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Seasonal changes in mesozooplankton swimmer community and fecal pellets collected by sediment trap moored at the Northwind Abyssal Plain in the western Arctic Ocean

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Abstract

In the western Arctic Ocean, the long sea ice coverage period prevents year-round zooplankton sampling by ordinary ship-board observation. To overcome these problems, the analysis of zooplankton swimmers in samples collected by a year-round moored sediment trap may be a powerful tool. In this study, we studied seasonal changes in zooplankton swimmer community and fecal pellets collected by a sediment trap moored at fixed depths (180–260 m) of the Northwind Abyssal Plain in the western Arctic Ocean from October 2010 to September 2012. The fecal pellets were separated into four types: oval, cylinder, spherical and brown-colored pellets. The occurrence of brown-colored pellets was limited to the open water period (July–August) and reached 80% of the total at that time. Ship-board experiments showed that the brown-colored fecal pellets were egested by amphipods (*Themisto libellula*). The high occurrence of brown-colored fecal pellets during the open water period might be a reflection of the massive feeding activity of amphipods. Zooplankton swimmer flux ranged from 35–739 ind. m⁻² day⁻¹, and poecilostomatoid copepods were the most abundant (accounted for 69% of the annual mean). Seasonally, barnacle and bivalve larvae were abundant during August–September and August–November, respectively. These meroplanktonic larvae were considered to be transported by current flow from the southern continental shelf, whereas they were absent from summer to autumn in 2012. The annual changes in meroplanktonic larvae occurrence would be a reflection of the annual changes in water mass formation at the upper layer of the sediment trap moored station.

Key words : meroplanktonic larvae, amphipods, sediment trap, fecal pellets, western Arctic Ocean

Introduction

In the western Arctic Ocean, a drastic reduction in the sea-ice extent has been observed during the summer (Stroeve et al., 2007; Comiso et al., 2008; Markus et al., 2009), and the effects of this reduction on the marine ecosystem are cause for concern (Grebmeier, 2012). While the zooplankton community is important, year-round ship-board observation is impossible in the Arctic basin because of the seasonal ice coverage (which lasts for eight months). In the basin of the western Arctic Ocean, annual cycle in abundance and distribution of dominant copepods is reported based on ice station observation (Ashjian et al., 2003). However, most information on the zooplankton community in the western Arctic Ocean has been derived from net-samples collected during the limited open water summer season (Hopcroft et al., 2010; Matsuno et al., 2012). Because of this shortcoming,

seasonal changes in the zooplankton community and their grazing intensity in the Arctic Ocean are not fully understood.

A sediment trap can collect sinking materials throughout the year, and zooplankton swimmers and their fecal pellets are also included in the samples (Buesseler et al., 2007). On some occasions, the zooplankton active flux exceeded the passive particle flux and reached > 10 times of the passive flux mass in the Arctic Ocean (Sampei et al., 2009a, 2012). Because of their importance, seasonal changes in the zooplankton community in the Arctic Ocean were evaluated by analyzing swimmer samples collected with sediment traps at several regions, especially in the Beaufort Sea (Forbes et al., 1992; Ota et al., 2008; Makabe et al., 2010). Recently, seasonal changes in the population structure and life cycle of the dominant copepods were also evaluated around the Northwind Abyssal Plain (Matsuno et al., 2014, 2015).

Zooplankton fecal pellets have an important role in the ver-

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tical material flux (Turner, 2002). The morphology (size, shape and color) of the fecal pellets varies with the egested taxa/species (Hansen and Bech, 1996 ; Urban-Rich et al., 1998). Thus, seasonal changes in the composition of the morphology of the fecal pellet could be treated as indices of seasonal changes in the grazing intensity of various zooplankton taxa in upper layers. Previously, the carbon flux estimation of fecal pellets was reported in the Arctic Ocean during winter (Sampei et al., 2009b). However, little information is available for seasonal changes in the morphology of the fecal pellets.

In the present study, we studied the seasonal changes in a zooplankton swimmer community and fecal pellet morphology based on the samples collected by a sediment trap moored at the Northwind Abyssal Plain in the western Arctic Ocean over two years (from October 2010 to September 2012). In this study, additional ship-board fecal pellet egestion experiments were conducted on each dominant zooplankton species/taxa. The identification of species/taxa was made for the fecal pellets based on their morphology using this reference data.

Materials and Methods

Field sampling

Samples were collected by sediment trap (SMD26 S-6000, open mouth area 0.5 m², Nichiyu Giken Kogyo Co. Ltd., Tokyo, Japan) rotated at 10–15 day intervals and moored at 180–260 m of St. NAPt (Northwind Abyssal Plain trap, 75°00'N, 162°00'W) from 4 October 2010 to 28 September 2011 (first year) and from 4 October 2011 to 18 September 2012 (second year) (Fig. 1). The end of the trap rope was

fixed to the sea bottom (bottom depth : 1,975 m). The sample cups were filled with 5% buffered formalin before deploying the sediment trap.

After retrieving the trap, the 52 samples were sieved gently with 1 mm mesh, and 1/10 subsamples of the passed fraction (<1 mm size) were filtered through a polycarbonate membrane filter, dried and weighed with an analytical balance to calculate the total mass flux (mg dry mass [DM] m⁻² day⁻¹) (Onodera et al., 2015). As supplement environmental information, the depth and temperature at the sediment trap were monitored every hour. The current speed at St. NAPt was estimated by a physical ocean general circulation model : the Center for Climate System Research Ocean Component Model version 4.9 (cf. Watanabe et al., 2015). Weekly data on the averaged percentage of ice coverage around St. NAPt (74.5–75.5°N, 161.5–162.5°W) during the mooring period were calculated from the sea ice concentration data set (http://iridl.ldeo.columbia.edu/SOURCES/IGOSS/nmc/.Reyn_SmithOIv2/, Reynolds et al., 2002). Daily chlorophyll *a* data, measured by MODIS/Aqua at 9 km resolution, were smoothed by calculating a 9-day running mean.

Microscopic analysis

All fractions of > 1 mm and 1/10 fractions of < 1 mm samples were used for the identification and enumeration of zooplankton taxa/species under a stereomicroscope. The species identification of the copepods mainly followed Brodsky (1967), Heron et al. (1984) for *Oncaea* spp., Frost (1974) for *Calanus* spp., Miller (1988) for *Neocalanus* spp. and Frost (1989) for *Pseudocalanus* spp.

The flux (F , ind. m⁻² day⁻¹) of the zooplankton swimmers were calculated with the following equation :

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

where N is the number of individuals (ind.), 0.5 is the mouth area (m²) of the sediment trap and d is the sampling interval (days).

The fecal pellets that occurred in the <1 mm fraction samples were categorized into four morphological types (oval, cylinder, spherical and brown-colored) and enumerated under a dissecting microscope. The size of each fecal pellet was measured for the longest axis of the fecal pellet (fecal pellet length) by using an eyepiece micrometer with a precision of 0.01 mm.

Data analysis

The zooplankton flux data (F : ind. m⁻² day⁻¹) for each species was log transformed ($\log_{10}[X+1]$) prior to analysis to reduce the bias of flux. Similarities between the samples were examined using the Bray-Curtis index. For grouping the samples, the similarity indices were coupled with hierarchical agglomerative clustering using a complete linkage method (Unweighted Pair Group Method using Arithmetic

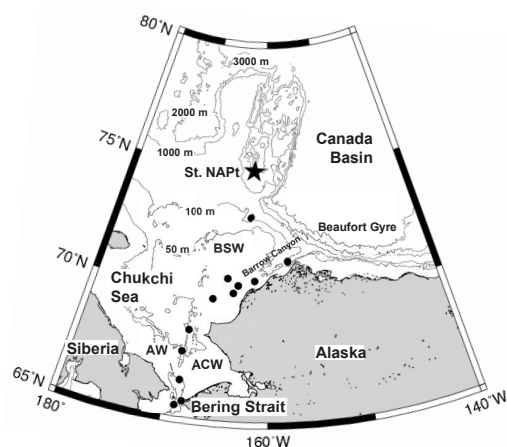


Fig. 1. Location of St. NAPt (Northwind Abyssal Plain trap, star) in the western Arctic Ocean, where the sediment trap was moored at 180–260 m during October 2010 to September 2012. Locations of zooplankton net sampling, which were used for ship-board experiments during July to September 2013, are shown with solid circles. ACW : Alaskan Coastal Water, AW : Anadyr Water and BSW : Bering Shelf Water.

mean : UPGMA) (Field et al., 1982). To identify the species most responsible for the similarity between the zooplankton community groups, tests by SIMPER analysis were performed based on the abundance data. All of these analyses were conducted using PRIMER v6 software (PRIMER-E Ltd.). Inter-group differences in the zooplankton flux were tested by a one-way ANOVA and Tukey-Kramer Test. These statistical analyses were conducted using StatView v5 software (SAS Institute Inc.).

Ship-board experiment

For the zooplankton fecal pellet egestion experiments, fresh zooplankton was collected by vertical tows of a ring net (mouth diameter 80 cm, mesh size 335 μm) at 12 stations in the Chukchi Sea during July and September 2013 (Table 1, Fig. 1). After collecting the samples, 10% v/v soda (saturated CO_2 in water) was added immediately to avoid gut evacuation. Fresh zooplankton were sorted by each taxon/species and copepodid stage (for copepods) and placed into 30 mL GF/F filtered sea water. The following species/taxa were used for the experiments : copepods (*Calanus glacialis* C5, *C. hyperboreus* C6F, *Eucalanus bungii* C6F, *Metridia longa* C6F, *Neocalanus cristatus* C5, *N. flemingeri* C5 and *N. plumchrus* C5), appendicularians (*Oikopleura vanhoeffeni*), barnacle larvae, amphipods (*Themisto libellula*), euphausiids and decapod larvae (hermit crab). After several-hours incubation, fecal pellets were collected by Pasteur pipette, preserved with 5% v/v borax-buffered formalin and stored in a refrigerator. In the land laboratory, morphotype identification and length measurement were made for each fecal pellet following the same procedure mentioned above.

Results

Hydrography

The trap mooring depth was mainly stable between 180–190 m (mean : 184 m, first year) and 250–260 m (mean : 256 m, second year) but temporarily deepened to approximately 300 m in July 2012 (Fig. 2a). This change was thought to be caused by the temporal strong current velocity at that time (Onodera et al., 2015). Temperature at the sediment trap ranged from -1.56°C to -0.07°C , and rapid changes in temperature were reflected by the changes in the depth of the trap (Fig. 2a, 2b). The current velocity simulated by the ocean circulation model showed a slow current around the trap ($< 2.7 \text{ cm s}^{-1}$ [mean 1.0 cm s^{-1}] at 188 m and $< 1.2 \text{ cm s}^{-1}$ [mean 0.3 cm s^{-1}] at 275 m) (Fig. 2c). From two time CTD casts at the station, four water masses were identified at 0–500 m in the water column : i.e., the Surface Mixed Layer (SML, 0–25 m), Pacific Summer Water (PSW, 25–100 m), Pacific Winter Water (PWW, 100–250 m) and the Atlantic Water (AW, > 250 m) (Fig. 2d, 2e) (McLaughlin et al., 2011). The water mass was PWW at 180–190 m depth in the first year, and AW was at 250–260 m depth in the second year.

The sea ice concentration around St. NAPt showed clear seasonal changes. Sea ice decreased from late July, melted completely from mid-August to early October, increased rapidly in mid-October and covered completely from November to June (Fig. 3a). High chl. *a* was observed during the open water period (August–September) (Fig. 3a). The total mass flux ranged from $0.1\text{--}215.9 \text{ mg DM m}^{-2} \text{ day}^{-1}$, showed large seasonality and peaked during November–December in both years (Fig. 3a). At St. NAPt, the daylight hours showed great seasonal changes : polar night occurred from mid-

Table 1. Information of ship-board experiments in the western Arctic Ocean during July–September 2013. Bl : Barnacle larvae, Cg : *Calanus glacialis*, Ch : *Calanus hyperboreus*, Dl : decapod larvae, Eb : *Eucalanus bungii*, Eu : euphausiids, Ml : *Metridia longa*, Nc : *Neocalanus cristatus*, Nf : *Neocalanus flemingeri*, Np : *Neocalanus plumchrus*, Tl : *Themisto libellula*, Ov : *Oikopleura vanhoeffeni*.

Sampling date	Position		Net towed depth (m)	Taxa/species
	Lat. ($^\circ\text{N}$)	Lon. ($^\circ\text{W}$)		
7 July 2013	65–29	168–55	51	Bl, Cg, Eb, Nc, Np, Tl
10 July 2013	69–48	166–19	40	Bl, Cg, Eb, Eu, Nf, Np, Tl, Ov
12 July 2013	70–44	164–36	31	Bl, Cg, Np
13 July 2013	70–37	161–33	31	Bl, Cg, Nf, Np, Ov
14 July 2013	70–06	164–54	35	Bl, Cg, Eu, Nc, Nf, Np, Tl, Ov
14 July 2013	70–24	163–30	30	Bl, Cg, Eu, Nf, Np, Ov
15 July 2013	68–31	168–32	46	Bl, Cg, Eb, Nc, Nf, Np, Ov
16 July 2013	67–38	168–57	45	Bl, Cg, Dl, Eb, Eu, Nc, Nf, Np, Tl, Ov
31 Aug. 2013	65–41	168–17	38	Ov
31 Aug. 2013	66–30	168–45	48	Ov
3 Sep. 2013	71–25	157–31	114	Ch, Eu, Ml
27 Sep. 2013	73–09	162–17	150	Ch, Ml

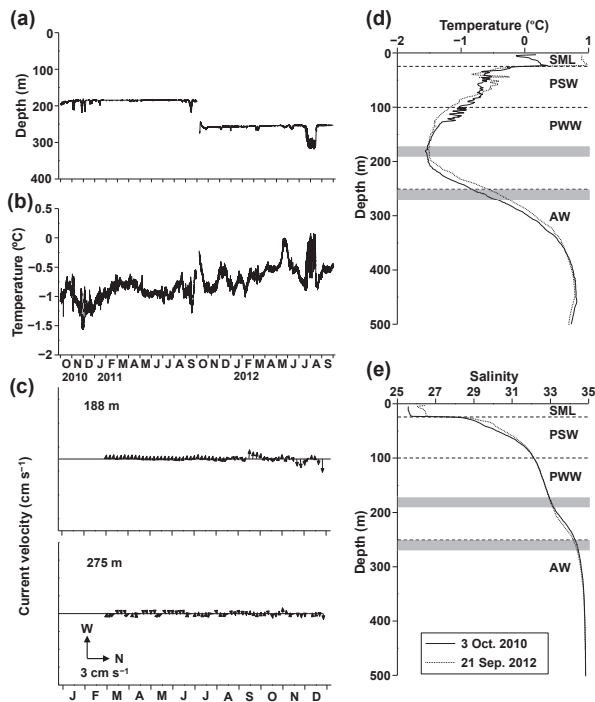


Fig. 2. Seasonal changes in depth (a) and temperature (b) monitored by the moored sediment trap at St. NAPt during October 2010 to September 2012. Current velocity at 188 m and 275 m of St. NAPt (c) estimated by a physical ocean general circulation model. Temperature (d) and salinity (e) observed from CTD casts at St. NAPt on 30 October 2010 and 21 September 2012. Shades indicate the trap depths (180–190 m and 250–260 m). SML : Surface Mixed Layer (0–25 m), PSW : Pacific Summer Water (25–100 m), PWW : Pacific Winter Water (100–250 m) and AW : Atlantic Water (>250 m).

November to early February, and the midnight Sun occurred from early May to mid-August (Fig. 3b).

Fecal pellets

For the fecal pellets collected by sediment trap, oval and spherical pellets were dominant and accounted for 60% and 30% of the annual mean number, respectively (Fig. 3c). The occurrence of brown-colored pellets showed clear seasonality and occurred only during July–August, reaching 80% of the fecal pellet number at that time. The fecal pellet length varied with each type: oval pellets were 0.07–0.88 mm ($\text{mean} \pm \text{SD} = 0.26 \pm 0.12$ mm), cylinder pellets were 0.25–1.20 mm (0.58 ± 0.26 mm), spherical pellets were 0.04–0.26 mm (0.09 ± 0.03 mm) and brown-colored pellets were 0.09–1.02 mm (0.25 ± 0.08 mm) (Fig. 4). Seasonal changes in the pellet size were slightly observed, but were not significant ($p > 0.05$, Tukey–Kramer Test).

The ship-board experiments results showed that oval and cylinder pellets were egested by various species, brown-colored pellets were egested only by the amphipod *T. libellula*, and spherical pellets were not egested by any species (Fig. 5). Oval pellets were egested by appendicularians (*O. van-*

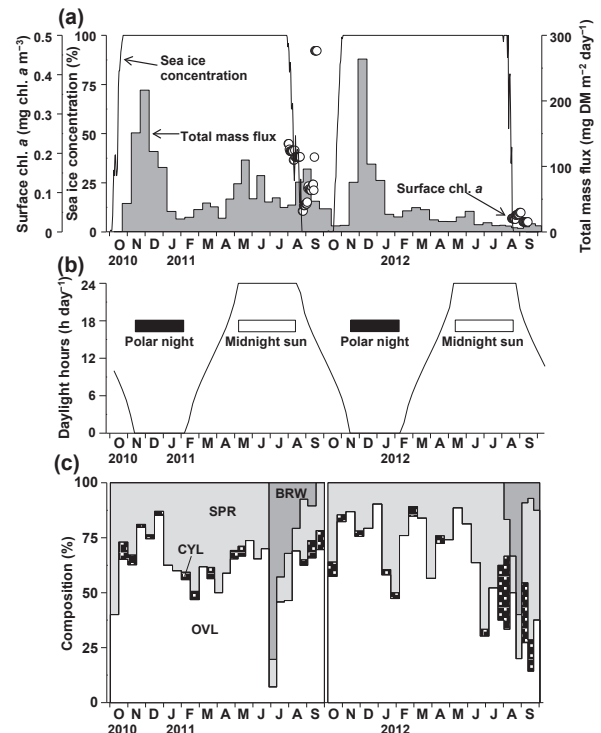


Fig. 3. Seasonal changes in sea ice concentration, surface chl. *a* (from satellite) and total mass flux (a), daylight hours (b) and composition in number of four types of fecal pellets (c). Based on morphology, four types of fecal pellets were identified: oval (OVL), cylinder (CYL), spherical (SPR) and brown-colored (BRW) types.

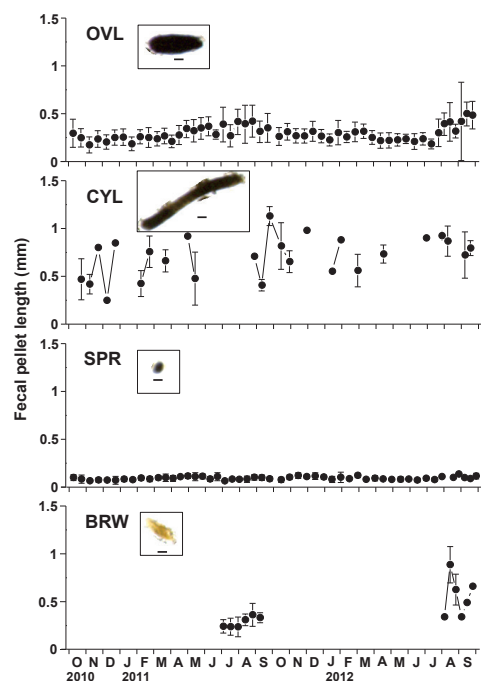


Fig. 4. Seasonal changes in length of fecal pellets. Symbols and bars indicate means and standard deviations, respectively. OVL : oval, CYL : cylinder, SPR : spherical and BRW : brown-colored type. Example pictures are shown for each morphological type. Scale bars : 100 μm .

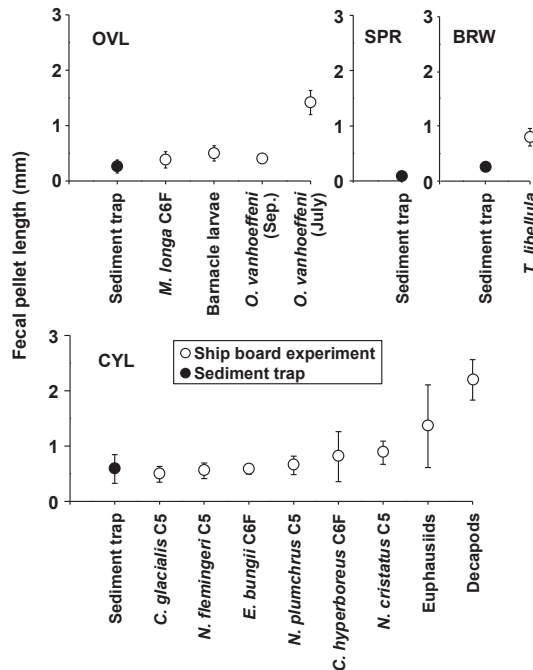


Fig. 5. Fecal pellet length collected by sediment trap or those egested by each species observed for ship-board experiments during July to September 2013. Symbols and bars indicate means and standard deviations, respectively.

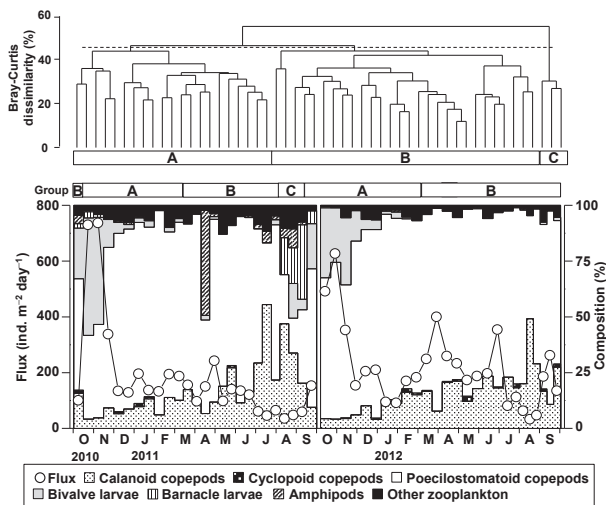


Fig. 6. Based on zooplankton flux, three groups (A-C) were identified by cluster analysis for zooplankton swimmers at St. NApT (upper panel). Seasonal changes in zooplankton flux and taxonomic composition of zooplankton group (lower panel).

hoeffeni), copepods (*M. longa*) and barnacle larvae (Fig. 5). The cylinder pellets were egested by six copepods (*C. glacialis* C5, *C. hyperboreus* C6F, *E. bungii* C6F, *N. cristatus* C5, *N. flemingeri* C5 and *N. plumchrus* C5), euphausiids and decapod larvae. The fecal pellet length in the experiment was similar to or larger than those by the sediment trap (Fig. 5).

Zooplankton community

The zooplankton flux ranged from 35–739 ind. m⁻² day⁻¹ and was greater during October–November in both years (Fig. 6). For taxonomic composition, the poecilostomatoid copepods were dominant (69% of the annual mean flux) followed by calanoid copepods (17%) (Fig. 6). From the viewpoint of seasonality, barnacle and bivalve larvae were abundant during August–September 2011 and August–November of 2010 and 2011, respectively (Fig. 6). It was remarkable that both barnacle and bivalve larvae were absent during August–September in 2012.

Based on the zooplankton flux, the 56 zooplankton swimmer samples were largely classified into three groups (A–C) (Fig. 6). The occurrence of each group showed clear seasonality. For both years, group A was observed from September to February and group B occurred from March to July (Fig. 6). Group C was observed in August 2011, but was not seen in 2012.

From the SIMPER analysis, the dominant poecilostomatoid copepod *Oncaea parila* contributed to separate groups A–C and B–C (Table 2). For calanoid copepods, *C. hyperboreus*, *Paraeuchaeta glacialis*, *Heterorhabdus norvegicus*, *M. longa* and *Scaphocalanus brevicornis* were identified to characterize each group. Bivalve larvae characterized separating groups A–B and A–C, and barnacle larvae separated groups A–C and B–C (Table 2).

For the abundance of each taxon, calanoid copepods, poecilostomatoid copepods, total copepods, barnacle larvae, bivalve larvae and total zooplankton were significantly varied between groups (Table 3). Group A was characterized by the dominance of total zooplankton, total copepods, poecilostomatoid copepods and bivalve larvae, and group C was characterized by the dominance of amphipods and barnacle larvae.

Discussion

Fecal pellets

Zooplankton fecal pellets have roles in the acceleration of the vertical material flux to the deep-sea and as food resources for detritivorous zooplankton (Taguchi and Saino, 1998; Turner, 2002). Fecal pellets were also thought to be food resources for copepods and appendicularians in the Arctic Ocean (Sampei et al., 2009b). Especially, small poecilostomatoid copepods are known to attach on fecal pellets for grazing (coprophagy) (Steinberg et al., 1998), which results in the comminution (coprorhexy) of the fecal pellets (Poulsen and Kjørboe, 2005). In this study, the detritivorous copepods (*Oncaea* spp.) numerically dominated (Fig. 6). This fact suggested that the fecal pellets collected by the

Table 2. Ranking of taxa according to their relative contribution (%) to the multivariate similarities between pairs of the mesozooplankton groups (A–C) identified by the cluster analysis for mesozooplankton community collected by the sediment trap at St. NAPt in the western Arctic Ocean from October 2010 to September 2012 (cf. Fig. 6).

Group	A	B
B	Bivalve larvae (12%) <i>Limacina helicina</i> (7%) <i>Scaphocalanus brevicornis</i> (5%) <i>Calanus hyperboreus</i> (5%)	
C	<i>Oncaea parila</i> (12%) Barnacle larvae (10%) Bivalve larvae (8%) <i>Paraeuchaeta glacialis</i> (7%)	Barnacle larvae (12%) <i>Oncaea parila</i> (10%) <i>Metridia longa</i> (6%) <i>Heterorhabdus norvegicus</i> (6%)

Table 3. Dominant mesozooplankton fluxes collected by the sediment trap at St. NAPt in the western Arctic Ocean from October 2010 to September 2012. Values are means and standard deviations of the three groups identified by Bray–Curtis dissimilarity (cf. Fig. 6). Differences between groups were tested by a one-way ANOVA and Tukey–Kramer test. Any groups not connected by the underlines were significantly different ($p < 0.05$). Numbers in the parentheses indicate the number of samples included for each group. *: $p < 0.05$, **: $p < 0.01$, ***: $p < 0.001$, NS: not significant.

Species/Taxa	Flux (ind. m ⁻² day ⁻¹)			one-way ANOVA	Tukey–Kramer Test
	A (21)	B (28)	C (3)		
Copepods					
Calanoid copepods	19.4±8.5	27.6±14.0	15.4±2.7	*	Not detected
Cyclopoid copepods	0.6±1.0	0.7±1.0	0	NS	
Poecilostomatoid copepods	175.4±93.1	119.2±83.0	11.9±7.0	**	C <u>B</u> A
Total copepods	195.4±98.1	147.4±92.7	27.4±4.3	*	C <u>B</u> A
Amphipods	0.8±0.8	3.3±13.4	2.1±1.8	NS	
Barnacle larvae	2.0±5.0	0.1±0.4	11.4±7.7	***	B <u>A</u> C
Bivalve larvae	61.8±113.2	1.2±4.4	3.5±3.9	*	B <u>C</u> A
Total zooplankton	270.7±203.1	158.4±92.5	49.0±11.8	**	C <u>B</u> A

sediment trap in this study were affected by coprophagy and coprorhexy of *Oncaea* spp.

Morphology (size, shape and color) of fecal pellets varies with the egested taxa/species and their food components (Riser et al., 2002; Wilson et al., 2008). In this study, fecal pellets were separated into four types, and oval and spherical pellets were numerically dominant throughout the year (Fig. 3c). From the ship-board experiments, the oval pellets were egested by appendicularians (*O. vanhoeffeni*), copepod *M. longa* and barnacle larvae (Fig. 5). Many individuals of *M. longa* were collected by the sediment trap (Matsuno et al., 2014, 2015). *Metridia longa* are known to have no diapause phase in the Arctic Ocean and continue grazing throughout the year (Båmstedt and Ervik, 1984; Grønvik and Hopkins, 1984). These facts suggested that the oval fecal pellets egested by *M. longa* may have been included in the sediment trap samples. *Oikopleura vanhoeffeni* also occurs during July–September and actively grazes on the ice-edge bloom (Acuña et al., 1999). From the egestion experiments, the fecal pellet length egested by *O. vanhoeffeni* was large, especially that in July, which was larger than in September (Fig.

5). This result was due to the differences in the body length of the specimens used for the experiments between the sampling dates (trunk length was 3.3 mm in July versus 0.5 mm in September). Thus, oval pellets in the sediment trap may have been egested by *M. longa* and *O. vanhoeffeni*.

While the composition of the cylinder pellets was low in the sediment trap samples (Fig. 3c), various species (six copepods, euphausiids and decapod larvae) egested cylinder fecal pellets in the ship-board experiments (Fig. 5). The morphology of fecal pellets is known to vary with taxa; copepods egest cylinder pellets, euphausiids egest cylinder or filiform pellets and appendicularians egest oval pellets (Riser et al., 2002; Wilson et al., 2008). The results of this study (copepods, euphausiids and decapod larvae egested cylinder pellets) corresponded with the previous study. While the fecal pellet length of the cylinder pellet showed large seasonal fluctuations, a significant seasonal pattern was not detected (Fig. 4). These results were caused by the mixture of the cylinder pellets, which were egested by various taxa/species.

Spherical pellets composed 30% of the total pellet number (Fig. 3c), while no species egested spherical pellets during the

ship-board experiments (Fig. 5). Small spherical pellets (<100 µm) are known to be egested by copepod nauplii and microzooplankton (e.g., radiolarians) (Gowing and Silver, 1985 ; Gowing et al., 2001 ; Turner, 2002). Because the mean length of the spherical pellets in this study was 90 µm, they might be egested by copepod nauplii and microzooplankton. An alternative explanation is that the large-sized other morphotype fecal pellets might be broken into small spherical pellets through the decomposition by bacteria (Ploug et al., 1999 ; Goldthwait et al., 2005) and coprophagy or coprorhexy by poecilostomatoid copepods (Smetacek, 1980 ; Lampitt et al., 1990) during the course of sinking.

Brown-colored pellets occurred during a limited season (July–August) (Fig. 3c), and only the amphipod *T. libellula* egested the brown-colored pellets during the ship-board experiments (Fig. 5). Macro-sized amphipods can feed on various food, from small copepods to marine snow (Lampitt et al., 1993). Because amphipods can feed on various food items, changes in fecal pellet morphotype with food types were reported for the sea ice associated amphipod *Gammarus wilkitzkii*. Thus, they egested yellow-green colored pellets during ice-algae feeding, while they egested brown-colored pellets during carnivorous feeding (Werner, 2000). These facts suggested that the brown-colored pellets collected by the sediment trap in this study may have been egested by carnivorous amphipods. The seasonal restricted peak of brown-colored pellets (July–August) would be a reflection of the high grazing activity of amphipods in the upper layer during that time. Because this period corresponded with the timing of the ice-edge bloom (July–August) (Fig. 3a), the grazing intensities were expected to be high not only for herbivores (copepods and appendicularians) but also for carnivores (amphipods).

Zooplankton community

Within the zooplankton taxa, the occurrence of meroplankton (barnacle and bivalve larvae) showed clear seasonality. Barnacle larvae were abundant during August–September, and bivalve larvae occurred during August–November (Fig. 6). The benthic adults of these larvae are known to distribute mainly in the Chukchi Sea shelf (Feder et al., 2007 ; Schonberg et al., 2014). Because the bottom depth was deep (ca. 1,900 m) at St. NAPt, the larvae released by sympatric benthic adults may not be the case in this study. Barnacle (*Balanus crenatus*) adults release their larvae during phytoplankton blooms (Crisp, 1962 ; Clare and Walker, 1986), and the larvae spend two to three weeks in the water column before settling to the sea bottom (Herz, 1933). Bivalves are also known to release their larvae during the two months after a phytoplankton bloom (Lammens, 1967). The released larvae by benthic adults in the shelf during the phytoplankton bloom to post-bloom might be transported to St. NAPt. The current forcing horizontal transport of various zooplankton

from Chukchi Sea shelf to the basin has well known (Ashjian et al., 2005). The later occurrence period of barnacle and bivalve larvae (August–November) than the open water bloom (August–September) may be a reflection of the northward transport of larvae to St. NAPt in this study.

Seasonal change was also the case for holoplankton (Fig. 6). Seasonal changes in this zooplankton group were governed by various calanoid copepods (Table 2). For calanoid copepods at St. NAPt, *C. hyperboreus*, *H. norvegicus*, *M. longa* and *P. glacialis* were dominant, and seasonal changes in the flux of each species was related to their vertical migration behavior (in terms of diel, seasonal and ontogenetic sense) (Matsuno et al., 2014, 2015). Thus, seasonal changes in the zooplankton community in this study were determined by two factors : 1) the occurrences of meroplanktonic larvae transported from shelf region and 2) seasonal changes in the vertical migration intensity of holoplanktonic calanoid copepods.

For the inter-annual changes in the zooplankton community, barnacle and bivalve larvae were abundant during August–September 2011, while they were both absent during August–September 2012 (Fig. 6). Because these larvae may be transported from the shelf region, their absence during summer 2012 suggested that inter-annual changes in the current flow in the upper layer of St. NAPt may have occurred, i.e., weakened current from the shelf in summer 2012. For the water current around St. NAPt, the northward current dominated throughout the year (Fig. 1), and a meso-scale eddy (diameter is 60–70 km) frequently occurred off of Barrow during the open water season (Kawaguchi et al., 2012 ; Watanabe et al., 2014). Because the eddy included high amounts of particles and zooplankton and was transported westward by the Beaufort Gyre, the presence of the eddy increased the vertical material flux at St. NAPt during autumn (Watanabe et al., 2014).

Based on the same trap samples of this study, inter-annual changes in the total mass flux and the diatom community were reported (Onodera et al., 2015). They showed that the total mass flux during summer 2012 was lower than that in summer 2011 (cf. Fig. 3a), and the ice-algae *Fossula arctica* dominated in the diatom community during summer 2011, while it was absent in summer 2012 (Onodera et al., 2015). These inter-annual changes were likely caused by the inflow of the oligotrophic water mass from the Canada basin to the upper layer of St. NAPt during summer 2012 (Onodera et al., 2015 ; Watanabe et al., 2015). Because the bottom depth was deep for the Canada basin (ca. 3,000 m), the low abundance of barnacle and bivalve larvae was expected for the water mass that originated from there. Therefore, inter-annual changes in barnacle and bivalve larvae (no occurrence during summer 2012, Fig. 6) was caused by the water mass inflow from the Canada basin, which contained few benthic

larvae, during summer 2012 (Onodera et al., 2015 ; Watanabe et al., 2015).

Conclusion

Through this study, the following two points were evidence of the biological application of the sediment trap samples. First, the water mass formation in the upper layer can alter transport the zooplankton flux to a deep layer. Second, the feeding intensity of the surface zooplankton community can affect the vertical flux of fecal pellets to the deep-sea in the Arctic Ocean.

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Literature cited

- Acuña, J.L., Deibel, D., Bochdansky, A.B. and Hatfield, E. (1999) *In situ* ingestion rates of appendicularian tunicates in the north-east water Polynya (NE Greenland). *Mar. Ecol. Prog. Ser.*, **186**, 149–160.
- Ashjian, C.J., Campbell, R.G., Welch, H.E., Butler, M. and Keuren, D.V. (2003) Annual cycle in abundance, distribution, and size in relation to hydrography of important copepod species in the western Arctic Ocean. *Deep-Sea Res. I*, **50**, 1235–1261.
- Ashjian, C.J., Gallagher, S.M. and Plourde, S. (2005) Transport of plankton and particles between the Chukchi and Beaufort Seas during summer 2002, described using a Video Plankton Recorder. *Deep-Sea Res. II*, **52**, 3259–3280.
- Båmstedt, U. and Ervik, A. (1984) Local variations in size and activity among *Calanus finmarchicus* and *Metridia longa* (Copepoda, Calanoida) overwintering on the west coast of Norway. *J. Plankton Res.*, **6**, 843–857.
- Brodsky, K.A. (1967) *Calanoida of the Far-eastern Seas and Polar Basin of the USSR*. Israel Program Scientific Translation, Jerusalem.
- Buesseler, K.O., Antia, A.N., Chen, M., Fowler, S.W., Gardner, W.D., Gustafsson, O., Harada, N., Michaelas, A.F., van der Loeff, M.R., Sarin, M., Steinberg, D.K. and Trull, T. (2007) An assessment of the use of sediment traps for estimating upper ocean particle fluxes. *J. Mar. Res.*, **65**, 345–416.
- Clare, A.S. and Walker, G. (1986) Further studies on the control of the hatching process in *Balanus balanoides* (L.). *J. Exp. Mar. Biol. Ecol.*, **97**, 295–304.
- 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. doi : 10.1029/2007GL031972.
- Crisp, D.J. (1962) Release of larvae by barnacles in response to the available food supply. *Anim. Behav.*, **10**, 382–383.
- Feder, H.M., Jewett, S.C. and Blanchard, A.L. (2007) Southern Chukchi Sea (Alaska) macrobenthos. *Polar Biol.*, **30**, 261–275.
- 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.
- Forbes, J.R., Macdonald, R.W., Carmack, E.C., Iseki, K. and O'Brien, M.C. (1992) Zooplankton retained in sequential sediment traps along the Beaufort Sea shelf break during winter. *Can. J. Fish. Aquat. Sci.*, **49**, 663–670.
- Frost, B.W. (1974) *Calanus marshallae*, a new species of calanoid copepod closely allied to the sibling species *C. finmarchicus* and *C. glacialis*. *Mar. Biol.*, **26**, 77–99.
- Frost, B.W. (1989) A taxonomy of the marine calanoid copepod genus *Pseudocalanus*. *Can. J. Zool.*, **67**, 525–551.
- Goldthwait, S.A., Carlson, C.A., Henderson, G.K. and Alldredge, A.L. (2005) Effects of physical fragmentation on remineralization of marine snow. *Mar. Ecol. Prog. Ser.*, **305**, 59–65.
- Gowing, M.M. and Silver, M.W. (1985) Minipellets : A new and abundant size class of marine fecal pellets. *J. Mar. Res.*, **43**, 395–418.
- Gowing, M.M., Garrison, D.L., Kunze, H.B. and Winchell, C.J. (2001) Biological components of Ross Sea short-term particle fluxes in the austral summer of 1995–1996. *Deep-Sea Res. I*, **48**, 2645–2671.
- Grebmeier, J.M. (2012) Shifting patterns of life in the Pacific Arctic and sub-Arctic Seas. *Annu. Rev. Mar. Sci.*, **4**, 63–78.
- Grønvik, S. and Hopkins, C.C.E. (1984) Ecological investigations of the zooplankton community of Balsfjorden, northern Norway : generation cycle, seasonal vertical distribution, and seasonal variations in body weight and carbon and nitrogen content of the copepod *Metridia longa* (Lubbock). *J. Exp. Mar. Biol. Ecol.*, **80**, 93–107.
- Hansen, B. and Bech, G. (1996) Bacteria associated with a marine planktonic copepod in culture. I. Bacterial genera in seawater, body surface, intestines and fecal pellets and succession during fecal pellet degradation. *J. Plankton Res.*, **18**, 257–273.
- Heron, G.A., English, T.S. and Damkaer, D.M. (1984) Arctic Ocean Copepoda of the genera *Lubbockia*, *Oncaea*, and *Epicalymma* (Poecilostomatoida : Oncaeidae), with remarks on distributions. *J. Crust. Biol.*, **4**, 448–490.
- Herz, L.E. (1933) The morphology of the later stages of *Balanus crenatus* Bruguiere. *Biol. Bull.*, **64**, 432–442.
- Hopcroft, R.R., Kosobokova, K.N. and Pinchuk, A.I. (2010) Zooplankton community patterns in the Chukchi Sea during summer 2004. *Deep-Sea Res. II*, **57**, 27–39.
- Kawaguchi, Y., Itoh, M. and Nishino, S. (2012) Detailed survey of a large baroclinic eddy with extremely high temperatures in the western Canada Basin. *Deep-Sea Res. I*, **66**, 90–102.
- Lammens, J.J. (1967) Growth and reproduction in a tidal flat population of *Macoma balthica* (L.). *Neth. J. Sea Res.*, **3**, 315–382.

- Lampitt, R.S., Noji, T. and von Bodungen, B. (1990) What happens to zooplankton fecal pellets? Implications for material flux. *Mar. Biol.*, **104**, 15–23.
- Lampitt, R.S., Wishner, K.F., Turley, C.M. and Angel, M.V. (1993) Marine snow studies in the northeast Atlantic Ocean : distribution, composition and role as a food source for migrating plankton. *Mar. Biol.*, **116**, 689–702.
- Makabe, R., Hattori, H., Sampei, M., Ota, Y., Fukuchi, M., Fortier, L. and Sasaki, H. (2010) Regional and seasonal variability of zooplankton collected using sediment traps in the southeastern Beaufort Sea, Canadian Arctic. *Polar Biol.*, **33**, 257–270.
- 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. doi : 10.1029/2009JC005436.
- 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., Fujiwara, A., Onodera, J., Watanabe, E., Imai, I., Chiba, S., Harada, N. and Kikuchi, T. (2014) Seasonal changes in mesozooplankton swimmers collected by sediment trap moored at a single station on the Northwind Abyssal Plain in the western Arctic Ocean. *J. Plankton Res.*, **36**, 490–502.
- Matsuno, K., Yamaguchi, A., Fujiwara, A., Onodera, J., Watanabe, E., Harada, N. and Kikuchi, T. (2015) Seasonal changes in the population structure of dominant planktonic copepods collected using a sediment trap moored in the western Arctic Ocean. *J. Nat. Hist.*, **49**, 2711–2726.
- McLaughlin, F., Carmack, E., Proshutinsky, A., Krishfield, R.A., Guay, C., Yamamoto-Kawai, M., Jackson, J.M. and Williams, B. (2011) The rapid response of the Canada Basin to climate forcing : From bellwether to alarm bells. *Oceanography*, **24**, 146–159.
- Miller, C.B. (1988) *Neocalanus flemingeri*, a new species of Calanidae (Copepoda : Calanoida) from the subarctic Pacific Ocean, with a comparative redescription of *Neocalanus plumchrus* (Marukawa) 1921. *Prog. Oceanogr.*, **20**, 223–273.
- Onodera, J., Watanabe, E., Harada, N. and Honda, M.C. (2015) Diatom flux reflects water-mass conditions on the southern Northwind Abyssal Plain, Arctic Ocean. *Biogeosciences*, **12**, 1373–1385.
- Ota, Y., Hattori, H., Makabe, R., Sampei, M., Tanimura, A. and Sasaki, H. (2008) Seasonal changes in nauplii and adults of *Calanus hyperboreus* (Copepoda) captured in sediment traps, Amundsen Gulf, Canadian Arctic. *Polar Sci.*, **2**, 215–222.
- Ploug, H., Grossart, H.P., Azam, F. and Jorgensen, B.B. (1999) Photosynthesis, respiration, and carbon turnover in sinking marine snow from surface waters of Southern California Bight : implications for the carbon cycle in the ocean. *Mar. Ecol. Prog. Ser.*, **179**, 1–11.
- Poulsen, L.K. and Kiørboe, T. (2005) Coprophagy and coprophagy in the copepods *Acartia tonsa* and *Temora longicornis* : clearance rates and feeding behavior. *Mar. Ecol. Prog. Ser.*, **299**, 217–227.
- Reynolds, R.W., Rayner, N.A., Smith, T.M., Stokes, D.C. and Wang, W. (2002) An improved in situ and satellite SST analysis for climate. *J. Climate*, **15**, 1609–1625.
- Riser, C.W., Wassmann, P., Olli, K., Pasternak, A. and Arashkevich, E. (2002) Seasonal variation in production, retention and export of zooplankton faecal pellets in the marginal ice zone and central Barents Sea. *J. Mar. Sys.*, **38**, 175–188.
- Sampei, M., Sasaki, H., Hattori, H., Forest, A. and Fortier, L. (2009a) Significant contribution of passively sinking copepods to the downward export flux in Arctic waters. *Limnol. Oceanogr.*, **54**, 1894–1900.
- Sampei, M., Forest, A., Sasaki, H., Hattori, H., Makabe, R., Fukuchi, M. and Fortier, L. (2009b) Attenuation of the vertical flux of copepod fecal pellets under Arctic sea ice : evidence for an active detrital food web in winter. *Polar Biol.*, **32**, 225–232.
- Sampei, M., Sasaki, H., Forest, A. and Fortier, L. (2012) A substantial export flux of particulate organic carbon linked to sinking dead copepods during winter 2007–2008 in the Amundsen Gulf (southeastern Beaufort Sea, Arctic Ocean). *Limnol. Oceanogr.*, **57**, 90–96.
- Schonberg, S.V., Clarke, J.T. and Dunton, K.H. (2014) Distribution, abundance, biomass and diversity of benthic infauna in the Northeast Chukchi Sea, Alaska : Relation to environmental variables and marine mammals. *Deep-Sea Res. II*, **102**, 144–163.
- Smetacek, V.S. (1980) Zooplankton standing stock, copepod fecal pellets and particulate detritus in Kiel Bight. *Est. Coast. Mar. Sci.*, **11**, 477–490.
- Steinberg, D.K., Pilskaln, C.H. and Silver, M.W. (1998) Contribution of zooplankton associated with detritus to sediment trap ‘swimmer’ carbon in Monterey Bay, California, USA. *Mar. Ecol. Prog. Ser.*, **164**, 157–166.
- 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. doi : 10.1029/2007GL029703.
- Taguchi, S. and Saino, T. (1998) Net zooplankton and the biological pump off Sanriku, Japan. *J. Oceanogr.*, **54**, 573–582.
- Turner, J.T. (2002) Zooplankton fecal pellets, marine snow and sinking phytoplankton blooms. *Aquat. Microb. Ecol.*, **27**, 57–102.
- Urban-Rich, J., Hansell, D.A. and Roman, M.R. (1998) Analysis of copepod fecal pellet carbon using a high temperature combustion method. *Mar. Ecol. Prog. Ser.*, **171**, 199–208.
- Watanabe, E., Onodera, J., Harada, N., Honda, M.C., Kimoto, K., Kikuchi, T., Nishino, S., Matsuno, K., Yamaguchi, A., Ishida, A. and Kishi, M.J. (2014) Enhanced role of eddies in the Arctic marine biological pump. *Nat. Commun.*, **5**, 3950. doi : 10.1038/ncomms4950.
- Watanabe, E., Onodera, J., Harada, N., Aita, M.N., Ishida, A. and Kishi, M.J. (2015) Wind-driven interannual variability of sea ice algal production over the western Arctic Chukchi Borderland. *Biogeosciences*, **12**, 6147–6168.
- Werner, I. (2000) Faecal pellet production by Arctic under-ice amphipods—transfer of organic matter through the ice/water interface. *Hydrobiologia*, **426**, 89–96.
- Wilson, S.E., Steinberg, D.K. and Buesseler, K.O. (2008) Changes in fecal pellet characteristics with depth as indicators of zooplankton repackaging of particles in the mesopelagic zone of the subtropical and subarctic North Pacific Ocean. *Deep-Sea Res. II*, **55**, 1636–1647.