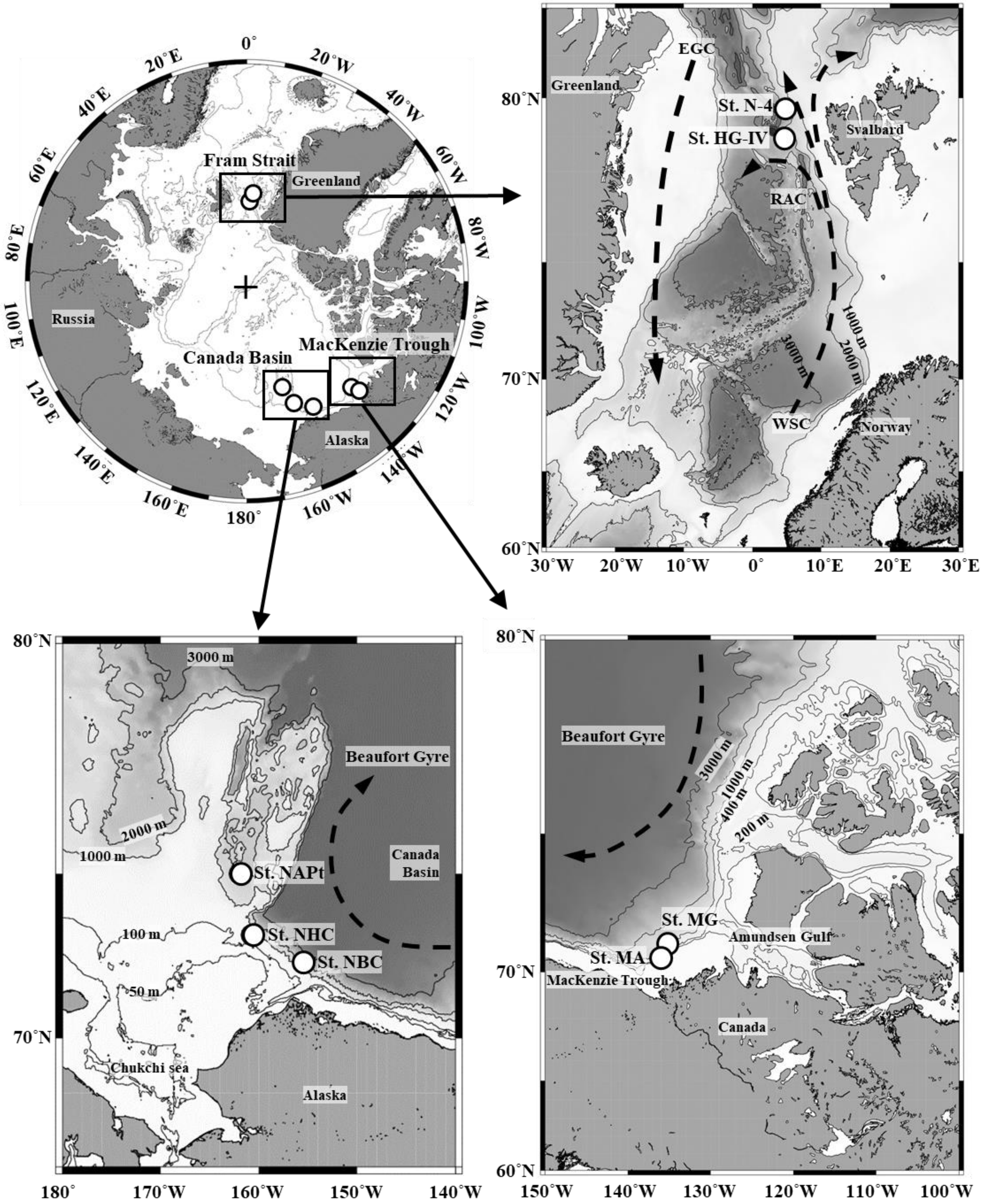
Fig. 5. Seasonal changes in occurrence of copepod groups identified by cluster analysis on flux (cf. Fig. 4) at each station in the Arctic Ocean. Copepods groups were identified 10 groups (A-J) by Bray-Curtis similarity (cf. Fig. 4). Cross: no data,

slash: not available, blank: no sampling.

Table 1. Information of trap deployments and collected samples by means of sediment traps at each investigated station in the Arctic Ocean.

Table 2. Size categories of the prosome length for identifying the *Calanus* species in the Fram Strait (cf. Hirche et al., 1994; Kosobokova and Hirche, 2016).

Table 3. Mean flux and contribution in percent for species in clustering groups (cf. Fig. 4a) in the Arctic Ocean. The dominant species were shown based on the contribution percent according to SIMPER.



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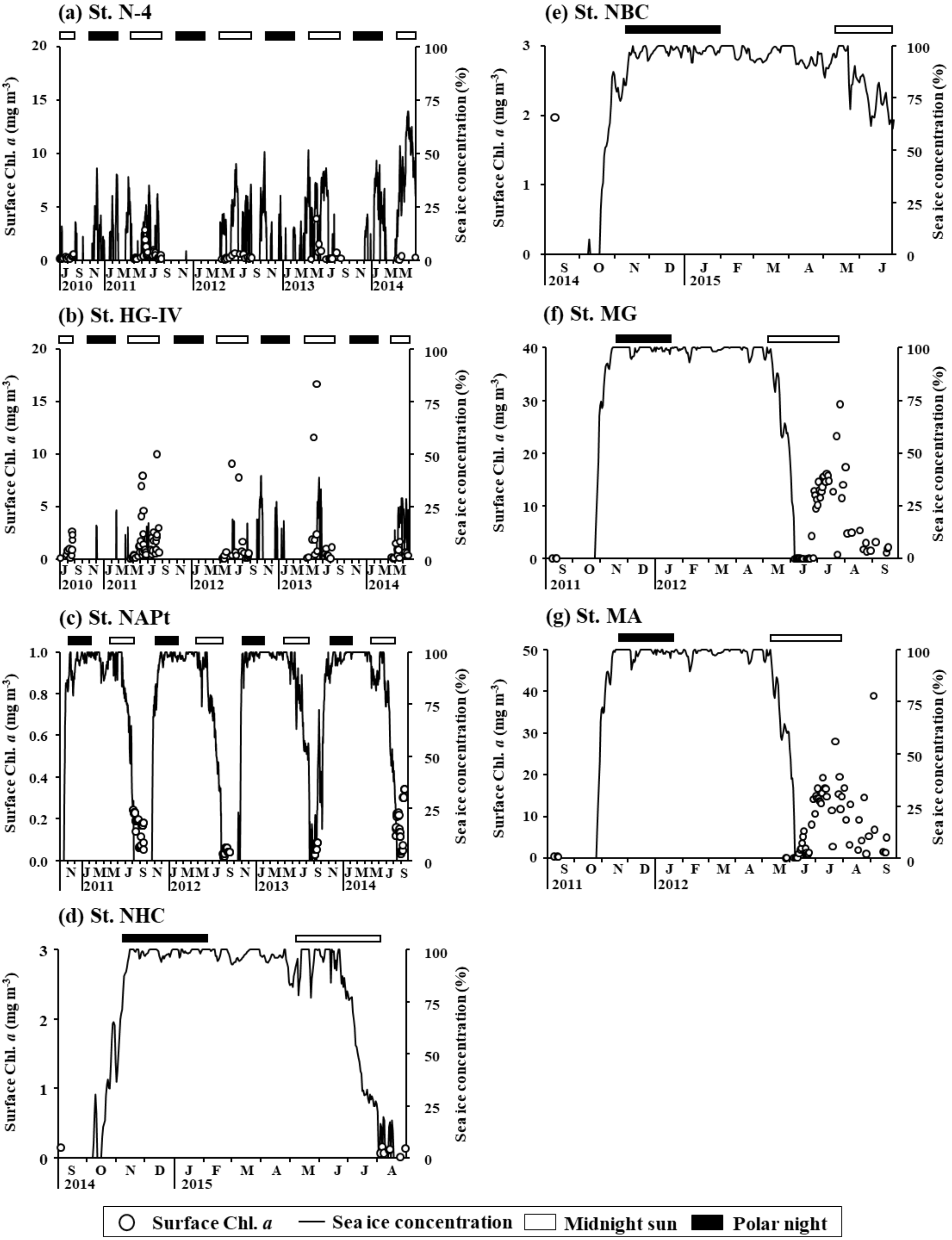

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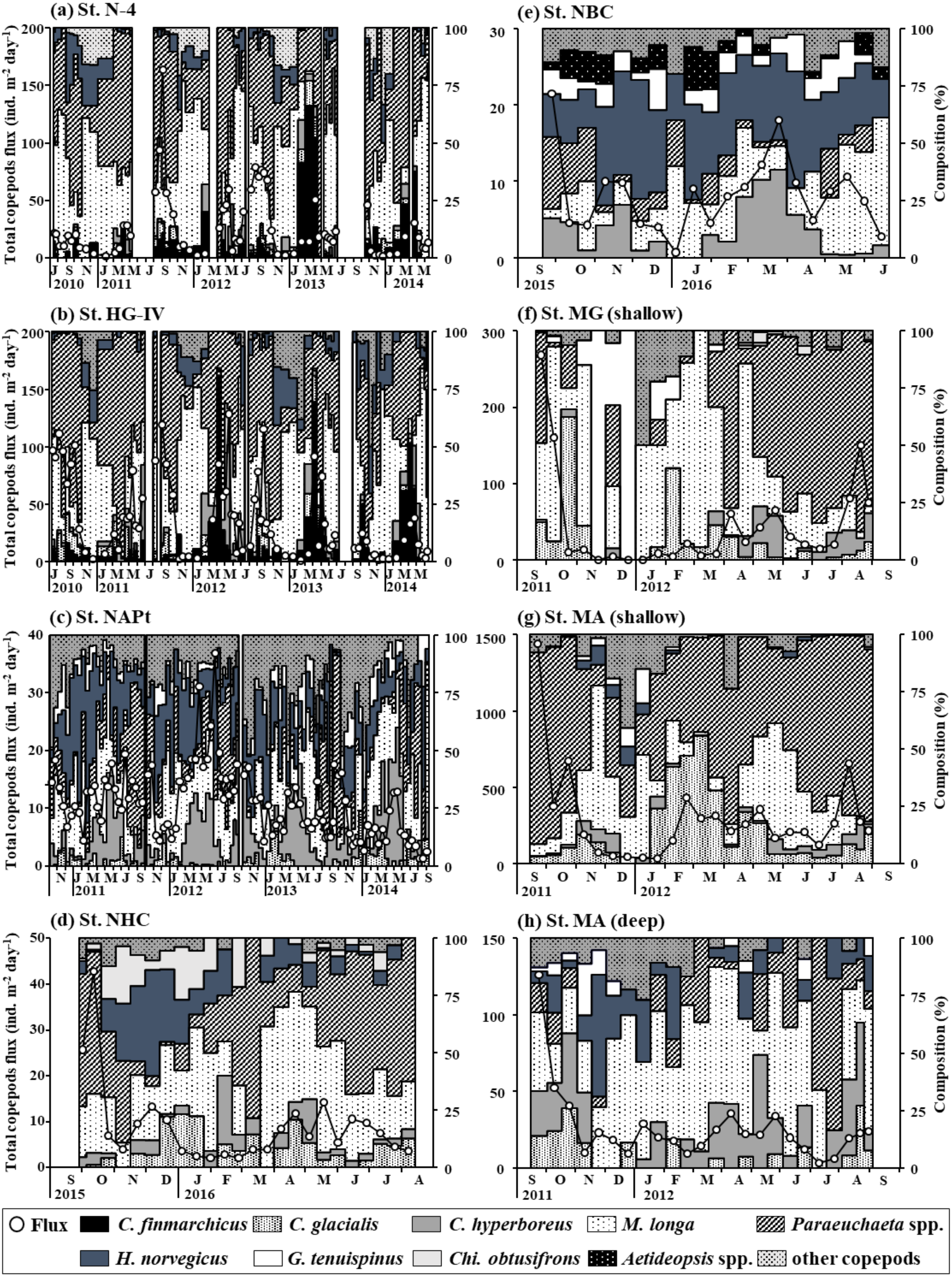

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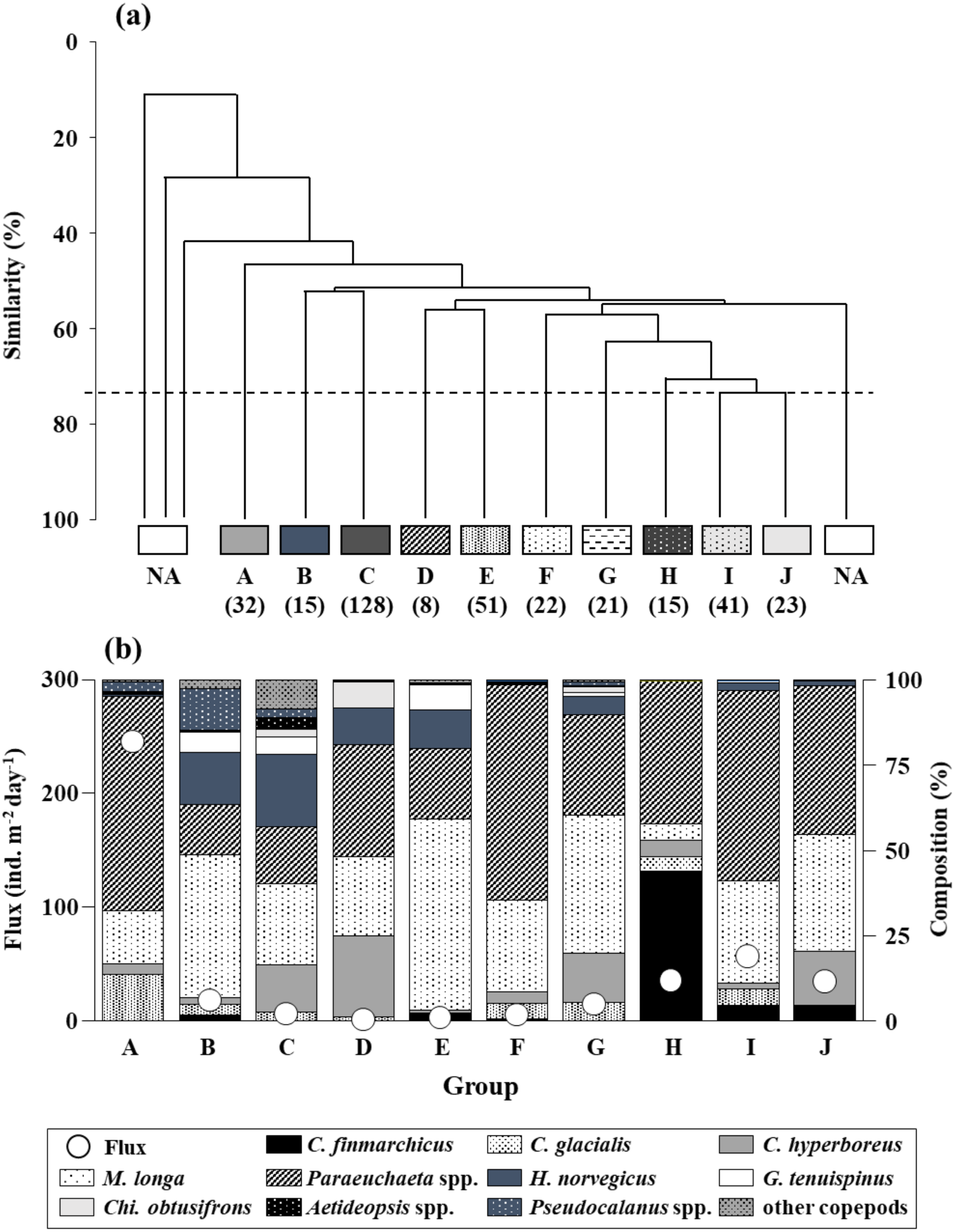

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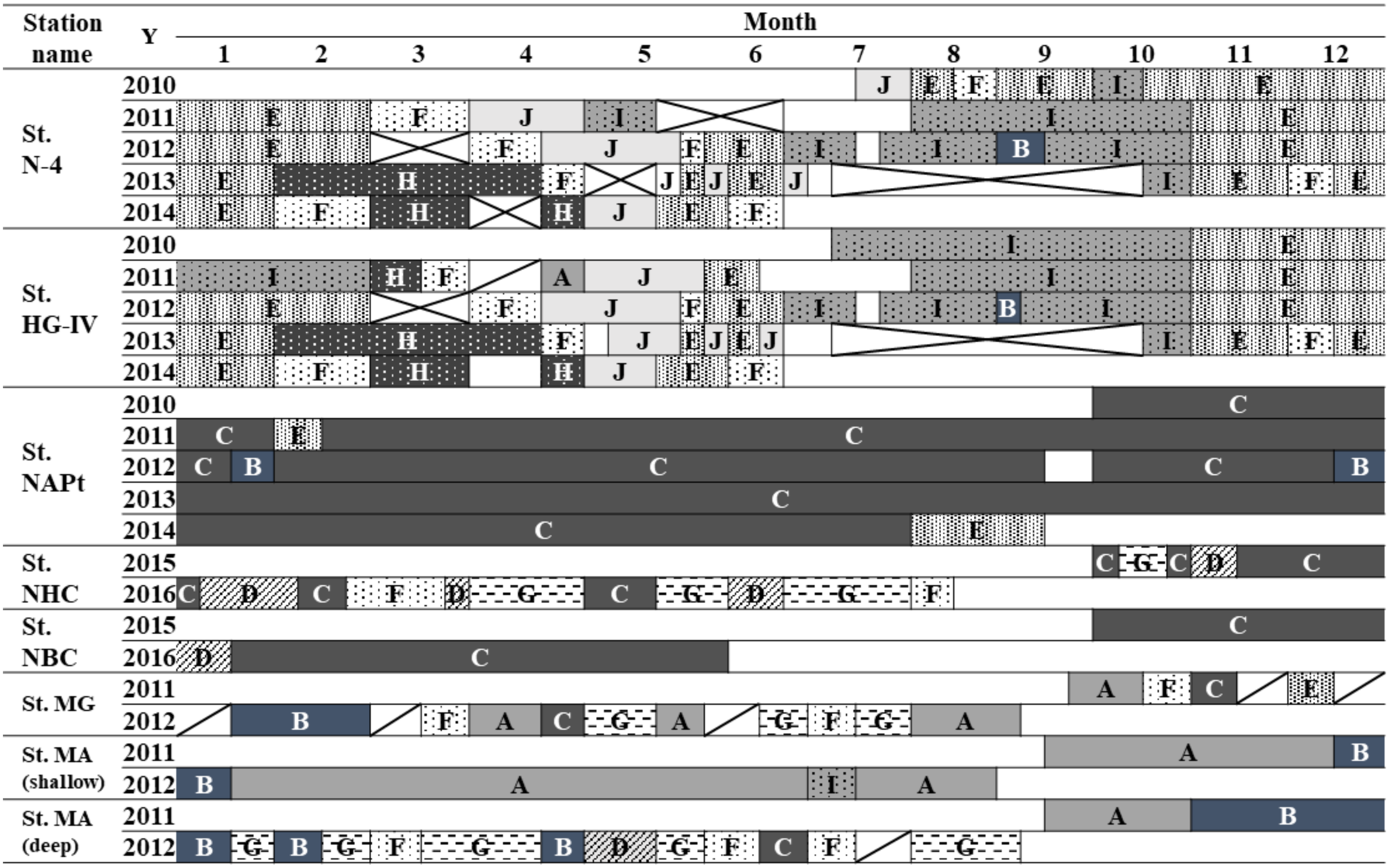

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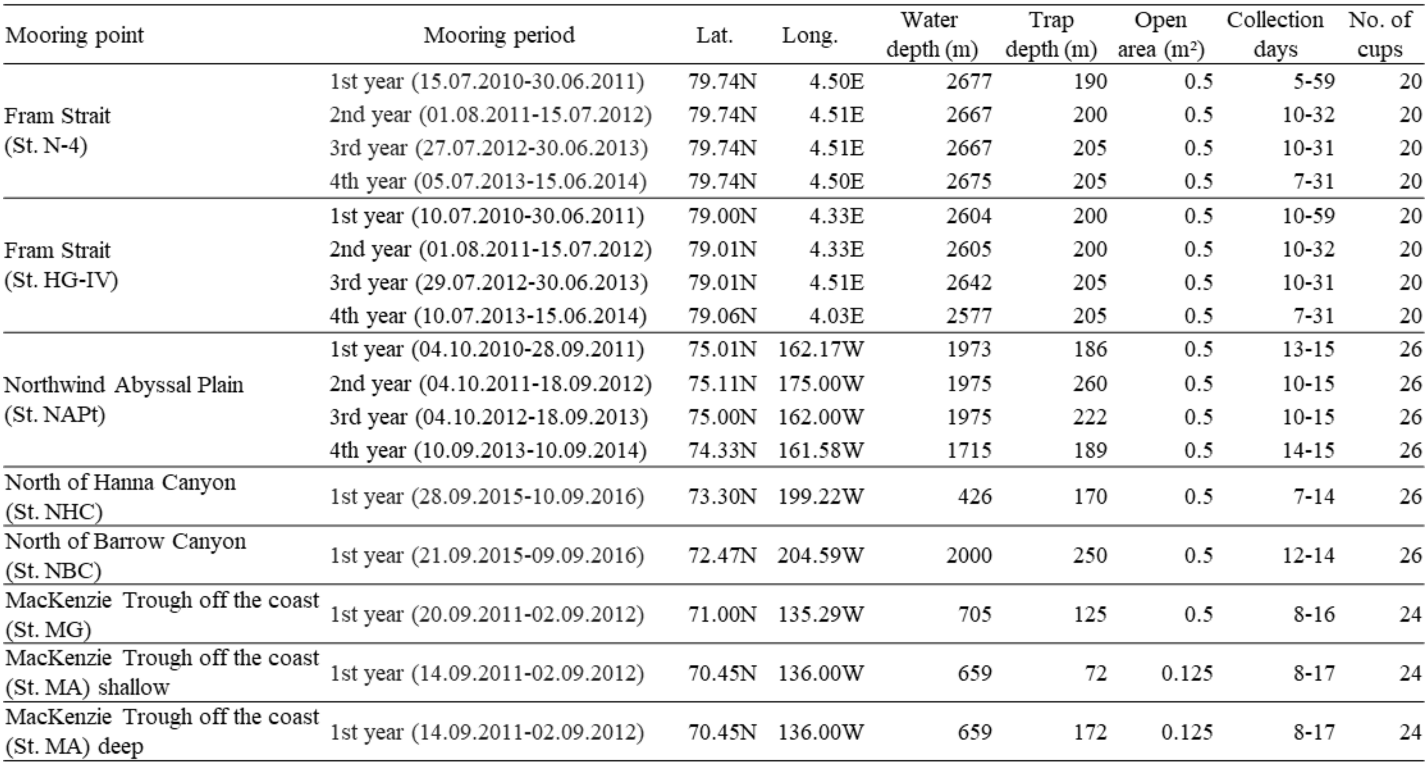
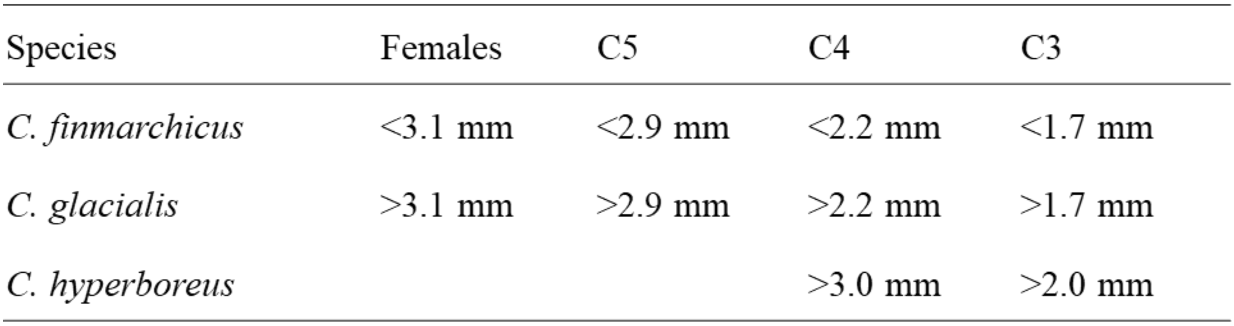


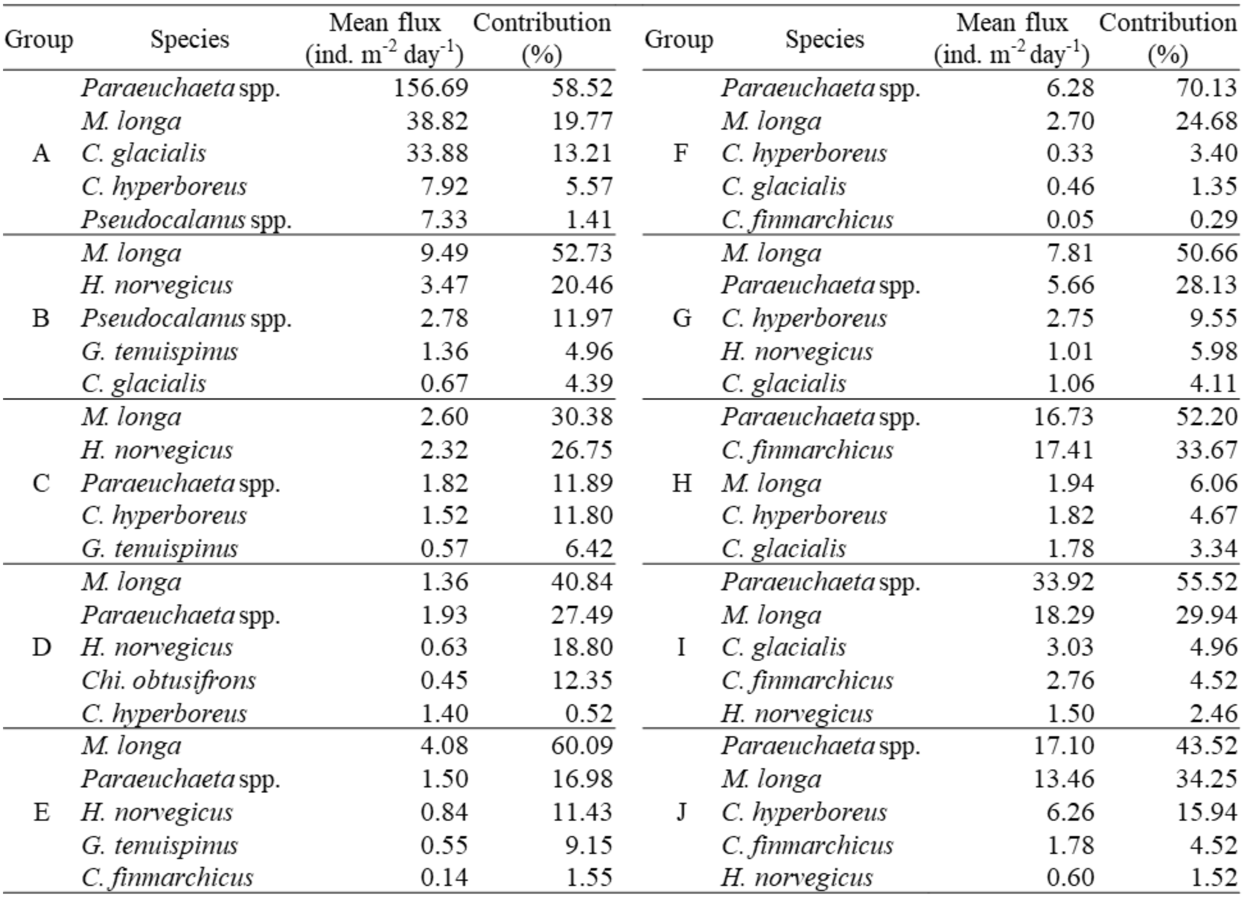
Mooring point	Mooring period	Lat.	Long.	Water depth (m)	Trap depth (m)	Open area (m²)	Collection days	No. of cups
Fram Strait (St. N-4)	1st year (15.07.2010-30.06.2011)	79.74N	4.50E	2677	190	0.5	5-59	20
	2nd year (01.08.2011-15.07.2012)	79.74N	4.51E	2667	200	0.5	10-32	20
	3rd year (27.07.2012-30.06.2013)	79.74N	4.51E	2667	205	0.5	10-31	20
	4th year (05.07.2013-15.06.2014)	79.74N	4.50E	2675	205	0.5	7-31	20
Fram Strait (St. HG-IV)	1st year (10.07.2010-30.06.2011)	79.00N	4.33E	2604	200	0.5	10-59	20
	2nd year (01.08.2011-15.07.2012)	79.01N	4.33E	2605	200	0.5	10-32	20
	3rd year (29.07.2012-30.06.2013)	79.01N	4.51E	2642	205	0.5	10-31	20
	4th year (10.07.2013-15.06.2014)	79.06N	4.03E	2577	205	0.5	7-31	20
Northwind Abyssal Plain (St. NAPt)	1st year (04.10.2010-28.09.2011)	75.01N	162.17W	1973	186	0.5	13-15	26
	2nd year (04.10.2011-18.09.2012)	75.11N	175.00W	1975	260	0.5	10-15	26
	3rd year (04.10.2012-18.09.2013)	75.00N	162.00W	1975	222	0.5	10-15	26
	4th year (10.09.2013-10.09.2014)	74.33N	161.58W	1715	189	0.5	14-15	26
North of Hanna Canyon (St. NHC)	1st year (28.09.2015-10.09.2016)	73.30N	199.22W	426	170	0.5	7-14	26
North of Barrow Canyon (St. NBC)	1st year (21.09.2015-09.09.2016)	72.47N	204.59W	2000	250	0.5	12-14	26
MacKenzie Trough off the coast (St. MG)	1st year (20.09.2011-02.09.2012)	71.00N	135.29W	705	125	0.5	8-16	24
MacKenzie Trough off the coast (St. MA) shallow	1st year (14.09.2011-02.09.2012)	70.45N	136.00W	659	72	0.125	8-17	24
MacKenzie Trough off the coast (St. MA) deep	1st year (14.09.2011-02.09.2012)	70.45N	136.00W	659	172	0.125	8-17	24

Table 2. Size categories of the prosome length for identifying the *Calanus* species in the Fram Strait (cf. Hirche et al., 1994; Kosobokova and Hirche, 2016).



Species	Females	C5	C4	C3
C. finmarchicus	<3.1 mm	<2.9 mm	<2.2 mm	<1.7 mm
C. glacialis	>3.1 mm	>2.9 mm	>2.2 mm	>1.7 mm
C. hyperboreus			>3.0 mm	>2.0 mm

Table 3. Mean flux and contribution in percent for species in clustering groups (cf. Fig. 4a) in the Arctic Ocean. The dominant species were shown based on the contribution percent according to SIMPER.



Group	Species	Mean flux (ind. m^{-2} day^{-1})	Contribution (%)	Group	Species	Mean flux (ind. m^{-2} day^{-1})	Contribution (%)
A	*Paraeuchaeta* spp.	156.69	58.52	F	*Paraeuchaeta* spp.	6.28	70.13
	M. longa	38.82	19.77		*M. longa*	2.70	24.68
	C. glacialis	33.88	13.21		*C. hyperboreus*	0.33	3.40
	C. hyperboreus	7.92	5.57		*C. glacialis*	0.46	1.35
	Pseudocalanus spp.	7.33	1.41		*C. finmarchicus*	0.05	0.29
B	*M. longa*	9.49	52.73	G	*M. longa*	7.81	50.66
	H. norvegicus	3.47	20.46		*Paraeuchaeta* spp.	5.66	28.13
	Pseudocalanus spp.	2.78	11.97		*C. hyperboreus*	2.75	9.55
	G. tenuispinus	1.36	4.96		*H. norvegicus*	1.01	5.98
	C. glacialis	0.67	4.39		*C. glacialis*	1.06	4.11
C	*M. longa*	2.60	30.38	H	*Paraeuchaeta* spp.	16.73	52.20
	H. norvegicus	2.32	26.75		*C. finmarchicus*	17.41	33.67
	Paraeuchaeta spp.	1.82	11.89		*M. longa*	1.94	6.06
	C. hyperboreus	1.52	11.80		*C. hyperboreus*	1.82	4.67
	G. tenuispinus	0.57	6.42		*C. glacialis*	1.78	3.34
D	*M. longa*	1.36	40.84	I	*Paraeuchaeta* spp.	33.92	55.52
	Paraeuchaeta spp.	1.93	27.49		*M. longa*	18.29	29.94
	H. norvegicus	0.63	18.80		*C. glacialis*	3.03	4.96
	Chi. obtusifrons	0.45	12.35		*C. finmarchicus*	2.76	4.52
	C. hyperboreus	1.40	0.52		*H. norvegicus*	1.50	2.46
E	*M. longa*	4.08	60.09	J	*Paraeuchaeta* spp.	17.10	43.52
	Paraeuchaeta spp.	1.50	16.98		*M. longa*	13.46	34.25
	H. norvegicus	0.84	11.43		*C. hyperboreus*	6.26	15.94
	G. tenuispinus	0.55	9.15		*C. finmarchicus*	1.78	4.52
	C. finmarchicus	0.14	1.55		*H. norvegicus*	0.60	1.52