



Title	Ingestion rates and grazing impacts of Arctic and Pacific copepods in the western Arctic Ocean during autumn
Author(s)	Matsuno, Kohei; Fujiwara, Amane; Hirawake, Toru; Yamaguchi, Atsushi
Citation	北海道大学水産科学研究彙報, 69(2), 93-102
Issue Date	2019-12-09
DOI	10.14943/bull.fish.69.2.93
Doc URL	http://hdl.handle.net/2115/76384
Type	bulletin (article)
File Information	bull.fish.69.2.93.pdf



[Instructions for use](#)

Ingestion rates and grazing impacts of Arctic and Pacific copepods in the western Arctic Ocean during autumn

Kohei MATSUNO¹⁾²⁾³⁾, Amane FUJIWARA⁴⁾, Toru HIRAWAKE²⁾⁵⁾ and Astushi YAMAGUCHI¹⁾²⁾

(Received 14 August 2019, Accepted 17 September 2019)

Abstract

Increasing numbers of Pacific copepods are being transported from the Bering Sea to the Arctic Ocean, so there is clear potential to affect the structure and composition of the Arctic food web. We investigated the grazing impacts of Arctic and Pacific copepods in the western Arctic Ocean using shipboard experiments during autumn. Ingestion rates for both Arctic and Pacific species were low and linked to low food availability. The ingestion rates varied with species, but were not related to chlorophyll *a*. The maximum ingestion rates calculated by the Michaelis–Menten equation were higher in the Arctic species (3.6% body carbon day⁻¹) than in the Pacific species (0.10% body carbon day⁻¹). The community grazing impacts were 0–0.57% remove day⁻¹, and the Pacific copepods contributed 0.1–1.7% for this parameter. Even if Pacific copepods are transported into the Arctic Ocean and ingest the natural protist assemblage, their impact is spatially and seasonally limited, and, at present, Pacific copepods are unlikely to cause a shift in the protist biomass of the western Arctic Ocean during autumn.

Key words : ingestion rate, grazing impact, Pacific copepods, Arctic Ocean

Introduction

Zooplankton are secondary producers in the marine ecosystem of the western Arctic Ocean and are an important food resource for fishes and marine mammals (Lowry et al., 2004 ; Nakano et al., 2016). In the western Arctic Ocean, the mesozooplankton biomass is dominated by Arctic copepods, especially *Calanus glacialis*, *Calanus hyperboreus*, *Metridia longa* and *Pseudocalanus* spp. Pacific copepods, including *Calanus marshallae*, *Neocalanus cristatus*, *Neocalanus flemingeri*, *Neocalanus plumchrus*, *Eucalanus bungii* and *Metridia pacifica*, are also abundant in the Chukchi Sea owing to the inflow of Pacific water through the Bering Strait. The Pacific water is a mixture of Anadyr water, Bering Shelf water and Alaskan Coastal water (Coachman et al., 1975). Because the origin of Pacific copepods is different from these waters, the spatial distribution of the zooplankton community structure is indicative of water masses in the Chukchi Sea

(Hopcroft et al., 2010 ; Ershova et al., 2015a ; Pinchuk and Eisner, 2017).

The shelf region of the western Arctic Ocean is shallow (ca. 50 m depth), and almost all of the primary production in the water column sinks to the sea floor without removal by zooplankton (Grebmeier et al., 1988). In recent years, the inflow of Pacific water from the Bering Sea into the western Arctic Ocean has increased, based on mooring observations in the Bering Strait (Woodgate et al., 2010, 2012). This water transports not only heat flux but also Pacific copepods, facilitating the northward shift of zooplankton and increases the abundance of Pacific copepods in Arctic waters (Matsuno et al., 2011 ; Nelson et al., 2014 ; Ershova et al., 2015b). The abundance of Pacific copepods increased slightly from 1946 to 2012 (Ershova et al., 2015b), and Pacific copepod abundance in southern areas of the Chukchi Sea has increased almost 10-fold in recent years (Matsuno et al., 2011). The grazing impact and effect on protist diversity of this changing

¹⁾ Laboratory of Marine Biology, Graduate School of Fisheries Sciences, Hokkaido University, 3-1-1 Minato-cho, Hakodate, Hokkaido 041-8611, Japan

(北海道大学大学院水産科学研究院海洋生物学分野)

²⁾ Arctic Research Centre, Hokkaido University, Kita-21 Nishi-11 Kita-ku, Sapporo, Hokkaido, 001-0021, Japan

(北海道大学北極域研究センター)

³⁾ Antarctic Climate & Ecosystems Cooperative Research Centre, 20 Castray Esplanade, Battery Point, Tasmania 7004, Australia

(オーストラリア南極気候生態系研究協力センター)

⁴⁾ Institute of Arctic Climate and Environment Research, Japan Agency for Marine–Earth Science and Technology, 2-15 Natsushima-cho, Yokosuka, Kanagawa 237-0061, Japan

(海洋研究開発機構北極環境変動総合研究センター)

⁵⁾ Laboratory of Marine Environment and Resource Sensing, Graduate School of Fisheries Sciences, Hokkaido University, 3-1-1 Minato-cho, Hakodate, Hokkaido 041-8611, Japan

(北海道大学大学院水産科学研究院海洋計測学分野)

zooplankton community are poorly understood.

For herbivorous zooplankton, the proportion (%) of primary production that is grazed by zooplankton is known as the daily ration and is a useful parameter for measuring the impact of zooplankton grazing on the phytoplankton community. In the Chukchi Sea, studies have shown that mesozooplankton and microzooplankton each graze 22% of primary production, while the remainder of the production is removed from the upper layers of the ocean by passive settling (Campbell et al., 2009; Sherr et al., 2009). The feeding preferences of zooplankton grazers may influence the diversity of the prey communities (protists) as individuals might graze on specific species (Porter, 1973) or on cells of certain sizes (Wilson, 1973). For example, sub-Antarctic and Arctic copepods are known to prefer dinoflagellates and ciliates over diatoms (Atkinson, 1996; Campbell et al., 2009, 2016), possible due to a shortage of suitable phytoplankton prey.

Around the western Arctic Ocean, a few studies have investigated zooplankton grazing: for Arctic copepods (*Calanus glacialis*, *Calanus hyperboreus*, and *Metridia longa*); small copepods (*Pseudocalanus* spp.) in the Chukchi Sea (Campbell et al., 2009); and for Arctic copepods (*Calanus* spp.), small copepods (*Pseudocalanus* spp.), Pacific copepods (*Metridia pacifica*, *Eucalanus bungii*, *Neocalanus cristatus* and *Neocalanus* spp.) and krill (*Thysanoessa raschii* and *T. inermis*) in the Bering Sea (Campbell et al., 2016). However, there is no information regarding the grazing activity (ingestion rates and food selectivity) of Pacific copepods transported into the Arctic Ocean. This information is important, particularly when evaluating the impact on the zooplankton community of climate change. In this study, we evaluate the ingestion rates and grazing impacts of Arctic and Pacific copepods in the western Arctic Ocean during autumn using ship-based grazing experiments.

Materials and Methods

Field sampling and grazing experiments

Zooplankton net sampling and copepod grazing experiments were conducted at 11 stations in the western Arctic Ocean (Fig. 1) from 4 September to 12 October, 2010, onboard the R/V *Mirai*. Fresh zooplankton were collected by vertical towing of a ring net (mouth diameter 80 cm, mesh size 335 μm) from 150 m depth to the surface or from 5 m above the seafloor at stations where the water depth was less than 150 m. The towing speed of the net was 0.5 m s^{-1} to reduce damage to live copepods. After collection, actively swimming copepods were picked immediately and placed in filtered seawater from the sampling site. The species and stages used in the experiments were the Arctic copepods *Calanus glacialis* C5, *C. hyperboreus* C6F and *Metridia longa* C6F; and the Pacific copepods *Neocalanus cristatus* C5, *N. flemingeri* C5, *N. plumchrus* C5 and *Eucalanus bungii*

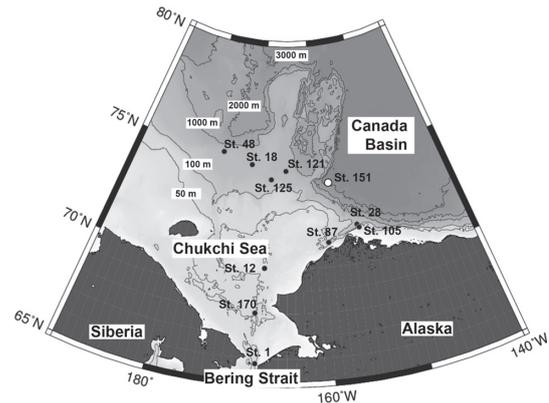


Fig. 1. Locations of stations (closed dots) in the western Arctic Ocean sampled from 4 September to 12 October 2010. At St. 151 (open dot), only chlorophyll *a* data were collected.

C6F. Additionally, we also sorted the copepods from the remaining aliquot of the fresh samples to measure of individual dry weights. The sorted specimens were rinsed with Milli-Q water, placed into preweighed aluminum pans, and stored in a freezer at -20°C . At the same stations, we also collected zooplankton samples by vertical hauls with a NOR-PAC net (mouth diameter 45 cm, mesh size 335 μm). These samples were immediately preserved with 5% buffered formalin for later analyses of abundance. The volume of water filtered through the net was estimated using a flowmeter mounted in the mouth of the net. At each site, temperature and salinity were measured by CTD (Sea-Bird Electronics Inc., SBE 911 Plus) casts. Seawater for the grazing experiments was collected from the maximum fluorescence layer (13.7–48 m, mean depth 30 m) using a rosette multisampler mounted on the CTD. The water samples were filtered through 200 μm mesh to remove copepods from the water used in the grazing experiments. Measurements of size-fractionated (>20 , 2–20, and <2 μm) chlorophyll *a* (chl.*a*) concentrations in the water used for grazing trials were performed with a fluorometer (Turner Designs, Inc., 10-AU). Finally, to determine the abundance of the protist community initially present in waters used in the grazing trials, 1 L of water was collected and preserved with 1% glutaraldehyde at every station except station 151.

Copepods were acclimated for approximately one hour at $1-3^{\circ}\text{C}$, and then actively swimming animals were selected for tests. The copepods were placed into 0.6 or 2.4 L polycarbonate bottles filled with the same water as the size-fractionated chl.*a* sample from the chlorophyll maximum layer, and the bottles were sealed with parafilm to prevent the formation of air bubbles on the insides of the bottles. The numbers of copepods used in each experimental bottle were adjusted based on bottle size (Table 1). These handling procedures were completed within two hours of net sampling.

During each experiment, control bottles filled with the

Table 1. Summary of grazing experiments in the western Arctic Ocean from 4 September to 12 October 2010. Chlorophyll *a* is showing initial value of the grazing experiment.

Station	Species/stage	Chl. <i>a</i> ($\mu\text{g L}^{-1}$)	Specimen numbers	Bottle volume (mL)	Numbers per liter	Abundance at each stage (ind. m^{-3})	Abundance of all stages (ind. m^{-3})
1	<i>C. glacialis</i> C5	0.74	1-3	600	1.7-5.0	48.4	158.8
1	<i>C. glacialis</i> C5	0.74	10-30	2,380	4.2-12.6	48.4	158.8
1	<i>N. flemingeri</i> C5	0.74	1-3	600	1.7-5.0	5.4	5.4
1	<i>N. flemingeri</i> C5	0.74	3-9	2,380	1.3-3.8	5.4	5.4
12	<i>C. glacialis</i> C5	1.13	10-30	2,380	4.2-12.6	86.2	105.3
12	<i>N. cristatus</i> C5	1.13	4-6	2,380	1.7-2.5	1.4	1.4
12	<i>E. bungii</i> C6F	1.13	10-30	2,380	4.2-12.6	9.0	180.6
18	<i>C. glacialis</i> C5	0.21	10-30	2,380	4.2-12.6	4.7	174.3
18	<i>M. longa</i> C6F	0.21	1-3	600	1.7-5.0	1.9	7.5
28	<i>C. glacialis</i> C5	0.52	3-9	600	5.0-15.0	78.8	156.6
28	<i>C. hyperboreus</i> C6F	0.52	1-3	600	1.7-5.0	0.5	0.5
28	<i>N. cristatus</i> C5	0.52	1-3	600	1.7-5.0	0.9	0.9
28	<i>N. plumchrus</i> C5	0.52	2-6	600	3.3-10.0	0.5	0.5
48	<i>C. glacialis</i> C5	0.25	1-3	600	1.7-5.0	5.0	20.4
48	<i>M. longa</i> C6F	0.25	1-3	600	1.7-5.0	6.4	11.4
87	<i>C. glacialis</i> C5	4.12	1-3	600	1.7-5.0	75.1	258.1
87	<i>N. flemingeri</i> C5	4.12	1-3	600	1.7-5.0	0.8	0.8
105	<i>C. glacialis</i> C5	0.81	1-3	600	1.7-5.0	1.7	14.9
121	<i>C. glacialis</i> C5	0.66	1-3	600	1.7-5.0	8.7	28.1
121	<i>C. hyperboreus</i> C6F	0.66	1-3	600	1.7-5.0	0.2	0.2
121	<i>M. longa</i> C6F	0.66	1-3	600	1.7-5.0	1.4	14.2
125	<i>C. glacialis</i> C5	0.32	2-6	2,380	0.8-2.5	15.3	44.3
125	<i>C. hyperboreus</i> C6F	0.32	1-3	2,380	0.4-1.3	0.5	1.0
125	<i>M. longa</i> C6F	0.32	2-6	2,380	0.8-2.5	0.5	15.3
151	<i>C. glacialis</i> C5	0.43	1-3	600	1.7-5.0	10.3	14.5
151	<i>N. flemingeri</i> C5	0.43	1-3	600	1.7-5.0	0.5	0.5
170	<i>C. glacialis</i> C5	1.13	1-3	600	1.7-5.0	19.5	19.5
170	<i>N. plumchrus</i> C5	1.13	1-3	600	1.7-5.0	1.4	1.4

same water source as the experimental bottles were used to estimate natural changes in protist assemblages and abundances during the incubation period. Three replicates of both the experimental and control bottles were prepared and incubated for 24 hours in an on-deck incubation system with continuously flowing seawater to maintain ambient water temperatures. The bottles were not fixed in the on-deck incubation system, which provided natural mixing of the protists in the experimental bottles via ship movement. The incubation system was artificially shaded to adjust the light intensity to match that where the incubation water was collected. After the incubation, dead copepods were removed and counted. Size-fractionated chl.*a* was measured for the controls and experimental bottles using the method described above. For experiments using the larger (2.4 L) experimental bottles, with the exception of St. 125 (Table 1), 1 L of the postgrazing water was preserved with 1% glutaraldehyde for three stations (e.g., St. 1, 12 and 18) to assess grazing selectiv-

ity on microzooplankton species.

Sample analyses

The NORPAC net samples were used to identify and count of the copepods under a stereomicroscope (Nikon SMZ1000-BD, $\times 0.8$ -8.0 magnification). Calanoid copepods were identified to species and copepod stage. For species identification of the calanoid copepods, we referred to Frost (1974) for *Calanus* spp. and to Miller (1988) for *Neocalanus* spp. From the data counts, we calculated abundances (ind. m^{-3} or ind. m^{-2}) of the dominant species using the filtered water volume and net towing depth.

To determine the dry weights of the dominant copepods, the frozen individual samples were freeze-dried (Tokyo Rika Inc., FDU 540). Dry weights (mg ind. $^{-1}$) were measured ($\pm 1 \mu\text{g}$) with a microbalance (Mettler Toledo MT5).

For initial and postgrazing water, the 1 L preserved (1% glutaraldehyde) samples were stored on a stone table for more

than 1 day to allow the protist cells to settle to the bottoms of the bottles. Then, the samples were concentrated to 20 mL using a siphon. Subsamples (0.1–0.5 mL, depending on the cell density in the subsample) were mounted on glass microscope slides, and diatoms and ciliates were counted and identified to the species level under an inverted microscope with 40–600x magnification. Because the maximum magnification was 600x, protists larger than 10 μm were included in this study. Species were identified to the lowest possible level (species or genus). For species identification, we referred to Hasle and Syvertsen (1997) and Hoppenrath et al. (2009) for diatoms; and to Maeda (1997) and Taniguchi (1997) for ciliates. For observation of dinoflagellates, part of each subsample was stained with Calcofluor (1 mg mL⁻¹) and examined under an epifluorescence microscope (Nikon TE-200EF) with UV light excitation. Species identification of dinoflagellates followed Fukuyo et al. (1997) and Hoppenrath et al. (2009). For other taxa (silicoflagellates and chrysophytes), species identification followed Thronsen (1997) and Toriumi (1997).

Data analysis

Based on the size-fractionated chl.*a* of initial, control and grazing experiment waters, growth rates (k), clearance rates (F , mL ind.⁻¹ day⁻¹) and ingestion rates (I , ng chl.*a* ind.⁻¹ day⁻¹) were calculated using the following equations (Frost, 1972):

$$kt = \ln(C_e/C_0) \quad (1)$$

$$kc = \ln(C_c/C_0) \quad (2)$$

$$F = V^*(k_c - k_i)/Z \quad (3)$$

$$I = F^*C_0((e^{kt}-1)/k_i) \quad (4)$$

where C_e is the average chl.*a* in the experimental samples, C_c is the average chl.*a* in the control samples, C_0 is the initial chl.*a*, V is the volume of the experimental bottle, and Z is the number of individuals incubated.

Conversion from dry weight of copepods (mg ind.⁻¹) to carbon biomass ($\mu\text{g C ind.}^{-1}$) was based on published equations. The equations were applied for *C. glacialis* from Forest et al. (2011) and for the other copepods (*E. bungii*, *N. cristatus* and *N. flemingeri*) from Ueda et al. (2008). To calculate the weight-specific clearances (mL μgC^{-1} day⁻¹) and ingestion rates (% body carbon day⁻¹), the individual carbon weights ($\mu\text{gC ind.}^{-1}$) and C : chl-*a* ratios (30 were empirically determined for this region) were used from reference (Sherr et al., 2003). The relationships described by the Michaelis-Menten equation were fitted to the data with curve fitting routines:

$$I = (V_{max} * C) / (K_m + C) \quad (5)$$

where I is the ingestion rate (% body carbon day⁻¹), V_{max} is the maximum ingestion rate, K_m is the food concentration at which the ingestion rate is half of V_{max} , and C is the food concentration in terms of chlorophyll *a*.

To clarify the factors governing the weight-specific clearances and ingestion rates, we performed an analysis of covariance (ANCOVA) using StatView v5 with the experimental copepod species and initial chl.*a* concentrations as independent variables.

For samples from St. 1, 12 and 18, protist abundances (cells L⁻¹) were determined on pre- and postgrazing experiments following the methods outlined above. To convert the abundance to carbon biomass, we referred to the database for diatoms for each species (Leblanc et al., 2012). For calculating biomasses of dinoflagellates and ciliates, the size of each species was measured, and cell volumes were calculated using the equations of Sun and Liu (2003), and the carbon biomass was then expressed using allometric equations for each taxon group (Menden-Deuer and Lassard, 2000). Based on the biomass, the proportions of the microzooplankton in the diet and prey fields were calculated.

Total biomass (mgDM m⁻³) for each copepod species was calculated using the abundance (ind. m⁻³) for each copepodite stage from the NORPAC net samples multiplied by the individual dry weight (mg ind.⁻¹), as provided by references (Conover and Huntley, 1991; Ashjian et al., 2003; Kobari et al., 2003, 2008; Lane et al., 2008) and from unpublished data from the western Arctic Ocean. Eventually, the grazing impacts (ng chl.*a* m⁻³ day⁻¹) and removal percentages (% remove day⁻¹) of chlorophyll were estimated by multiplying the biomass (mgDM m⁻³) and ingestion rates (ng chl.*a* mgDM⁻¹ day⁻¹) for each species.

Results

Food conditions in grazing experiment

Total chlorophyll *a* concentrations ranged between 0.21 and 4.12 $\mu\text{g L}^{-1}$ (0.94 \pm 1.10), and were low in the basin region, and high in the shelf region of the Chukchi Sea, especially around Barrow Canyon (St. 87) (Table 1). For size-fractionated chl.*a*, the small-size class (<2 μm) dominated at nearly all stations, although the proportion of the large-size class (>20 μm) increased for the off-Barrow stations (Fig. 2a). Protist community compositions varied latitudinally: dinoflagellates were abundant around the Bering Strait, diatoms dominated in the shelf region, and ciliates and dinoflagellates were dominant in the basin region (Fig. 2b). A larger portion of the biomass than of the abundance of ciliates and dinoflagellates composed (Fig. 2c).

Clearance and ingestion rates by size fractions

Clearance rates by the experimental copepods varied between size fractions, with almost all of the values being positive for the >20 and <2 μm fractions, while 71% (=20/28) of values were negative for the 2–20 μm fraction (Figs. 3a, b, c). The ANCOVA revealed significant relationships between the total clearance rates and species ($p < 0.01$) and the interac-

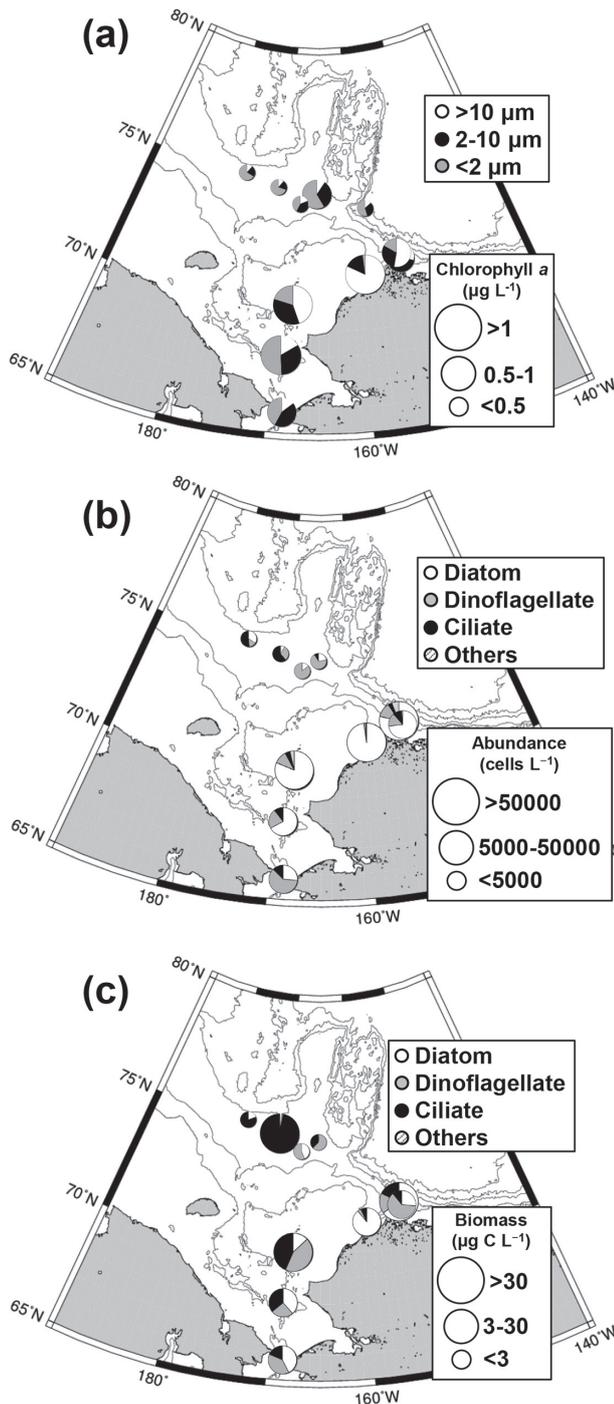


Fig. 2. Spatial distributions of size-fractionated chlorophyll *a* (a), microplankton abundance (b) and microplankton biomass (c) in the western Arctic Ocean from 4 September to 12 October 2010. Circle sizes indicate the magnitude of each value.

tions ($p < 0.01$) of species and chl.*a* (Table 2).

Ingestion rates were similar to clearance rates: positive values were shown for the >20 and <2 μm fractions, while 75% (=21/28) of values were negative for the 2–20 μm fraction (Fig. 4a, b, c). From the fit of the Michaelis–Menten equation, the ingestion rates of *M. longa* were higher than

Table 2. Results of ANCOVA on clearance and ingestion rates with species and chl.*a* in the western Arctic Ocean from 4 September to 12 October 2010.

Parameter	d.f.	SS	<i>F</i> -value	<i>p</i> -value
Clearance rate				
Species	6	0.473	6.1	**
Chl. <i>a</i>	1	0.031	2.4	NS
Species \times chl. <i>a</i>	6	0.36	4.6	**
Error	14	0.182	–	–
Ingestion rate				
Species	6	0.088	5.6	**
Chl. <i>a</i>	1	0.014	5.3	NS
Species \times chl. <i>a</i>	6	0.1	6.4	**
Error	14	0.037	–	–

those of *C. glacialis*. Additionally, the ingestion rates of the Arctic species (including *C. glacialis*, *C. hyperboreus* and *M. longa*) were higher than those of the Pacific species (including *Eucalanus bungii*, *Neocalanus cristatus*, *N. flemingeri*, and *N. plumchrus*). In particular, the V_{max} values for Arctic and Pacific copepods were 3.6% body carbon day⁻¹ and 0.10% body carbon day⁻¹, respectively. The ANCOVA also detected similar results to those for clearance rates (Table 2).

Prey preferences in microzooplankton

The proportions of microzooplankton in the field varied with the location of each station (Fig. 2). For *C. glacialis*, *N. cristatus* and *E. bungii*, the proportions of microzooplankton in the diets were slightly higher than in the field, but a significant difference was not detected due to large standard deviations (Fig. 5). However, *N. flemingeri* showed a significant preference for microzooplankton as prey (*U*-test, $p < 0.05$).

Comparison of grazing impacts among the species

The grazing impacts and removal percentages based on total chl.*a* for each species are shown in Table 3. These values varied greatly depending on stations and species (Table 3). For the mean removal percentages for each species, the Arctic copepod *C. glacialis* showed the highest ($0.080 \pm 0.17\%$ remove day⁻¹), followed by the Pacific copepod *N. flemingeri* ($0.014 \pm 0.024\%$ remove day⁻¹), and the Arctic copepod *M. longa* ($0.013 \pm 0.013\%$ remove day⁻¹). However, there were no significant differences among the species for removal percentages and grazing impacts (one-way ANOVA, $p = 0.82$ – 0.83). Additionally, the comparisons between Arctic and Pacific copepods on the removal percentages and grazing impacts were not significantly different ($p = 0.29$ – 0.30).

Discussion

Food selectivity by copepods

Several methods are used to measure the ingestion rates of

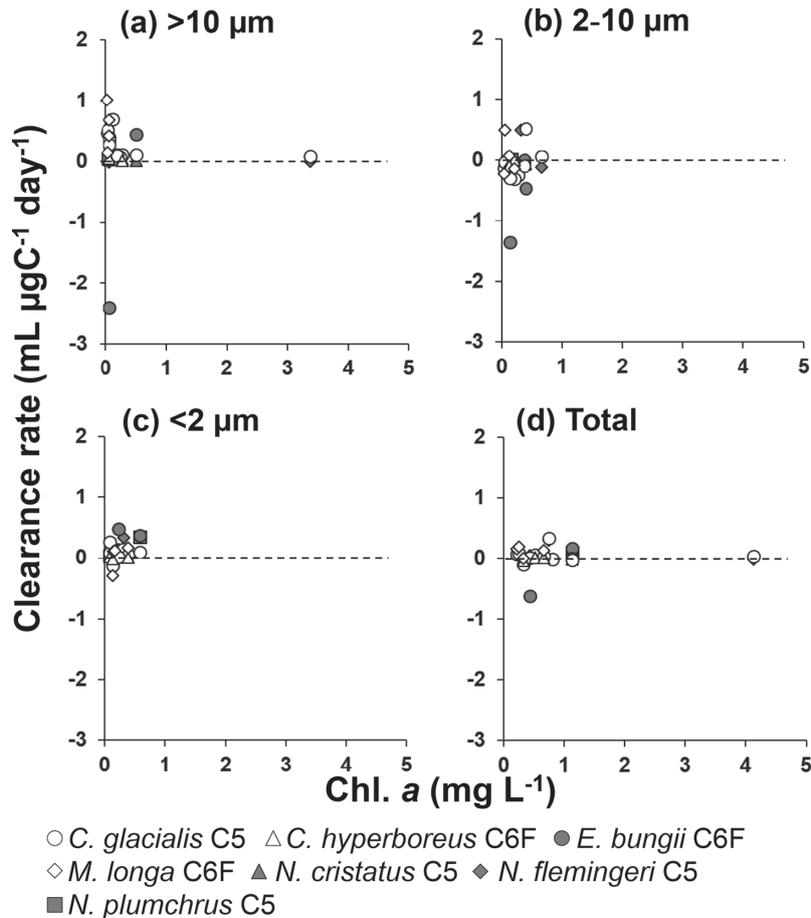


Fig. 3. Copepod clearance rates ($\text{mL } \mu\text{gC}^{-1} \text{ day}^{-1}$) of ambient chlorophyll *a* concentrations in the $>20 \mu\text{m}$ size fraction (a), $2\text{--}20 \mu\text{m}$ (b), $<2 \mu\text{m}$ (c) and total (d). Symbols represent copepod species and stages. Open symbols; Arctic species; closed symbols; Pacific species.

zooplankton (Bámstedt et al., 1991). While the methods employing bottle incubations require considerable effort for sample analysis, they have the advantage of enabling the evaluation of food selectivity by zooplankton (Atkinson, 1996). Considering their prey preferences, copepods generally prefer microzooplankton (Atkinson, 1996; Campbell et al., 2009). In this study, almost all copepods exhibited no food selectivity except *N. flemingeri* because of large variations in the food conditions. This means that the Pacific copepods can graze microzooplankton assemblages more efficiently than the Arctic species, which means that the Pacific species have the potential to change the microzooplankton community in the western Arctic Ocean during autumn. However, *N. flemingeri* feeds nonselectively on all prey items during spring in the eastern Bering Sea (Campbell et al., 2016). To obtain more accurate evaluations for food selectivity of the species, more experiments are needed in the Arctic during different seasons.

On the other hand, many species were not consumed by copepods. Concerning the ingestion rates based on size-fractionated chl.*a*, almost all values in the $2\text{--}20 \mu\text{m}$ fraction were negative, which could be an illustration of a trophic cas-

cade-effect (cf. Carpenter et al., 1985). In this case, mesozooplankton grazed selectively on microzooplankton, which decreased the abundance of microzooplankton and led to an increase in the $2\text{--}20 \mu\text{m}$ fraction, as it was released from grazing pressure by the microzooplankton. As an explanation, extremely low food concentrations during the grazing experiments might have caused the high $2\text{--}20 \mu\text{m}$ fraction, but unfortunately, we could not determine the case.

Grazing impacts and effects on the protist community

Taxa-specific maximum ingestion rates generally followed allometric theory, with Arctic copepods having higher feeding rates than Pacific copepods. This was not surprising as all Pacific species were thought to be just before or in the diapause phase (e.g., Miller et al., 1984), while the Arctic copepod *M. longa* does not have a clear diapause phase (Bámstedt and Ervik, 1984; Grønvik and Hopkins, 1984).

Considering the grazing impacts by the copepods on chlorophyll *a*, we found that the removal percentages varied greatly with sampling stations and species. According to Campbell et al. (2016), grazing impacts (i.e., % remove per day on chl.*a*) in the eastern Bering Sea during spring are

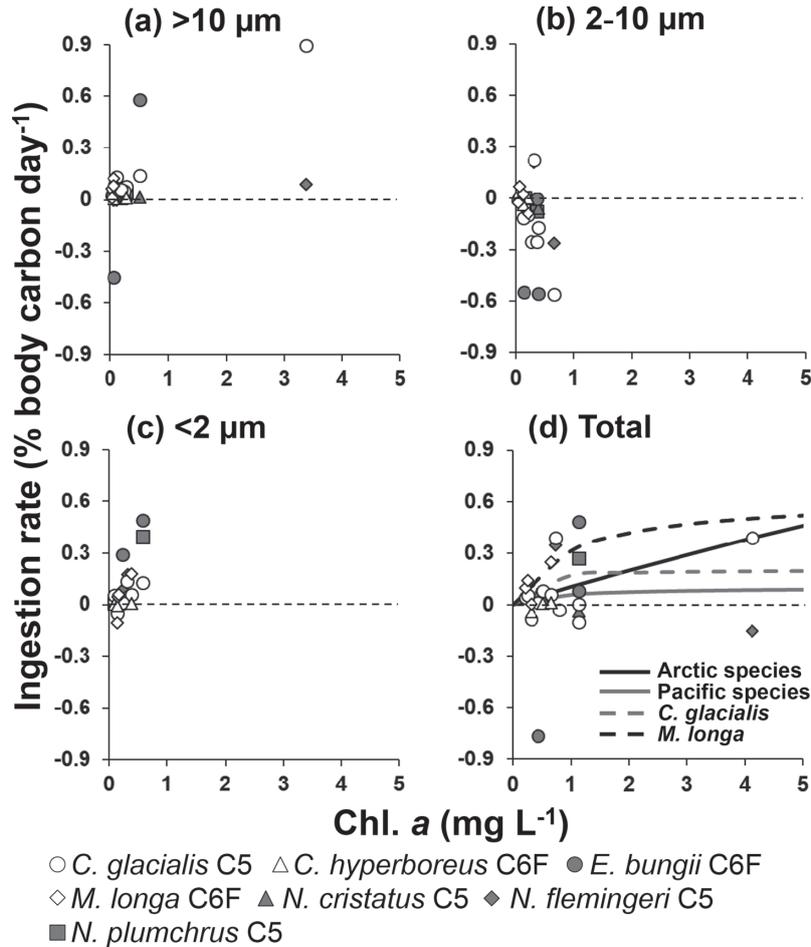


Fig. 4. Copepod ingestion rates (% body carbon day⁻¹) of ambient chlorophyll *a* concentrations in the >20 μm size fraction (a), 2-20 μm (b), <2 μm (c) and total (d). Symbols represent copepod species and stages. The curve fits for the Michaelis-Menten functions are shown for *C. glacialis*; *M. longa*; Arctic species (including *C. glacialis*, *C. hyperboreus* and *M. longa*) and Pacific species (including *Eucalanus bungii*, *Neocalanus cristatus*, *N. flemingeri*, and *N. plumchrus*).

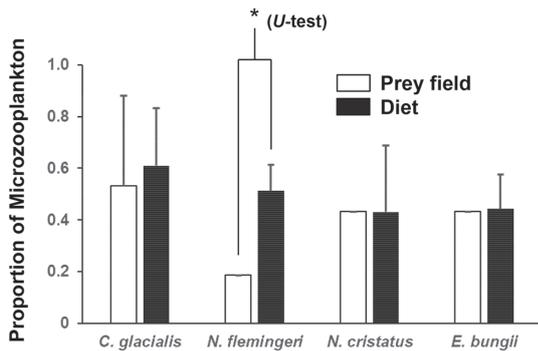


Fig. 5. Comparison of the proportion of microzooplankton between the prey and diet fields for each copepod species in the western Arctic Ocean from 4 September to 12 October 2010. *: $p < 0.05$.

related to zooplankton biomass but not to chl.*a* or to primary production. Such a relationship was not detected in the Chukchi Sea during spring and summer by Campbell et al. (2009), but in our study in the western Arctic Ocean during autumn, the relationships between copepod biomass and their

grazing impacts were significantly positive ($r^2=0.373$, $p < 0.0001$). Important factors that could affect grazing by copepods include feeding behavior, food quality and feeding history of the copepods (Bámstedt et al., 1991). Thus, the combination of the grazing impacts from different seasons may cause the relationship between biomass and grazing impact to be unclear because of the differences in physiological status of copepods and their foods among the seasons.

We calculated the community grazing impacts by integrating all population grazing impacts at each station but could not assess the entire community grazing impact on the protist community because the six species of copepods examined in this study did not include all species in the study area (cf. Matsuno et al., 2012). However, the community grazing impacts of our results (0–0.57% remove day⁻¹) at each station were similar to the reported value in spring (0.6), and lower than that in summer (5.1) (Campbell et al., 2009). Removal rate have been reported to be 2.7% day⁻¹ in the eastern Bering Sea during spring (Campbell et al., 2016) and less than 2.5% day⁻¹ in the Atlantic sector in the Southern Ocean during sum-

Table 3. Clearance rate, ingestion rate, and grazing impact for each species on chl.*a* in the western Arctic Ocean from 4 September to 12 October 2010.

Station	Species	Clearance rate (ml mgDM ⁻¹ day ⁻¹)	Clearance rate (ml µgC ⁻¹ day ⁻¹)	Ingestion rate (ng chl. <i>a</i> mgDM ⁻¹ day ⁻¹)	Ingestion rate (ng chl. <i>a</i> µgC ⁻¹ day ⁻¹)	Chl. <i>a</i> (mg m ⁻³)	Total abundance (ind. m ⁻³)	Total biomass (mgDM m ⁻³)	Grazing impact (ng chl. <i>a</i> m ⁻³ day ⁻¹)	Grazing impact (% remove day ⁻¹)
Arctic copepods										
St.1	<i>C. glacialis</i>	169.20	0.33	66.31	0.13	0.74	158.77	58.69	3,891.86	0.52
St.12	<i>C. glacialis</i>	1.49	0.0026	0.79	0.0014	1.13	105.34	66.70	52.46	0.0047
St.18	<i>C. glacialis</i>	41.16	0.074	8.20	0.015	0.21	174.31	17.45	143.05	0.067
St.28	<i>C. glacialis</i>	30.97	0.056	15.04	0.027	0.52	156.60	68.85	1,035.84	0.20
St.48	<i>C. glacialis</i>	47.76	0.088	10.37	0.019	0.25	20.43	6.53	67.72	0.027
St.87	<i>C. glacialis</i>	18.20	0.032	73.03	0.13	4.12	258.12	88.03	6,428.18	0.16
St.105	<i>C. glacialis</i>	-6.97	-0.012	-5.56	-0.010	0.81	14.86	3.76	-20.90	-0.0026
St.121	<i>C. glacialis</i>	18.34	0.033	11.12	0.020	0.66	28.13	9.34	103.86	0.016
St.125	<i>C. glacialis</i>	-50.86	-0.092	-16.05	-0.029	0.32	44.32	17.61	-282.79	-0.088
St.151	<i>C. glacialis</i>	7.14	0.013	2.59	0.0047	0.43	14.46	8.43	21.87	0.0051
St.170	<i>C. glacialis</i>	-16.22	-0.029	-18.76	-0.034	1.13	19.48	14.67	-275.17	-0.024
St.28	<i>C. hyperboreus</i>	4.12	0.0063	2.07	0.0032	0.52	0.47	1.70	3.52	0.00068
St.121	<i>C. hyperboreus</i>	4.51	0.0068	2.76	0.0042	0.66	0.24	0.88	2.42	0.00037
St.125	<i>C. hyperboreus</i>	-28.68	-0.042	-9.29	-0.014	0.32	0.95	1.79	-16.59	-0.0052
St.18	<i>M. longa</i>	79.81	0.16	16.30	0.032	0.21	7.54	1.61	26.23	0.012
St.48	<i>M. longa</i>	96.37	0.19	23.01	0.046	0.25	11.35	3.43	78.85	0.031
St.121	<i>M. longa</i>	68.25	0.13	41.61	0.082	0.66	14.18	1.50	62.44	0.0095
St.125	<i>M. longa</i>	0.57	0.0011	0.37	0.00074	0.32	15.25	2.00	0.74	0.00023
Pacific copepods										
St.12	<i>E. bungii</i>	4.22	0.027	4.23	0.027	1.13	180.58	27.04	114.33	0.010
St.151	<i>E. bungii</i>	-98.01	-0.62	-40.37	-0.25	0.43	0.47	0.02	-0.92	-0.00022
St.170	<i>E. bungii</i>	25.94	0.16	25.54	0.16	1.13	5.57	4.13	105.62	0.0093
St.12	<i>N. cristatus</i>	-5.49	-0.013	-5.30	-0.013	1.13	1.37	6.96	-36.88	-0.0033
St.28	<i>N. cristatus</i>	11.01	0.026	5.27	0.013	0.52	0.93	4.75	25.03	0.0048
St.1	<i>N. flemingeri</i>	186.70	0.30	71.53	0.12	0.74	5.38	4.39	314.16	0.042
St.87	<i>N. flemingeri</i>	-7.57	-0.012	-31.70	-0.051	4.12	0.78	0.22	-6.89	-0.00017
St.151	<i>N. flemingeri</i>	26.51	0.043	10.03	0.016	0.43	0.47	0.38	3.82	0.00089
St.28	<i>N. plumchrus</i>	15.02	0.040	7.34	0.020	0.52	0.09	0.06	0.46	0.000089
St.170	<i>N. plumchrus</i>	35.46	0.095	33.30	0.090	1.13	0.28	0.19	6.27	0.00055

mer (Atkinson, 1996). Therefore, our results suggest that the grazing impacts of copepods on phytoplankton biomass (chlorophyll *a*) are small or nearly zero in the western Arctic Ocean during autumn.

The large variability in the grazing impacts of Arctic copepods arose from regional differences in abundances of *C. glacialis*, which are high over the shelf and low in the basin (Matsuno et al., 2012). In the western Arctic region, a decrease in sea ice cause increased in Pacific water inflow and results in increased inflow of Pacific copepods (Matsuno et al., 2011 ; Ershova et al., 2015b). Copepods transported from the Pacific could affect the protist in the Arctic and compete with endemic copepod species. However, based on our results, the grazing impacts by Pacific copepods were very small, and accounted for only 0.1–17% in comparison with

the co-occurring Arctic copepods. Pacific copepods in the Arctic have been observed mostly in the Chukchi Sea (especially the shelf region) but rarely in the basin area (Nelson, 2014 ; Ershova et al., 2015b). On a seasonal basis, the Pacific species are present mainly during the open-water season from July to October and have not been observed during other seasons in the western Arctic, based on mooring observations (Matsuno et al., 2014). This suggest that the grazing impact of Pacific copepods in the western Arctic Ocean is restricted to a small area (Chukchi Sea) during a short period (July–October).

Conclusions

A comparison of the grazing activity between co-occurring Arctic and Pacific copepods in the western Arctic Ocean dur-

ing autumn found that the grazing activity for both species was low. The ingestion rates were higher in Arctic species than in Pacific species, and the community grazing impacts showed a similar trend. Thus, even if Pacific copepods are transported into the Arctic Ocean and ingest the endemic protist assemblage there, their impacts are presumably limited both spatially and seasonally. Our results indicate that Pacific copepods are unlikely to cause a shift in the protist community of the western Arctic Ocean during autumn.

Acknowledgements

We are grateful to the captain, officers and crew of R.V. *Mirai* (JAMSTEC) for their help during the field-sample collections. We also express our sincere thanks to Dr. Ruth Eriksen and Dr. Kerrie Swadling for correcting the English in earlier versions of the manuscript. This study was supported by the Arctic Challenge for Sustainability (ArCS) Project. This study was partially supported by a Grant-in-Aid for JSPS Overseas Research Fellowships to KM. Part of this study was supported by a Grant-in-Aid for Scientific Research 17H01483 (A), 19H03037 (B), and 18K14506 (Early Career Scientists) from the Japanese Society for the Promotion of Science (JSPS).

References

- 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.
- Atkinson, A. (1996) Subantarctic copepods in an oceanic, low chlorophyll environment : ciliate predation, food selectivity and impact on prey population. *Mar. Ecol. Prog. Ser.*, **130**, 85–96.
- 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.
- Båmstedt, U., Eilertsen, H.C., Tande, K.S., Slagstad, D. and Skjoldal, R.H. (1991) Copepod grazing and its potential impact on the phytoplankton development in the Barents Sea. *Polar Res.*, **10**, 339–354, doi : 10.1111/j.1751-8369.1991.tb00658.x.
- Campbell, R.G., Sherr, E.B., Ashjian, C.J., Plourde, S., Sherr, B.F., Hill, V. and Stockwell, D.A. (2009) Mesozooplankton prey preference and grazing impact in the western Arctic Ocean. *Deep-Sea Res. II*, **56**, 1274–1289.
- Campbell, R.G., Asjian, C.J., Sherr, E.B., Sherr, B.F., Lomas, M.W., Ross, C., Alatalo, P., Gelfman, C. and Keuren, D.V. (2016) Mesozooplankton grazing during spring sea-ice conditions in the eastern Bering Sea. *Deep-Sea Res. II*, **134**, 157–172.
- Carpenter, S.R., Kitchell, J.F. and Hodgson, J.R. (1985) Cascading trophic interactions and lake productivity. *BioScience*, **35**, 634–639.
- Coachman, L.K., Aagaard, K. and Tripp, R.B. (1975) *Bering Strait : the regional physical oceanography*. University of Washington Press, Seattle, Washington.
- Conover, R.J. and Huntley, M. (1991) Copepods in ice-covered seas—distribution, adaptations to seasonally limited food, metabolism, growth patterns and life cycle strategies in polar seas. *J. Mar. Syst.*, **2**, 1–41.
- Ershova, E.A., Hopcroft, R.R. and Kosobokova, K.N. (2015a) Inter-annual variability of summer mesozooplankton communities of the western Chukchi Sea : 2004–2012. *Polar Biol.*, **38**, 1461–1481.
- Ershova, E.A., Hopcroft, R.R., Kosobokova, K.N., Matsuno, K., Nelson, R.J., Yamaguchi, A. and Eisner, L.B. (2015b) Long-term changes in summer zooplankton communities of the western Chukchi Sea, 1945–2012. *Oceanography*, **28**, 100–115, <http://dx.doi.org/10.5670/oceanog.2015.60>.
- Forest, A., Galindo, V., Darnis, G., Pineault, S., Lalande, G., Tremblay, J.-E. and Fortier, L. (2011) Carbon biomass, elemental ratios (C : N) and stable isotope composition ($\delta^{13}\text{C}$, $\delta^{15}\text{N}$) of dominant calanoid copepods during the winter-to-summer transition in the Amundsen Gulf (Arctic Ocean). *J. Plankton Res.*, **33**, 161–178.
- Frost, B.W. (1972) Effects of size and concentration of food particles on the feeding behavior of the marine planktonic copepod *Calanus pacificus*. *Limnol. Oceanogr.*, **17**, 805–815.
- 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.
- Fukuyo, Y., Inoue, H. and Takayama, H. (1997) Class Dinophyceae. pp. 31–112, Chihara, M. and Murano, M. (eds), *An illustrated guide to marine plankton in Japan*. Tokai University Press, Tokyo.
- Grebmeier, J.M., Mcroy, C.P. and Feder, H.M. (1988) Pelagic-benthic coupling on the shelf of the northern Bering and Chukchi Seas. I. Food supply source and benthic biomass. *Mar. Ecol. Prog. Ser.*, **48**, 57–67.
- 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.
- Hasle, G.R. and Syvertsen, E.E. (1997) Marine diatoms. pp. 5–385, Tomas, C.R. (eds), *Identifying marine phytoplankton*. Academic Press, San Diego.
- 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.
- Hoppenrath, M., Elbrächter, M. and Drebes, G. (2009) *Marine phytoplankton*. E. Schweizerbart'sche Verlagsbuchhandlung, Stuttgart.
- Kobari, T., Shinada, A. and Tsuda, A. (2003) Functional roles of interzonal migrating mesozooplankton in the western subarctic Pacific. *Prog. Oceanogr.*, **57**, 279–298.
- Kobari, T., Steinberg, D.K., Ueda, A., Tsuda, A., Silver, M.W. and Kitamura, M. (2008) Impacts of ontogenetically migrating copepods on downward carbon flux in the western subarctic Pacific Ocean. *Deep-Sea Res. II*, **55**, 1648–1660.
- Lane, P.V.Z., Llinás, L., Smith, S.L. and Pilz, D. (2008) Zooplankton distribution in the western Arctic during summer 2002 : hydrographic habitats and implications for food chain dynamics. *J. Mar. Syst.*, **70**, 97–133.
- Leblanc, K., Aristegui, J., Armand, L., Assmy, P., Beker, B., Bode, A., Breton, E., Cornet, V., Gibson, J., Gosselin, M.-P., Kopczynska, E., Marshall, H., Peloquin, J., Piontkovski, S., Poulton, A.J., Quéguiner, B., Schiebel, R., Shipe, R., Stefels, J., van Leeuwe,

- M.A., Varela, M., Widdicombe, C. and Yallop, M. (2012) A global diatom database—abundance, biovolume and biomass in the world ocean. *Earth Syst. Sci. Data*, **4**, 149–165.
- Lowry, L.F., Sheffield, G. and George, C. (2004) Bowhead whale feeding in the Alaskan Beaufort Sea, based on stomach contents analyses. *J. Cetacean Res. Manage.*, **6**, 215–223.
- Maeda, M. (1997) Suborder Oligotrichida. pp. 397–420, Chihara, M. and Murano, M. (eds), *An illustrated guide to marine plankton in Japan*. Tokai University Press, Tokyo.
- 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., 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.
- Menden-Deuer, S. and Lassard, E.J. (2000) Carbon to volume relationships for dinoflagellates, diatoms, and other protist plankton. *Limnol. Oceanogr.*, **45**, 569–579.
- 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.
- Miller, C.B., Frost, B.W., Batchelder, H.P., Clemons, M.J. and Conway, R.E. (1984) Life histories of large, grazing copepods in a subarctic ocean gyre : *Neocalanus plumchrus*, *Neocalanus cristatus*, and *Eucalanus bungii* in the Northeast Pacific. *Prog. Oceanogr.*, **13**, 201–243.
- Nakano, T., Matsuno, K., Nishizawa, B., Iwahara, Y., Mitani, Y., Yamamoto, J., Sakurai, Y. and Watanuki, Y. (2016) Diet and body condition of polar cod (*Boreogadus saida*) in the northern Bering Sea and Chukchi Sea. *Polar Biol.*, **39**, 1081–1086.
- Nelson, R.J., Ashjian, C.J., Bluhm, B.A., Conlan, K.E., Gradinger, R.R., Grebmeier, J.M., Hill, V.J., Hopcroft, R.R., Hunt, B.P.V., Joo, H.M., Kirchman, D.L., Kosobokova, K.N., Lee, S.H., Li, W.K.W., Lovejoy, C., Poulin, M., Sherr, E. and Young, K.V. (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.
- Pinchuk, A.I. and Eisner, L.B. (2017) Spatial heterogeneity in zooplankton summer distribution in the eastern Chukchi Sea in 2012–2013 as a result of large-scale interactions of water masses. *Deep-Sea Res. II*, **135**, 27–39.
- Porter, K.G. (1973) Selective grazing and differential digestion of algae by zooplankton. *Nature*, **244**, 179–180.
- Sherr, E.B., Sherr, B.F., Wheeler, P.A. and Thompson, K. (2003) Temporal and spatial variation in stocks of autotrophic and heterotrophic microbes in the upper water column of the central Arctic Ocean. *Deep-Sea Res. I*, **50**, 557–571.
- Sherr, E.B., Sherr, B.F. and Hartz, A.J. (2009) Microzooplankton grazing impact in the western Arctic Ocean. *Deep-Sea Res. II*, **56**, 1264–1273.
- Sun, J. and Liu, D. (2003) Geometric models for calculating cell biovolume and surface area for phytoplankton. *J. Plankton Res.*, **25**, 1331–1346.
- Taniguchi, A. (1997) Suborder Tintinnina. pp. 421–483, Chihara, M. and Murano, M. (eds), *An illustrated guide to marine plankton in Japan*. Tokai University Press, Tokyo.
- Thronsen, J. (1997) The planktonic marine flagellates. pp. 591–729, Tomas, C.R. (eds), *Identifying marine phytoplankton*. Academic Press, San Diego.
- Toriumi, S. (1997) Class Chrysophyceae. pp. 147–156, Chihara, M. and Murano, M. (eds), *An illustrated guide to marine plankton in Japan*. Tokai University Press, Tokyo.
- Ueda, A., Kobari, T. and Steinberg, D.K. (2008) Body length, weight and chemical composition of ontogenetically migration copepods in the western subarctic gyre of the North Pacific Ocean. *Bull. Plankton Soc. Japan*, **55**, 107–114 (in Japanese with English abstract).
- Wilson, D.S. (1973) Food size selection among copepods. *Ecology*, **54**, 909–914.
- Woodgate, R.A., Weingartner, T. and Lindsay, R. (2010) The 2007 Bering Strait oceanic heat flux and anomalous Arctic sea-ice retreat. *Geophys. Res. Lett.*, **37**, L01602, doi : 10.1029/2009GL041621.
- Woodgate, R.A., Weingartner, T. and Lindsay, R. (2012) Observed increases in Bering Strait oceanic fluxes from the Pacific to the Arctic from 2001 and their impacts on the Arctic Ocean water column. *Geophys. Res. Lett.*, **39**, L24603, doi : 10.1029/2012GL054092.