



Title	Comparison of the vertical distribution of pelagic copepod abundance, biomass and community structure between the Atlantic and Pacific sectors of the Arctic Ocean
Author(s)	Abe, Yoshiyuki; Hildebrandt, Nicole; Matsuno, Kohei; Niehoff, Barbara; Yamaguchi, Atsushi
Citation	北海道大学水産科学研究彙報, 70(1), 91-102
Issue Date	2020-08-24
Doc URL	http://hdl.handle.net/2115/79120
Type	bulletin (article)
File Information	bull.fish.70.1.91.pdf



[Instructions for use](#)

Comparison of the vertical distribution of pelagic copepod abundance, biomass and community structure between the Atlantic and Pacific sectors of the Arctic Ocean

Yoshiyuki ABE¹⁾, Nicole HILDEBRANDT²⁾, Kohei MATSUNO^{3,4)}, Barbara NIEHOFF²⁾
and Atsushi YAMAGUCHI^{3,4)}

(Received 30 April 2020, Accepted 27 May 2020)

Abstract

We compared copepod abundance, biomass and community structure in the Atlantic sector (Fram Strait) and Pacific sector (Canada Basin) of the Arctic Ocean by using vertical stratified zooplankton samples collected from 0–1,000 m or 0–1,500 m during daytime in summer. Abundance and biomass were high at the surface layer and decreased with increasing depth in both regions. Abundance and biomass in the surface layer in the Fram Strait were 6–18 times higher than those in the Canada Basin. According to cluster analysis, the copepod communities were separated into three groups that varied vertically and included both locations. Regional differences were marked for *Calanus finmarchicus*, which was distributed only in the Fram Strait. In the Canada Basin, Spinocalanidae composed 56.1% of calanoid copepod abundance for the bathypelagic groups and also contributed 7.5% of abundance throughout the water column. The dominance of Spinocalanidae may reflect the oligotrophic environment in the Pacific sector of the Arctic Ocean.

Key words : Copepods, Fram Strait, Canada Basin, Vertical distribution, Arctic Ocean, *Calanus finmarchicus*, Spinocalanidae

Introduction

Recently, atmospheric warming in the Arctic area has progressed 2–3 times faster than the global scale (Trenberth et al., 2007). Reduced sea ice coverage in summer has also been reported for the Arctic Ocean (Duarte et al., 2012 ; Naam, 2012). The reduction of sea ice is reported to be greater for the regions where the Arctic Ocean connects with the Atlantic and Pacific Oceans (Shimada et al. 2001, 2006 ; Stroeve et al., 2007 ; Comiso et al., 2008 ; Markus et al., 2009). The evaluation of the effects of sea ice reduction on marine ecosystems is an important and urgent issue in biological oceanography (Wassmann et al., 2015 ; Hunt et al., 2016).

Consequently, studies of marine zooplankton, especially copepod-predominant components, in the Arctic Ocean where it connects to the Atlantic and Pacific Oceans are of prime importance. For the Pacific sector in the Arctic Ocean, the transport of Pacific copepods through the Bering Strait has increased in recent years (Matsuno et al., 2011, 2016 ; Nelson et al., 2014 ; Ershova et al., 2016). More-

over, reproductive success (egg production and hatching) of the transported Pacific copepod *Neocalanus flemingeri* in the Arctic Ocean has been reported (Matsuno et al., 2015). In the Atlantic sector of the Arctic Ocean, the transported zooplankton biomass from the Atlantic Ocean is reported to be 2–3 times higher than that transported through the Pacific sector (Wassmann et al., 2015). Reproductive success of the transported Atlantic copepod *Calanus finmarchicus* in the Atlantic sector of the Arctic Ocean has also been reported (Gluchowska et al., 2017 ; Weydmann et al., 2018). These reports are important since they evaluate changes in copepod populations in each connecting region of the Arctic Ocean. However, information on differences in pelagic copepod community structure and vertical distributions in the Atlantic and Pacific sectors of the Arctic Ocean are scarce, which prevents an accurate evaluation of future forecasts of biological oceanography in each region (Wassmann et al., 2015 ; Hunt et al., 2016).

In the present study, we evaluate copepod community structure from the surface to deep layers (down to 1,500 m) in

¹⁾ Office for Enhancing Institutional Capacity, Hokkaido University
(北海道大学大学力強化推進本部)

²⁾ Helmholtz Centre for Polar and Marine Research, Alfred Wegener Institute
(ドイツ連邦共和国アルフレッドウェゲナー極地海洋研究所)

³⁾ Faculty of Fisheries Sciences, Hokkaido University
(北海道大学大学院水産科学研究院海洋生物学分野)

⁴⁾ Arctic Research Center, Hokkaido University
(北海道大学北極域研究センター)

the Atlantic and Pacific sectors of the Arctic Ocean. In addition to species identifications and enumeration, copepod biomass was quantified by measuring body length and applying length-mass regressions. Species diversity and similarity analyses were used to evaluate patterns of geographical and vertical change in the copepod community. The obtained results were compared with those in the Arctic Ocean and their adjacent seas, and the characteristics in the Atlantic and Pacific sectors were clarified. Finally, we discuss future prospects for the copepod community under global warming conditions in the Atlantic and Pacific sectors of the Arctic Ocean.

Material and methods

Field sampling

Zooplankton sampling in the Atlantic sector was conducted at one station (78°50'N, 1°59'W) in the Fram Strait on 1 July 2011. Samples were collected from 0–50, 50–200, 200–500, 500–1,000 and 1,000–1,500 m by vertical haul of a Multi Net (150 µm mesh, 0.25 m² mouth opening, Hydro-Bios Inc. Kiel) during daytime (17 : 59–18 : 47 local time) (Fig. 1). In the Pacific sector, zooplankton sampling was performed at one station (73°48'N, 159°58'W) in the Canada Basin on 27 September 2013. Samples were collected from 0–100, 100–250, 250–500 and 500–1,000 m by vertical haul of a Vertical Multiple Plankton Sampler (VMPS : Terazaki and Tomatsu, 1997 ; 62 µm mesh size, 0.25 m² mouth opening, Tsurumi-Seiki Co., Ltd. Yokohama) during daytime (06 : 22–06 : 38 local time). At each station, temperature and salinity were

measured by CTD (SBE-911plus, Sea-Bird Electronics Ltd., Washington). After collection, zooplankton samples were immediately preserved with 4% buffered formalin.

Samples and data analysis

In the land laboratory, enumeration and species identification of copepods were performed under a stereomicroscope. Calanoid copepods were identified at the species level, and the total length (*TL*) were measured by an ocular micrometer with a precision of 0.1 mm. The dry mass of calanoid copepods was estimated from *TL* using the following allometric equation :

$$\text{Log}_{10} DM = 2.546 \text{Log}_{10} TL - 6.697$$

where *DM* is individual dry mass (µg DM ind.⁻¹) and *TL* is total length (µm) (Mizdalski, 1988). *DM* was converted to carbon mass, assuming the carbon content of copepods is 44.7% of the *DM* (Båmstedt, 1986). For Harpacticoida, we used the following allometric equation :

$$\text{Log}_{10} CM = 1.950 \text{Log}_{10} TL - 5.577$$

where *CM* is the individual carbon mass (µg C ind.⁻¹) and *TL* is the total length (µm) (Uye et al., 2002).

For Cyclopoida, the dry mass was estimated by the following equation :

$$\text{Log}_{10} DM = 2.163 \log_{10} TL - 6.207$$

where *DM* is the individual dry mass (µg DM ind.⁻¹) and *TL* is the total length (µm) (Kaneko, 2005). The carbon content of Cyclopoida was assumed to be 42.5% of *DM* (James and Wilkinson, 1988).

For Poecilostomatoida, we used the following allometric equation :

$$\text{Log}_{10} DM = 2.895 \log_{10} TL - 7.993$$

where *DM* is in the individual dry mass (µg DM ind.⁻¹) and *TL* is the total length (µm) (Nishibe, 2005). The carbon content of Poecilostomatoida was assumed to be 53% of *DM* (Nishibe and Ikeda, 2008).

For each sample, the species diversity index (*H'*) was calculated :

$$H' = -\sum ni / Ni \times \ln ni / Ni$$

where *ni* is the abundance (ind. m⁻²) of each species and *Ni* is the total abundance at the *i*th layer (Shannon and Weaver, 1949).

To quantitatively compare the vertical distributions, the depths where 50% of the population resided (50% distributed layer : *D*_{50%}, Pennak, 1943) were calculated for each species. *D*_{25%} and *D*_{75%} were also calculated.

To evaluate geographical and vertical changes in the copepod community, cluster analysis based on copepod abundance was performed. Abundance data (*X* : ind. m⁻²) for each species were log-transformed (log₁₀[*X*+1]). Then, similarities between samples were calculated using the Bray-Curtis



Fig. 1. Location of sampling stations in the Fram Strait (Atlantic sector of the Arctic Ocean) and in the Canada Basin (Pacific sector of the Arctic Ocean). For details of samplings, see the text.

similarity index (Bray and Curtis, 1957). To group samples, similarity indices were coupled with hierarchical agglomerative clustering using a complete linkage method (UPGMA : Unweighted Pair Group Method using Arithmetic mean) (Field et al., 1982). Nonmetric Multi-Dimensional Scaling (NMDS) ordination was executed to delineate the sample groups on a two-dimensional map. All analyses were performed with PRIMER v7 software (Primer-e Ltd., Albany, New Zealand).

Results

Hydrography

The temperature varied between -1.03 and 5.56°C in the Fram Strait (Fig. 2A). Low temperature (-1.03 – 0°C) was observed from the surface to 26 m, while the temperature increased below that layer and reached 5.56°C at 53 m. Below this peak, the temperature decreased with increasing depth. Salinity ranged between 32.92 and 35.16, and high salinity (> 35) was observed below 50 m and was stable below that layer. Dissolved oxygen was highest (8.47 ml L^{-1}) at the surface layer and remained at a high value of 6 ml L^{-1} throughout the water column. Chl. *a* varied between 0.02 and 1.18 mg m^{-3} and peaked at a depth of 15 m.

For the Canada Basin, the temperature varied between -1.61 and 0.79°C (Fig. 2B) and showed little change with depth. Salinity ranged between 32.92 and 35.16. Salinity was low (< 30) at 0–40 m, which is characteristic of Polar Surface Water at that layer. Salinity gradually increased with increasing depth and reached a peak below a depth of 500 m, similar to the value (> 35) in the Fram Strait. Dissolved oxygen was relatively high near the surface layer, peaked (8.90 ml L^{-1}) at 30 m, and subsequently decreased with increasing depth down to 200 m, below which it was stable. Chl. *a* ranged between 0.04 and 3.24 mg m^{-3} and reached a subsurface maximum at 36 m.

Comparison of hydrography between the sectors revealed greater differences, especially in temperature and salinity. Thus, surface salinity was lower in the Canada Basin than in the Fram Strait, while the Fram Strait was warmer than the Canada Basin through a wide range between 25 and 1,000 m.

Copepods

In the Fram Strait, both copepod abundance and biomass were highest at the surface 0–50 m ($3,132\text{ ind. m}^{-3}$ and 18.6 mg C m^{-3}) and decreased with increasing depth (Fig. 3A). Species diversity (H') was low at the surface layer (0.70), was high at 200–500 m (1.74) and remained high below that layer. In the Canada Basin, copepod abundance was high at 0–50 m (518 ind. m^{-3}), while high biomass was at 100–250 m (1.3 mg C m^{-3}) (Fig. 3B). Species diversity was high even in the surface layer, and the highest value (2.27) occurred at 100–250 m.

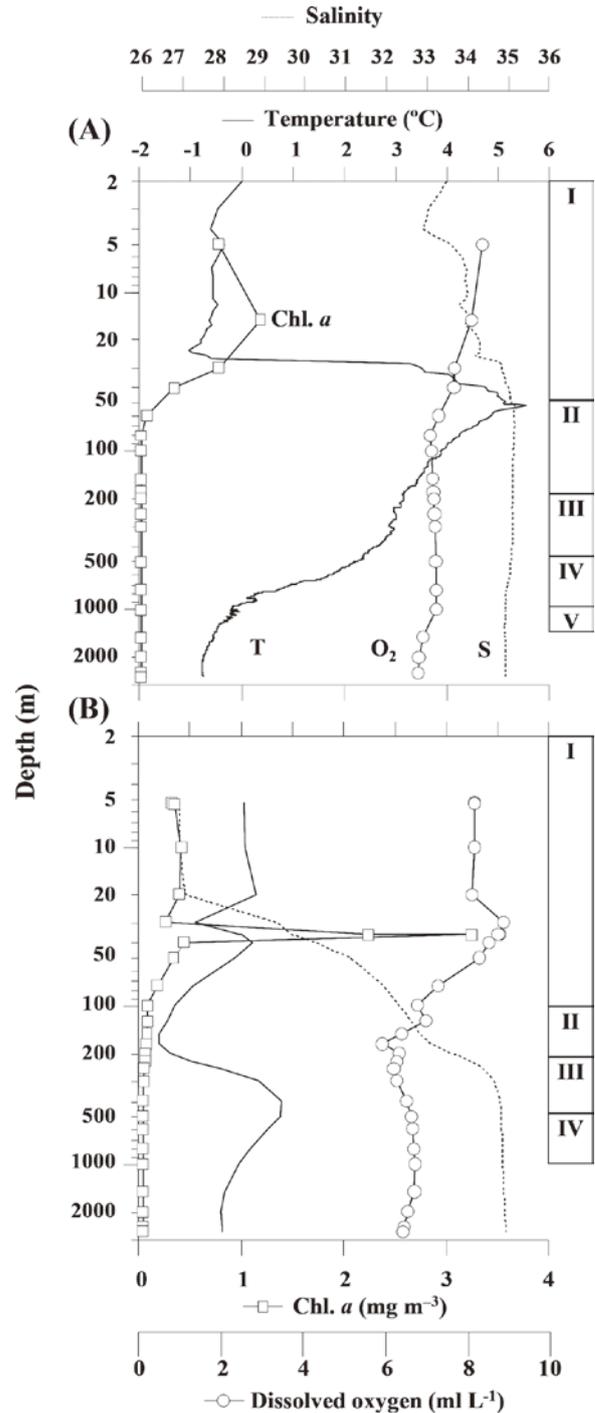


Fig. 2. Vertical distribution of temperature, salinity, dissolved oxygen and Chl. *a* in the Fram Strait (A) and the Canada Basin (B). Depth ranges of sampling layers are shown in the numbers in the right columns. Note that the depth scale is in log-scale.

For copepod composition by abundance, Cyclopoida accounted for 66% at the surface, while the proportion of Calanoida increased at deeper layers in the Fram Strait (Fig. 4A). On the other hand, in the Canada Basin, Cyclopoida accounted for 55% at the surface, but Poecilostomatoida

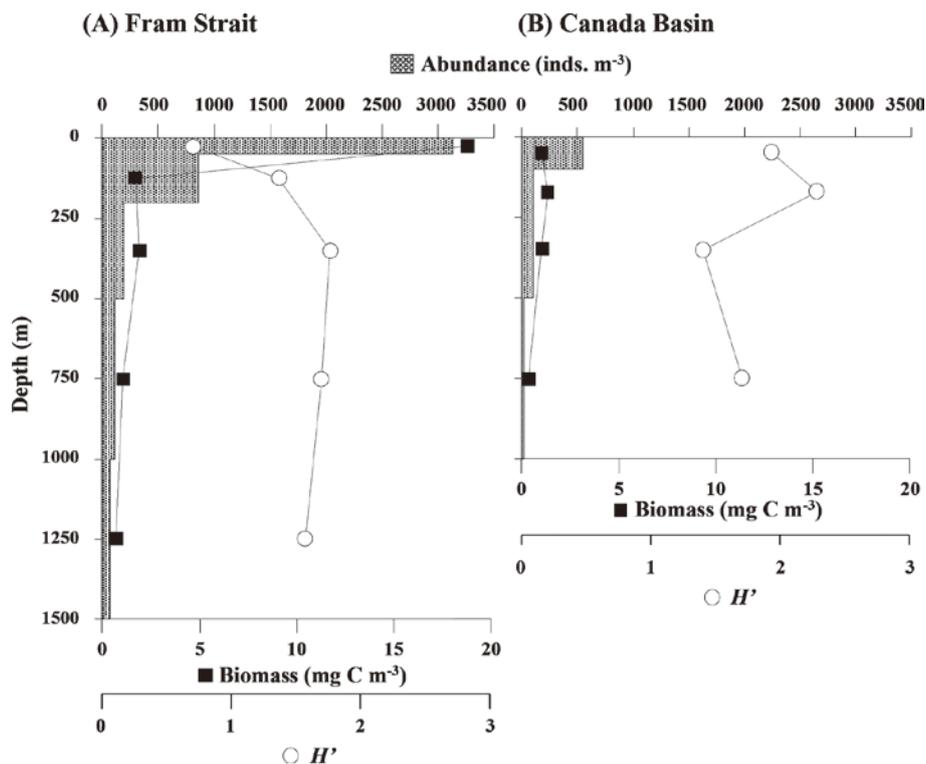


Fig. 3. Vertical distribution of copepod abundance, biomass and species diversity indices (H') based on their abundance data in the Fram Strait (A) and Canada Basin (B).

dominated at 65%–68% below 250 m (Fig. 4B). For copepod composition by biomass, Calanoida predominated (78–99%) throughout the water column in both regions (Fig. 4C, 4D).

The results of cluster analyses and NMDS analyses are shown in Fig. 5. According to the cluster analyses, the copepod community was separated into three groups at 78% Bray–Curtis dissimilarity. The copepod communities were separated vertically rather than geographically. Thus, we named the groups from shallow to deep: epipelagic, mesopelagic and bathypelagic. The epipelagic group contained samples from 0–50 and 50–200 m in the Fram Strait and 0–100 m in the Canada Basin. The mesopelagic group included samples at 200–500 and 500–1,000 m in the Fram Strait and 100–250 and 250–500 m in the Canada Basin. The bathypelagic group contained the deepest samples in both regions.

The standing stock and vertical distribution (50% distribution depth ($D_{50\%}$) and distribution core ($D_{25\%}$ – $D_{75\%}$)) of copepods in the Fram Strait and in the Canada Basin are shown in Fig. 6. Most of the dominant species were well corresponded with the two regions. The dominant species was *Oithona* spp. ($D_{50\%}$: 32–63 m) in the epipelagic group. *Oncaea* spp. ($D_{50\%}$: 319–324 m) and *Microcalanus* spp. ($D_{50\%}$: 245–542 m) dominated the mesopelagic group. Regional differences were marked for *Calanus finmarchicus*, which was distributed in the epipelagic layer ($D_{50\%}$: 49 m) only in

the Fram Strait. *Spinocalanus* spp. was common to both regions and was the characteristic species in the bathypelagic group.

Vertical changes in the family composition of calanoid copepods in terms of abundance and biomass are shown in Fig. 7. In abundance, Calanidae dominated the epipelagic group in both regions (reached 93.0% in the Fram Strait and 58.3% in the Canada Basin). Clausocalanidae including *Microcalanus* spp. dominated the mesopelagic group in both regions (composed 53.0% in the Fram Strait and 63.6% in the Canada Basin). For the bathypelagic group, Clausocalanidae dominated in the Fram Strait (63.1%), while Spinocalanidae dominated in the Canada Basin (56.1%).

Concerning biomass, Calanidae dominated throughout the water column in both regions (composed >60.0% in the Fram Strait and >60.9% in the Canada Basin). The predominance of Calanidae was marked at 0–50 m in the Fram Strait (98.6%). In the mesopelagic group, the compositions of Aetideidae, Heterorhabditidae and Metridinidae varied in both regions. In the bathypelagic group, Spinocalanidae (19.4%) was dominant in the Canada Basin.

Discussion

Methodological note

We applied different mesh size sampling gears in each region (Fram Strait: 150 μ m, Canada Basin: 62 μ m). The

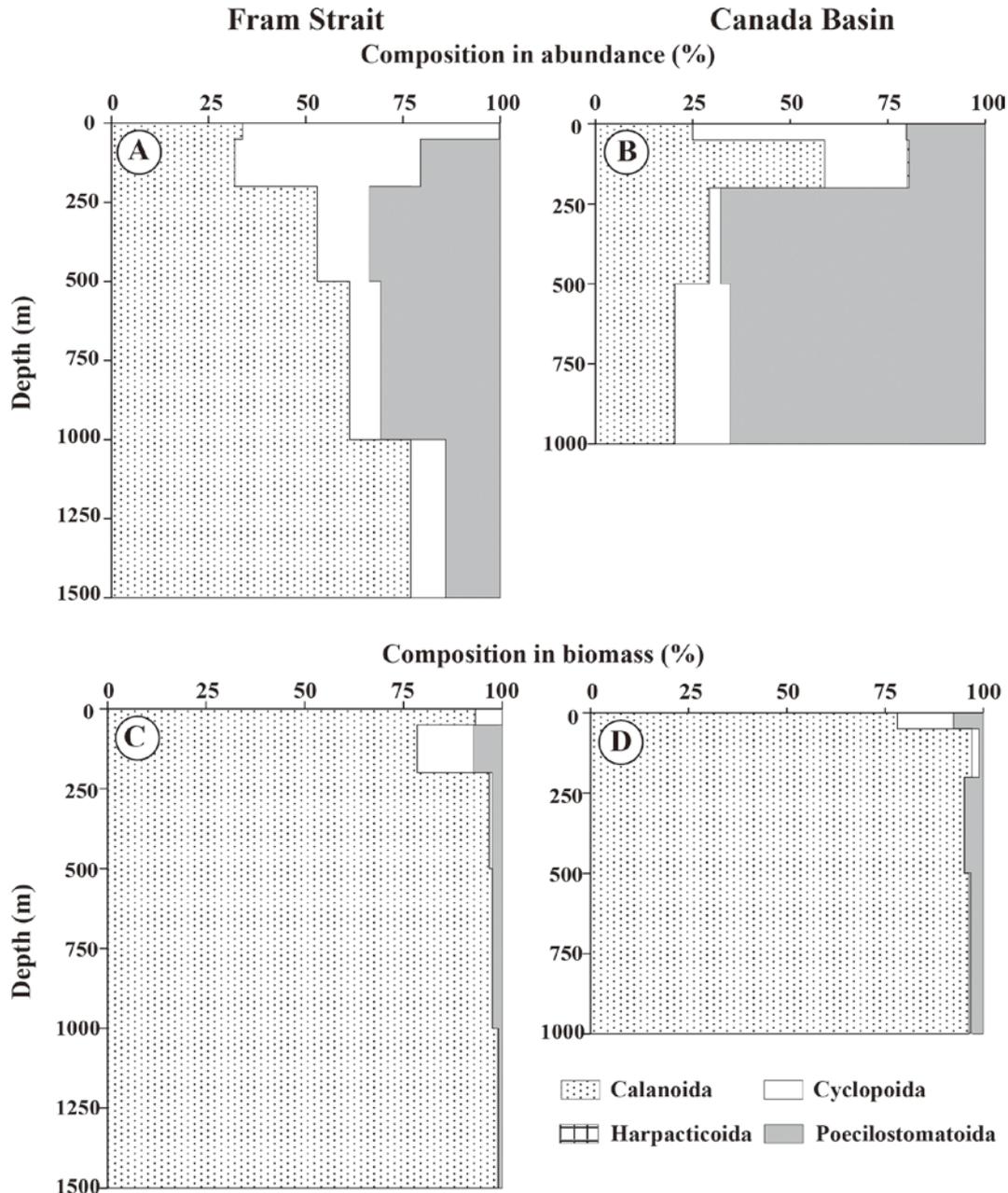


Fig. 4. Vertical changes in composition of four orders (Calanoida, Cyclopoida, Harpacticoida and Poecilostomatoida) of copepods in abundance (A), (B) and biomass (C), (D) in the Fram Strait (left) and Canada Basin (right).

bias due to the use of different mesh sizes should be considered. The use of smaller mesh sizes has been associated with an increased composition of small copepods (Cyclopoida in the epipelagic layer and Poecilostomatoida in the meso- and bathypelagic layer), especially in abundance (Böttger-Schnack, 1996 ; Yamaguchi et al., 2002 ; Homma et al., 2011). In the present study, the composition of Poecilostomatoida in terms of abundance was 0.2–33.6% in the Fram Strait using a 150- μ m mesh net but 19.5–67.8% in the Canada Basin using a 62- μ m mesh net (Fig. 4A, B). In terms of biomass, since the individual mass of small Poecilostomatoida was low, large body-sized Calanoida predominated in

both regions (Fig. 4C, D). In terms of depth composition, Homma et al. (2011) compared the composition in terms of abundance at different layers (epipelagic layer : 0–250 m ; mesopelagic layer : 250–1,000 m ; bathypelagic layer : 1,000–3,000 m) by applying different mesh sizes. While abundance increased with the use of smaller mesh sizes, few effects were detected for the depth composition in terms of copepod abundance (Homma et al., 2011).

The sampling period also varied between the two regions (1 July in the Fram Strait and 27 September in the Canada Basin). Both periods were in summer, which corresponds to the period after sea ice melting in both regions. Consistent

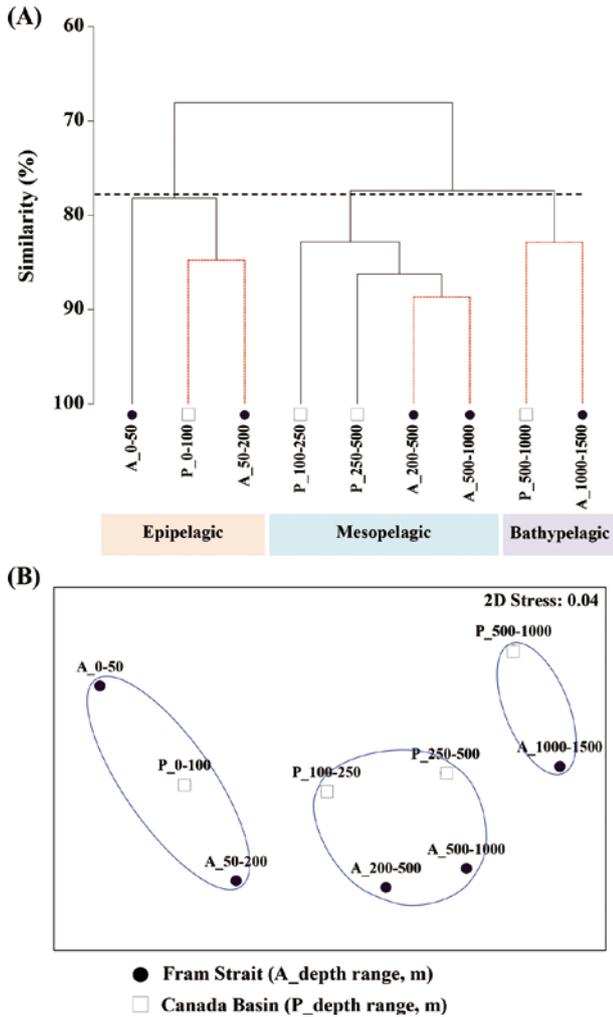


Fig. 5. Results of the cluster analysis based on zooplankton abundance using Bray-Curtis similarity (A). Two-dimensional representation of nonmetric multi-dimensional scaling plots (B). The dotted line in (A) and circles in (B) indicate percentage similarity at 78%.

with this study, studies of summer zooplankton distribution down to greater depths in the Arctic Ocean have used time intervals ranging from one month (Mumm, 1993 ; Auel and Hagen, 2002 ; Kosobokova and Hopcroft, 2010) to three months (Mumm et al., 1998 ; Kosobokova and Hirche, 2000). Thus, the difference in sampling periods in this study (ca. three months) is within the ranges of previous studies.

As mentioned above, the applied mesh size and sampling period differed between locations. Due to differences in mesh size, the abundance of small copepods such as Cyclopoida and Poecilostomatoida would be biased. For biomass, the effect of different mesh sizes would be minor because of the low individual mass of the small copepods. For differences in sampling period, since both locations were sampled in the same summer season, little effect would be expected for the vertical distribution and community structure of copepods.

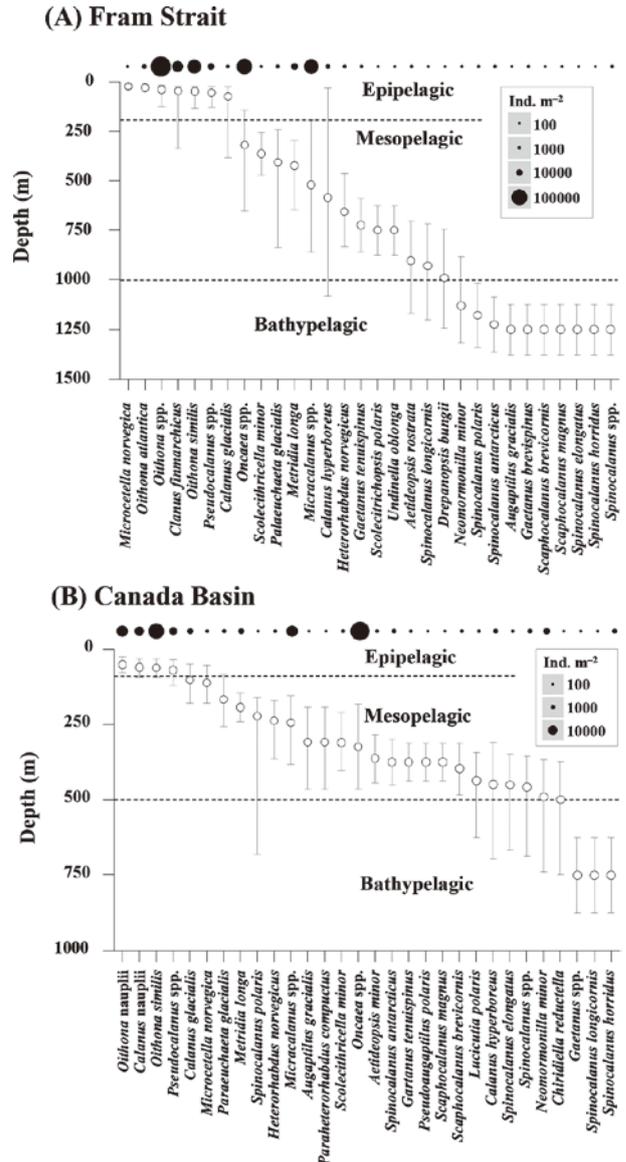


Fig. 6. Standing stock and vertical distribution of copepods in the Fram Strait (A) and Canada Basin (B). For each species or taxon, the upper solid circles indicate abundance (ind. m⁻² : water column), and the lower open circles indicate 50% distribution depth (D_{50%}). The vertical bars indicate depth ranges where 25% (D_{25%}) and 75% (D_{75%}) of the population are distributed. The dashed lines indicate boundaries of copepod communities identified from the cluster analysis (cf. Fig. 5).

Regional comparison

In terms of regional differences, it is notable that both abundance and biomass at the surface layer were 6–18 times higher in the Fram Strait than in the Canada Basin (Fig. 3). Considering differences in mesh size (coarse 150 μm in the Fram Strait), these results suggest that extremely high abundances of copepods occurred at the surface layer of the Fram Strait. With respect to regional differences in the zooplankton community in the Arctic Ocean, Kosobokova and

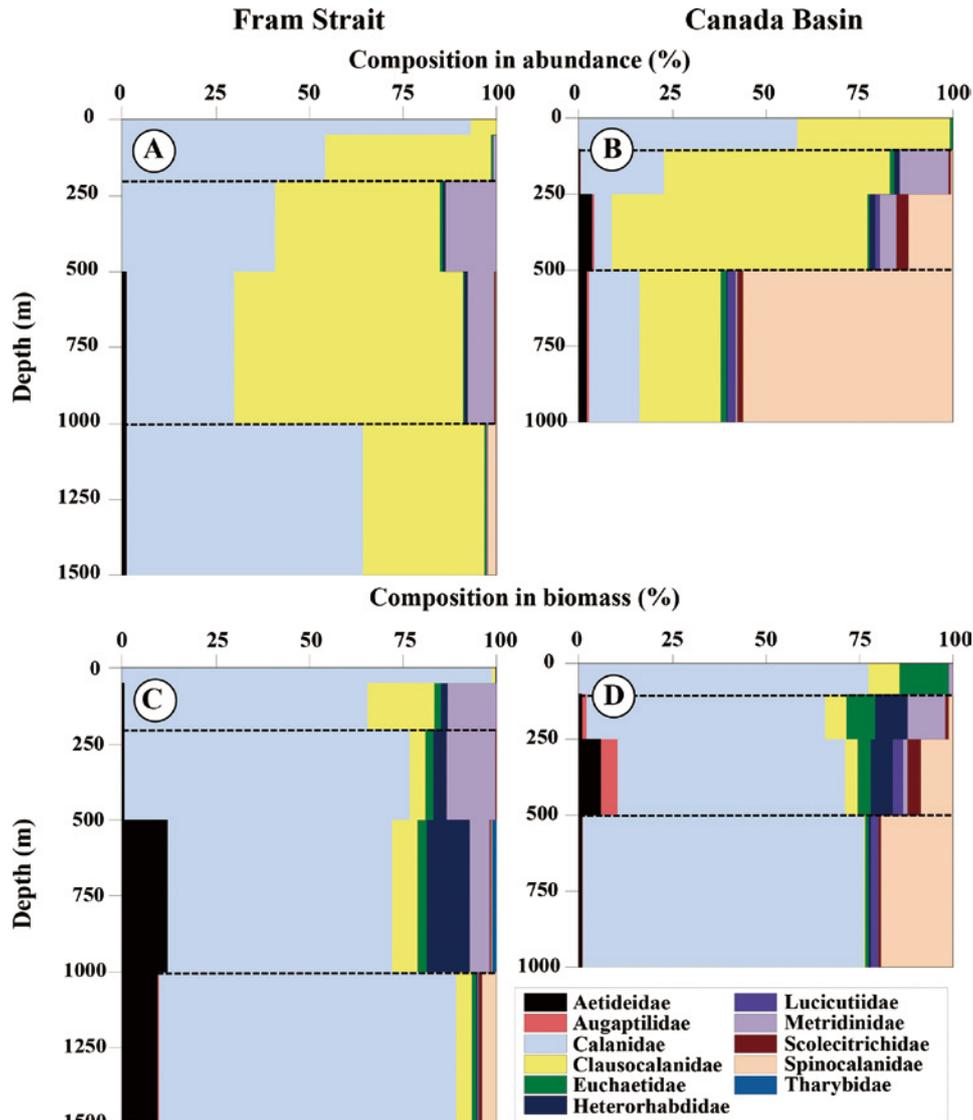


Fig. 7. Vertical changes in the composition of families of calanoid copepods in terms of abundance (A, B) and biomass (C, D) in the Fram Strait (left) and Canada Basin (right). Dashed lines indicate the boundaries of the copepod community identified from the cluster analysis (cf. Fig. 5).

Hirche (2000) revealed that the distribution of the Atlantic copepod *C. finmarchicus* was restricted to east of the Lomonosov Ridge, while the abundance and biomass of various zooplankton taxa (appendicularians, chaetognaths and ostracods) decreased in the western basins, i.e., the Canada and Makarov Basins, due to the elimination of Atlantic water in these regions. In the present study, *C. finmarchicus* did not occur in the Canada Basin (Fig. 6). The presence/absence of transported copepods from the Atlantic Ocean may induce regional differences in the abundance and biomass of copepods at the surface layer. Thus, transported copepods from the Atlantic Ocean would provide high abundance and biomass at the surface layer of the Fram Strait.

The species diversity of copepods is known to be high in the meso- and bathypelagic zones of oceans worldwide (Roe, 1988 ; Scotto di Carlo et al., 1984 ; Richter, 1994 ; Yama-

guchi et al., 2002 ; Homma et al., 2010). In this study, species diversity in the Fram Strait peaked at the mesopelagic layer (Fig. 3A). However, in the Canada Basin, species diversity was even high at the surface layer (Fig. 3B). This may be due to the cold water temperature throughout the water column in the Canada Basin (Fig. 2B). Deep-sea copepods are adapted to cold water temperatures, allowing them to extend their vertical distribution to the surface layer. The occurrence of deep-sea copepods near surface layer may elevate species diversity in this layer. This pattern was confirmed by the $D_{50\%}$ data of the copepods. Seven species had $D_{50\%}$ above a depth of 250 m in the Fram Strait, while eleven species had $D_{50\%}$ above 250 m in the Canada Basin (Fig. 6). In addition to these species numbers, in the Fram Strait, the predominance of Atlantic *C. finmarchicus* may reduce species diversity at the surface layer, and species diversity showed a

peak at 200–500 m.

Despite regional differences in abundance and species diversity, the copepod communities were separated into three groups that varied vertically at both geographical locations (Fig. 5). For copepods in the Arctic Ocean, it has been reported that vertical changes in abundance, biomass and species composition are more prominent than regional changes (Kosobokova and Hirche, 2000 ; Auel and Hagen, 2002 ; Kosobokova and Hopcroft, 2010 ; Kosobokova et al., 2011). Within the 0–1,500 m water column, the zooplankton community was classified into four groups in the central Arctic Ocean : 0–50, 50–200, 200–1,000, 1,000–1,500 m (Auel and Hagen, 2002). Similar classification of the copepod community into three groups (0–300, 300–1,000 and 1,000–3,000 m) was reported in the Greenland Sea (Richter, 1994). Although the depth ranges differed slightly, the vertical classification of the copepod community in this study is similar to these reports (Fig. 5). These observations suggest that vertical classifications are present for the copepod community throughout the Arctic Ocean.

While the community structures were similar between the two regions, prominent differences in the calanoid copepod community were observed, with a high composition of Spinocalanidae in the deep layer of the Canada Basin. Spinocalanidae composed 56.1% of the abundance in the bathypelagic groups and also contributed 7.5% of calanoid copepod abundance throughout the water column in the Canada Basin (Fig. 7). For the calanoid copepod community

below 200 m depth, Spinocalanidae was reported to be the second most dominant family following Clausocalanidae in the central Arctic Basin and the Canada Basin (Table 1). Spinocalanidae has been reported to compose 10–17% of calanoid copepod abundance below 200 m in the Canada Basin and the central Arctic Basin (Auel and Hagen, 2002 ; Kosobokova and Hopcroft, 2010).

On the other hand, the dominant copepod families below 200 m were Clausocalanidae, Calanidae and Metridinidae in the Fram Strait and Greenland Sea (Table 1). The dominance of these families is similar to that in the western and northern North Pacific and the Bering Sea (Table 1). In all of these regions, the composition of Spinocalanidae is reported to be extremely low, with values as low as 0.1–0.4% (Yamaguchi et al., 2002 ; Homma et al., 2011). These facts suggest that the composition of Spinocalanidae in the Pacific sector of the Arctic Ocean, including the Canada Basin, is much higher than in other oceanic regions.

Interestingly, dominance of Spinocalanidae in the calanoid copepod community has been reported for Pacific basins, including the Canada Basin and the Makarov Basin (Table 1). Both the biomass and composition of the Atlantic species decreased dramatically through the Nansen Basin to the Amundsen Basin along with a decreasing effect of the Atlantic water (Wassmann et al., 2015 ; Kosobokova and Hirche, 2000). The boundary between Atlantic and the Pacific expatriates in the Arctic Ocean is reported to be the Lomonosov Ridge (Bluhm et al., 2015). The dominance of Spinocalani-

Table 1. Regional comparison of copepod abundance, biomass and dominant calanoid families below 200 m in the Arctic Ocean and their adjacent seas.

Study area (depth range, m)	Sampling gear	Mesh size (μm)	Abundance (ind. m^{-2})	Biomass (mg C m^{-2})	Dominant families in deep sea (below 200 m)	Reference
Canada Basin (0–3,000)	Multi net	150	50,176	1,340	Clausocalanidae Spinocalanidae Calanidae	Kosobokova and Hopcroft 2010
Canada Basin (0–1,000)	VMPS	62	28,635	664	Clausocalanidae Spinocalanidae Calanidae	This study
Central Arctic Ocean (0–1,500)	Multi net	150	39,327		Clausocalanidae Spinocalanidae Calanidae	Auel and Hagen 2002
Fram Strait (0–3,000)	Multi net	150	187,189	2,488	Clausocalanidae Calanidae Metridinidae	This study
Greenland Sea (0–4,000)	Multi net	150	728,160	6,754	Clausocalanidae Calanidae Metridinidae	Richter 1994
Western subarctic Pacific (0–3,000)	VMPS	62	735,350	9,096	Clausocalanidae Metridinidae Eucalanidae	Yamaguchi et al. 2002
North Pacific (0–3,000)	VMPS	62	284,664	6,576	Clausocalanidae Metridinidae Calanidae	Homma et al. 2011
Bering Sea (0–3,000)	VMPS	62	213,413	4,341	Clausocalanidae Metridinidae Aetideidae	Homma et al. 2011

dae in the Pacific sector in the Arctic Ocean is related to the typical oligotrophic environment with no effect of Atlantic water in these regions.

Spinocalanidae is small in body size (0.6–2.2 mm for adult females ; Damkaer, 1975 ; Razouls et al., 2005–2020). Due to the difficulty of morphological identification by microscopic observation, few studies of Spinocalanidae are available. Recently, by applying molecular identification techniques, 28 morphospecies of Spinocalanidae were discriminated, while 39 species were detected using DNA sequence analyses and 42 using proteomic fingerprinting (Bode et al., 2017). Spinocalanidae is suggested to be polyphyletic and has an important role in material cycling in the meso- and bathypelagic layer (Bode et al., 2017). Among dominant Spinocalanidae in the Canada Basin, *Spinocalanus antarcticus* is an omnivorous detritus feeder with a looped shape mid-gut that is 1.7–1.9 times longer than its body length (Kosobokova et al., 2002). This looped gut permits the digestion of amorphous detrital ball and mineral particles and improves assimilation efficiency in food-limited bathy- and abyssopelagic realms (Kosobokova et al., 2002). Spinocalanidae is also reported to be adapted to the oxygen minimum layer and has important role in material cycling of the mesopelagic zone in the oligotrophic Arabian Sea (Wishner et al., 2008).

Because of the high stratification of ice melt water at the surface, the Arctic Basin is an oligotrophic environment, and size of phytoplankton is small, with limited primary production (Nishino et al., 2011). Moreover, in the Canada Basin, the occurrence of the anticyclonic circulation called the Beaufort Gyre increases stratification via the accumulation of less saline ice melt water at the surface and deep nutricline, resulting in dominance of small phytoplankton and low primary production (Nishino et al., 2011). Sediment trap experiments have revealed that the amount of sinking flux in the Canada Basin is similar for the oligotrophic subtropical North Pacific and is mainly composed of mineral particles (Onodera et al., 2009). Thus, food resources for deep-sea copepods in the Pacific sector of the Arctic Ocean are expected to be lower than in other oceanic regions. Under this resource-limited oligotrophic environment of the deep basin of the Arctic Ocean, Spinocalanidae may have an advantage in terms of the adaptation of the specialized digestive system (looped gut) of this family. Thus, the dominance of Spinocalanidae, especially in the Canada Basin may be related to low primary productivity in the Pacific sector of the Arctic Basin.

It also should be noted that both the abundance and biomass of total copepods through the water column in the Pacific sector of the Arctic Ocean were somewhat lower than in the other oceans. The abundance was 28,635 – 50,176 ind. m⁻² in the Pacific sector but 187,189–735,350 ind. m⁻² in the other locations (Table 1). Biomass was 664–1,340 mg C m⁻² in the Pacific Sector but 2,488–9,096 mg C m⁻² in

the other locations (Table 1). These facts suggest that low primary productivity in the oligotrophic Pacific sector may induce low zooplankton standing stock throughout the water column.

Future prospects

The Arctic Ocean ecosystem is undergoing changes in its adjacent connecting regions (Wassmann et al., 2015 ; Hunt et al., 2016). The reduction of sea ice is greatest in the Pacific sector of the Arctic Ocean (Stroeve et al., 2007 ; Comiso et al., 2008 ; Markus et al., 2009). Future prospects in the Canada Basin include low primary production due to the intensification of anticyclonic circulation, enhanced stratification via accumulation of less saline ice melt water at the surface and deepening of the nutricline (Nishino et al., 2011). In fact, the size of dominant phytoplankton has reportedly changed from nano-size to pico-size (Li et al., 2009). As a result of low productivity, zooplankton standing stocks are low throughout the water column in the Canada Basin (Kosobokova and Hopcroft, 2010 ; Matsuno et al., 2012). In the future, anticyclonic circulation will enhance the reduction of sea ice, resulting in low primary production and reduced vertical material flux to the deep. Under these conditions, dominance of Spinocalanidae, which is adapted to oligotrophic environments, may be expected in the meso- and bathypelagic layer in the Pacific sector of the Arctic Ocean in the future.

In the Atlantic sector of the Arctic Ocean, water advection from the Norwegian Sea through the Fram Strait accounts for a large part of the ocean current and has a large physical and biological impact on the Arctic Ocean (Cottier et al., 2005 ; Nilsen et al., 2006 ; Hunt et al., 2016). The amount of zooplankton biomass transported from the Atlantic Ocean is reported to be two to three times higher than that from the Pacific Ocean (Wassmann et al., 2015). Since 1990, increases in the temperature of water passing through the Fram Strait have been reported (Turrell et al., 2003 ; Holliday et al., 2008). According to long-term monitoring, the abundance of *C. finmarchicus* is higher in warm years (>6°C SST at the Atlantic sector in the Arctic Ocean) (Turrell et al., 2003 ; Holliday et al., 2008). Among Atlantic species, *C. finmarchicus* is the most important and accounted for 55% of copepod biomass throughout the water column at Fram Strait in the present study. This composition is comparable to the value of 40% of zooplankton biomass reported NE of the Svalbard Islands (Kosobokova, 2012). As the temperature of Atlantic water increases, the biomass of advected *C. finmarchicus* is expected to increase in the Atlantic sector of the Arctic Ocean. *C. finmarchicus* is an important prey of the Atlantic herring (*Clupea harengus*) and the Atlantic mackerel (*Scomber scombrus*) (Marshall and Orr, 1972 ; Prokopchuk and Sentyabov, 2006). Occurrence of more *C. finmarchicus* in the Atlantic sector of the Arctic Ocean may modify the

northward feeding migration route of these fishes and induce changes in the marine ecosystem.

Thus, as a future prospect, the copepod community is expected to change in both the Atlantic and Pacific sectors of the Arctic Ocean. The pattern of change is expected to vary between the two regions. Thus, in the Pacific sector of the Arctic Ocean, due to greater oligotrophy, dominance of Spinocalanidae at the deep layer is expected. On the other hand, because of warming of the intruding Atlantic water, dominance of *C. finmarchicus* at the surface layer is expected for the Atlantic sector in the Arctic Ocean.

Acknowledgements

We thank the captains, officers, crews and researchers on board the R/V *Polarstern*, AWI and the R/V *Mirai*, JAM-STEAC, for their great efforts during field sampling. Part of this study was supported by a Grant-in-Aid for Scientific Research 17H01483 (A), 18K14506 (Early Career Scientists), 19H03037 (B), 20K20573 (Pioneering) and 20H03054 (B) from the Japanese Society for the Promotion of Science (JSPS). This work was conducted within the Arctic Challenge for Sustainability (ArCS II) project.

References

- Auel, H. and Hagen, W. (2002) Mesozooplankton community structure, abundance and biomass in the central Arctic Ocean. *Mar. Biol.*, **140**, 1013-1021.
- Båmstedt, U. (1986) Chemical composition and energy content. pp. 1-58, Corner, E.D.S. and O'Hara, S.C.M. (eds), *The Biological Chemistry of Marine Copepods*, Clarendon Press, Oxford.
- Bluhm, B.A., Kosobokova, K.N. and Carmack, E.C. (2015) A tale of two basins: An integrated physical and biological perspective of the deep Arctic Ocean. *Prog. Oceanogr.*, **139**, 89-121.
- Bode, M., Laakmann, S., Kaiser, P., Hagen, W., Auel, H. and Cornils, A. (2017) Unravelling diversity of deep-sea copepods using integrated morphological and molecular techniques. *J. Plankton Res.*, **39**, 600-617.
- Böttger-Schnack, R. (1996) Vertical structure of small metazoan plankton, especially non-calanoïd copepods. I. Deep Arabian Sea. *J. Plankton Res.*, **18**, 1073-1101.
- Bray, J.B. and Curtis, J.T. (1957) An ordination of the upland forest communities of southern Wisconsin. *Ecol. Monogr.*, **27**, 325-349.
- Comiso, J.C., Parkinson, C.L., Gersten, R. and Stock, L. (2008) Accelerated decline in the Arctic sea ice cover. *Geophys. Res. Lett.*, **35**, L01703.
- Cottier, F.R., Tverberg, V., Inall, M., Svensen, H., Nilsen, F. and Griffith, C. (2005) Water mass modification in an Arctic fjord through cross-shelf exchange: the seasonal hydrography of Kongsfjorden, Svalbard. *J. Geophys. Res.*, **110**(C12), 1-18.
- Damkaer, D.M. (1975) Calanoïd copepods of the genera *Spinocalanus* and *Mimocalanus* from the central Arctic Ocean, with a review of the Spinocalanidae. NOAA Tech Rep NMFS CIRC-391, 88 pp.
- Duarte, C.M., Lenton, T., Wadhams, P. and Wassmann, P. (2012) Abrupt climate change in the Arctic. *Nature Climate Change*, **2**, 60-63.
- Ershova, E.A., Hopcroft, R.R., Matsuno, K. and Yamaguchi, A. (2016) Long-term changes in summer zooplankton communities of the western Chukchi Sea, 1945-2012. *Oceanography*, **28**, 100-115.
- Field, J.G., Clarke, K.R. and Warwick, R.M. (1982) A practical strategy for analyzing multispecies distribution patterns. *Mar. Ecol. Prog. Ser.*, **8**, 37-52.
- Gluchowska, M., Trudnowska, E., Goszczko, I., Kubiszyn, A.M., Blachowiak-Samolyk, K., Walczowski, W. and Kwasniewski, S. (2017) Variations in the structural and functional diversity of zooplankton over vertical and horizontal environmental gradients en route to the Arctic Ocean through the Fram Strait. *PLoS One*, **12**, e0171715.
- Holliday, N.P., Hughes, S., Bacon, S., Beszczynska-Möller, A., Hansen, B., Lavín, A., Loeng, H., Mork, K.A., Østerhus, S., Sherwin, T. and Walczowski, W. (2008) Reversal of the 1960s to 1990s freshening trend in the northeast North Atlantic and Nordic Seas. *Geophys. Res. Lett.*, **35**, L03614.
- Homma, T. and Yamaguchi, A. (2010) Vertical changes in abundance, biomass and community structure of copepods down to 3,000 m in the southern Bering Sea. *Deep-Sea Res. II*, **57**, 965-977.
- Homma, T., Yamaguchi, A., Bower, J.R. and Imai, I. (2011) Vertical changes in abundance, biomass, and community structure of copepods in the northern North Pacific and Bering Sea at 0-3,000 m depth, and their role on the vertical flux of surface-produced organic material. *Bull. Fish. Sci. Hokkaido Univ.*, **61**, 29-47.
- Hunt, G.L., Drinkwater, K.F., Arrigo, K., Berge, J., Daly, K.L., Danielson, S.L., Daase, M., Hop, H., Isla, E., Karnovsky, N.J., Laidre, K.L., Mueter, F.J., Murphy, E.J., Renaud, P.E., Smith, W.O. Jr, Trathan, P.N., Turner, J.M. and Wolf-Gladrow, D.A. (2016) Advection in polar and sub-polar environments: Impacts on high latitude marine ecosystems. *Prog. Oceanogr.*, **149**, 40-81.
- James, M.R. and Wilkinson, V.H. (1988) Biomass, carbon ingestion, and ammonia excretion by zooplankton associated with an upwelling plume in western Cook Strait, New Zealand. *NZ J. Mar. Freshw. Res.*, **22**, 249-257.
- Kaneko, M. (2005) Ecological studies of oncaeid copepods in the western subarctic Pacific. Master Thesis, Hokkaido University, Hakodate. (in Japanese).
- Kosobokova, K.N. (2012) *Zooplankton of the Arctic Ocean: community structure, ecology, spatial distribution*. GEOS, Moscow, 272 pp.
- Kosobokova, K.N. and Hirche, H.-J. (2000) Zooplankton distribution across the Lomonosov Ridge, Arctic Ocean: species inventory, biomass and vertical structure. *Deep-Sea Res. I*, **47**, 2029-2060.
- Kosobokova, K.N. and Hopcroft, R.R. (2010) Diversity and vertical distribution of mesozooplankton in the Arctic's Canada Basin. *Deep-Sea Res. II*, **57**, 96-110.
- Kosobokova, K.N., Hirche, H.-J. and Scherzinger, T. (2002) Feeding ecology of *Spinocalanus antarcticus*, a mesopelagic copepod with a looped gut. *Mar. Biol.*, **141**, 503-511.
- Kosobokova, K.N., Hopcroft, R.R. and Hirche, H.-J. (2011) Patterns of zooplankton diversity through the depths of the Arctic's central basins. *Mar. Biodiv.*, **41**, 29-50.
- Li, M.K.W., McLaughlin, F.A., Lovejoy, C. and Carmack, E.C. (2009) Smallest algae thrive as the Arctic Ocean freshens. *Science*, **326**, 539.

- Markus, T., Stroeve, J.C. and Miller, J. (2009) Recent changes in Arctic sea ice melt onset, freezeup, and melt season length. *J. Geophys. Res.*, **114**, C12024.
- Marshall, S.M. and Orr, A.P. (1972) *The Biology of a Marine Copepod*. Springer, Berlin, Heidelberg, 195 pp.
- Matsuno, K., Yamaguchi, A., Hirawake, T. and Imai, I. (2011) Year-to-year changes of the mesozooplankton community in the Chukchi Sea during summers of 1991, 1992 and 2007, 2008. *Polar Biol.*, **34**, 1349–1360.
- Matsuno, K., Yamaguchi, A., Shimada, K. and Imai, I. (2012) Horizontal distribution of calanoid copepods in the western Arctic Ocean during the summer of 2008. *Polar Sci.*, **6**, 105–119.
- Matsuno, K., Yamaguchi, A., Hirawake, T., Nishino, S., Inoue, J. and Kikuchi, T. (2015) Reproductive success of Pacific copepods in the Arctic Ocean and the possibility of changes in the Arctic ecosystem. *Polar Biol.*, **38**, 1075–1079.
- Matsuno, K., Abe, Y., Yamaguchi, A. and Kikuchi, T. (2016) Regional patterns and controlling factors on summer population structure of *Calanus glacialis* in the western Arctic Ocean. *Polar Sci.*, **10**, 503–510.
- Mizdalski, E. (1988) Weight and length data of zooplankton in the Weddell Sea in austral spring (1986) (ANT V/3). *Ber. Polarforsch.*, **55**, 1–72.
- Mumm, N. (1993) Composition and distribution of mesozooplankton in the Nansen Basin, Arctic Ocean, during summer. *Polar Biol.*, **13**, 451–461.
- Mumm, N., Auel, H., Hanssen, H., Hagen, W., Richter, C. and Hirche, H. (1998) Breaking the ice : large-scale distribution of mesozooplankton after a decade of Arctic and transpolar cruises. *Polar Biol.*, **20**, 189–197.
- Naam, R. (2012) Arctic sea ice : what, why and what next. Scientific American. Available at : <https://blogs.scientificamerican.com/guest-blog/arctic-sea-ice-what-why-and-what-next/>. (accessed on 12 April 2020)
- Nelson, R.J., Ashjian, C., Bluhm, B., Conlan, K., Gradinger, R., Grebmeier, J., Hill, V., Hopcroft, R., Hunt, B., Joo, H., Kirchner, D., Kosobokova, K.N., Lee, S., Li, W.K.W., Lovejoy, C., Poulin, M., Sherr, E. and Young, K. (2014) Biodiversity and biogeography of the lower trophic taxa of the Pacific Arctic region – sensitivities to climate change. pp. 269–336, Grebmeier, J.M. and Maslowski, W. (eds), *The Pacific Arctic Region : Ecosystem Status and Trends in a Rapidly Changing Environment*, Springer, Dordrecht.
- Nilsen, F., Gjevik, B. and Schauer, U. (2006) Cooling of the West Spitsbergen Current : isopycnal diffusion by topographic vorticity waves. *J. Geophys. Res.*, **111**(C8), 1–16.
- Nishibe, Y. (2005) The biology of oncaeid copepods (Poecilostomatoida) in the Oyashio region, western subarctic Pacific : its community structure, vertical distribution, life cycle and metabolism. Ph. D. Thesis, Hokkaido University, Hakodate.
- Nishibe, Y. and Ikeda, T. (2008) Metabolism and elemental composition of four oncaeid copepods in the western subarctic Pacific. *Mar. Biol.*, **153**, 397–404.
- Nishino, S., Kikuchi, T., Yamamoto-Kawai, M., Kawaguchi, Y., Hirawake, T. and Itoh, M. (2011) Enhancement/reduction of biological pump depends on ocean circulation in the sea-ice reduction regions of the Arctic Ocean. *J. Oceanogr.*, **67**, 305–314.
- Onodera, J. and Takahashi, K. (2009) Taxonomy and biostratigraphy of middle Eocene silicoflagellates in the central Arctic Basin. *Micropaleontol.*, **55**, 209–248.
- Pennak, R.W. (1943) An effective method of diagramming diurnal movements of zooplankton organisms. *Ecology*, **24**, 405–407.
- Prokopchuk, I. and Sentyabov, E. (2006) Diets of herring, mackerel, and blue whiting in the Norwegian Sea in relation to *Calanus finmarchicus* distribution and temperature conditions. *ICES J. Mar. Sci.*, **63**, 117–127.
- Razouls, C., de Bovée, F., Kouwenberg, J. and Desreumaux, N. (2005–2020) Diversity and geographic distribution of marine planktonic copepods. Sorbonne Université, CNRS. Available at : <http://copepodes.obs-banyuls.fr/en> (accessed on 10 April 2020)
- Richter, C. (1994) Regional and seasonal variability in the vertical distribution of mesozooplankton in the Greenland Sea. *Ber. Polarforsch.*, **154**, 1–87.
- Roe, H.S.J. (1988) Midwater biomass profiles over the Madeira Abyssal Plain and the contribution of copepods. *Hydrobiologia*, **167/168**, 169–181.
- Scotto di Carlo, B., Ianora, A., Fresi, E. and Hure, J. (1984) Vertical zonation patterns for Mediterranean copepods from the surface to 3,000 m at a fixed station in the Tyrrhenian Sea. *J. Plankton Res.*, **6**, 1031–1056.
- Shannon, C.E. and Weaver, W. (1949) *The Mathematical Theory of Communication*. The University of Illinois Press, Urbana, 117 pp.
- Shimada, K., Carmack, E.C., Hatakeyama, K. and Takizawa, T. (2001) Varieties of shallow temperature maximum waters in the western Canadian Basin of the Arctic. *Geophys. Res. Lett.*, **28**, 3441–3444.
- Shimada, K., Kamoshida, T., Itoh, M., Nishino, S., Carmack, E., McLaughlin, F., Zimmermann, S. and Proshutinsky, A. (2006) Pacific Ocean inflow : Influence on catastrophic reduction of sea ice cover in the Arctic Ocean. *Geophys. Res. Lett.*, **33**, L08605.
- Stroeve, J., Holland, M.M., Meier, W., Scambos, T. and Serreze, M. (2007) Arctic sea ice decline : Faster than forecast. *Geophys. Res. Lett.*, **34**, L09501.
- Trenberth, K.E., Jones, P.D., Ambenje, P., Bojariu, R., Easterling, D., Klein-Tank, A., Parker, D., Rahimzadeh, F., Renwick, J.A., Rusticucci, M., Soden, B. and Zhai, P. (2007) Observations : surface and atmospheric climate change. pp. 237–336, Solomon, S., Qin, D., Manning, M., Chen, Z., Marquis, M., Averyt, K.B., Tignor, M. and Miller, H.I. (eds), *Climate Change 2007 : The Physical Science Basis. Contribution of Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change*, Cambridge University Press, Cambridge.
- Turrell, W.R., Hansen, B., Hughes, S. and Østerhus, S. (2003) Hydrographic variability during the decade of the 1990s in the Northeast Atlantic and southern Norwegian Sea. *ICES Mar. Sci. Symp.*, **219**, 111–120.
- Uye, S., Aoto, I. and Onbé, T. (2002) Seasonal population dynamics and production of *Microsetella norvegica*, a widely distributed but little studied marine planktonic harpacticoid copepod. *J. Plankton Res.*, **24**, 143–153.
- Wassmann, P., Kosobokova, K.N., Slagstad, D., Drinkwater, K.F., Hopcroft, R.R., Moore, S.E., Ellingsen, I., Nelson, R.J., Carmack, E., Popova, E. and Berge, J. (2015) The contiguous domains of Arctic Ocean advection : Trails of life and death. *Prog. Oceanogr.*, **139**, 42–65.
- Weydman, A., Walczowski, W., Carstensen, J. and Kwaśniewski, S. (2018) Warming of Subarctic waters accelerates development of a key marine zooplankton *Calanus finmarchicus*. *Glob. Change Biol.*, **24**, 172–183.
- Wishner, K.F., Gelfman, C., Gowing, M.M., Outram, D.M.,

- Rapien, M. and Williams, R.L. (2008) Vertical zonation and distributions of calanoid copepods through the lower oxycline of the Arabian Sea oxygen minimum zone. *Prog. Oceanogr.*, **78**, 163-191.
- Yamaguchi, A., Watanabe, Y. and Ishida H., Harimoto, T., Furusawa, K., Suzuki, S., Ishizaka, J., Ikeda, T., Takahashi, M.M. (2002) Community and trophic structures of pelagic copepods down to greater depths in the western subarctic Pacific (WEST-COSMIC). *Deep-Sea Res. I*, **49**, 1007-1025.