Short-term changes of the mesozooplankton community and copepod gut pigment in the Chukchi Sea in autumn: Reflection of strong wind event

4

5 K. Matsuno¹*, A. Yamaguchi², S. Nishino³, J. Inoue¹ and T. Kikuchi³

6 [1]{Arctic Environment Research Center, National Institute of Polar Research, 10-3 Midori-

7 cho, Tachikawa, Tokyo 190-8518, Japan}

- 8 [2]{Laboratory of Marine Biology, Graduate School of Fisheries Sciences, Hokkaido
- 9 University, 3–1–1 Minato-cho, Hakodate, Hokkaido 041-8611, Japan}

10 [3]{Japan Agency for Marine-Earth Science and Technology, 2-15 Natsushima-cho,

11 Yokosuka, Kanagawa 237-0061, Japan}

12

13 * Correspondence to: K. Matsuno (matsuno.kohei@nipr.ac.jp, k.matsuno@fish.hokudai.ac.jp)

14

15 Abstract

16 To evaluate the effect of atmospheric turbulence on the marine ecosystem, high-frequency 17 sampling (two to four times per day) on the mesozooplankton community and the gut pigment 18 of dominant copepods were made at a fixed station in the Chukchi Sea from 10 to 25 19 September 2013. During the study period, a strong wind event (SWE) was observed on 18 September. After the SWE, the standing stock of chlorophyll a (chl. a) was increased, 20 21 especially for micro-size (> $10 \mu m$) fractions. Zooplankton abundance ranged from 23610 to 56809 ind. m⁻² and exhibited no clear changes with SWE. In terms of abundance, calanoid 22 copepods constituted the dominant taxa (mean: 57%), followed by barnacle larvae (31%). 23 24 Within the calanoid copepods, small-sized *Pseudocalanus* spp. (65%) and large-sized *Calanus* 25 glacialis (30%) dominated. In the population structure of C. glacialis, copepodid stage 5 (C5) 26 dominated, and the mean copepodid stage did not vary with SWE. The dominance of accumulated lipids in C5 and C6 females with immature gonads indicated that they were 27 preparing for seasonal diapause. The gut pigment of C. glacialis C5 was higher at night and 28 was correlated with ambient chl. a, and a significant increase was observed after SWE (2.6 vs 29

4.5 ng pigment ind.⁻¹). The grazing impact by C. glacialis C5 was estimated to be 4.14 mg C 1 2 $m^{-2} dav^{-1}$, which corresponded to 0.5–4.6% of the standing stock of micro-size phytoplankton. 3 Compared with the metabolic food requirement, their feeding on phytoplankton accounted for 12.6% of their total food requirement. These facts suggest that C. glacialis could not 4 5 maintain their population on solely phytoplankton food, and other food sources (i.e., microzooplankton) are important in autumn. As observed for the increase in gut pigment, 6 7 temporal phytoplankton bloom, which is enhanced by the atmospheric turbulence (SWE) in 8 autumn, may have a positive effect on copepod nutrition.

9

10 **1** Introduction

11 In marine ecosystems of the western Arctic Ocean, mesozooplankton is an important food 12 resource for pelagic fishes and whales (Lowry et al., 2004; Ashjian et al., 2010). In terms of biomass, mesozooplankton in the western Arctic Ocean is dominated by Arctic copepods. 13 14 Within the Arctic copepods, Calanus glacialis is a key species that dominates in the 15 zooplankton biomass and commonly occurs in the continental shelf throughout the Arctic 16 Ocean (Conover and Huntley, 1991; Lane et al., 2008). For the life cycle of C. glacialis, they 17 grow to C3–C4 at the epipelagic layer during the first summer, then descend to the deep layer 18 and enter diapause, developing to C5 at the epipelagic layer in the second summer, then down 19 to the deep layer and molting to the adult stage (C6) using stored lipid as energy (Longhurst et 20 al., 1984; Ashjian et al., 2003; Falk-Petersen et al., 2009).Concerning seasonal change, a 21 comparison of the zooplankton community between summer and autumn (Llinás et al., 2009) 22 and year-round changes based on the two-week sampling interval at a drifting ice station in 23 the Arctic basin were reported (Ashjian et al., 2003). However, short-term changes in the 24 zooplankton community based on high-frequency sampling (two to four times per day) have 25 not been reported.

Recently, a drastic reduction in the area of sea ice has been observed in the Arctic Ocean during summer, and the sea ice reduction was greatest in the western Arctic Ocean (Stroeve et al., 2007; Comiso et al., 2008; Markus et al., 2009). Furthermore, increases in frequency and magnitude of cyclones and a northward shift of their track during summer have been reported in recent years (Serreze et al., 2000; Cabe et al., 2001; Zhang et al., 2004; Sepp and Jaagus, 2011). While the importance of such changes is clear, little information is available regarding their effect on atmospheric turbulence in marine ecosystems in the western Arctic Ocean. From 10 to 25 September 2013, high-frequency sampling/observation was made at a fixed station in the Chukchi Sea, and the occurrence of strong wind events (SWE), vertical flux of nutrients and changes in primary production and microplankton communities were reported (Nishino et al., 2015; Yokoi et al., submitted). However, no information is available regarding how the mesozooplankton community responds to such atmospheric turbulence and oceanic environmental changes.

In the present study, we evaluated short-term changes of the mesozooplankton community in the Chukchi Sea during autumn based on the high-frequency samplings made simultaneously by Nishino et al. (2015) and Yokoi et al. (submitted). We estimated the grazing impact of dominant copepods based on their gut pigments and evaluated the effect of SWE (Nishino et al., 2015) and short-term changes of microplankton assemblages (Yokoi et al., submitted) on the mesozooplankton community in the Chukchi Sea in autumn.

13

14 2 Materials and Methods

15 2.1 Field sampling

Zooplankton samplings were conducted at a fixed station in the Chukchi Sea $(72^{\circ}45^{\circ}N)$. 16 17 168°15'W, depth 56 m) from 10 to 25 September 2013 (Fig. 1) (Nishino et al., 2015). Zooplankton samples were collected by vertical hauls with a NORPAC net (mouth diameter 18 19 45 cm, mesh size 335 µm; Motoda, 1957) and ring net (mouth diameter 80 cm, mesh size 335 20 µm) from 49 m depth to the sea surface two to four times per day (total of 47 times) including 21 both day and night. The large mesh size of NORPAC net (335 µm) may induce somewhat 22 underestimation of smaller zooplankton species and early stages of larger zooplankton species. 23 Zooplankton samples collected by NORPAC nets were preserved with 5% buffered formalin 24 immediately on board. The ring net samples were used for copepod gut pigment measurement. For evaluation of the diel vertical migration (DVM) of copepods, day and 25 26 night vertical stratified hauls with closing PCP nets (mouth diameter 45 cm, mesh size 62 µm; Kawamura, 1989) from two layers (0-20 m and 20-49 m) were made on 14 and 22 27 28 September. The samples from the PCP net were preserved with 5% buffered formalin.

At the fixed station, temperature, salinity and chlorophyll *a* (chl. *a*) fluorescence were measured by CTD (Sea-Bird Electronics Inc., SBE911Plus) casts at a frequency of two to four times per day. To evaluate size fractionated chl. *a*, water samples from the sea surface and the maximum fluorescence layer (16.8–27.7 m depth) were collected by a bucket and rosette multi-sampler mounted on CTD, respectively. Water samples were filtered through 20, 10 and 2-μm pore-size membranes and GF/F filters, and chl. *a* was extracted with N,Ndimethylformamide and measured with a fluorometer (Turner Designs, Inc., 10-AU-005).

5 2.2 Gut pigment

For fresh samples collected by ring nets, 10% v/v soda (saturated CO₂ in water) was added to 6 7 avoid copepod grazing, gut evacuation and decomposition of gut pigment. Fresh specimens 8 of C. glacialis copepodid stage 5 (C5) were sorted under a stereomicroscope. Batches of fifteen specimens were immersed in 6 ml N,N-dimethylformamide and stored in dark, cold 9 10 conditions overnight to extract chlorophyll and phaeopigments. After the extraction of 11 pigment, the chlorophyll and phaeopigments were measured with a fluorometer (Turner Designs, Inc., 10-AU-005). Chlorophyll and phaeopigments were summed and expressed as 12 gut pigments (ng pigment ind.⁻¹) (cf. Mackas and Bohrer, 1976). 13

14 The gut pigment of *C. glacialis* C5 was higher at nighttime than daytime. Assuming 15 their grazing at night, the grazing rate ($GR_{ind.}$, mg pigment ind.⁻¹ day⁻¹) of *C. glacialis* C5 was 16 calculated from following equation:

17
$$GR_{ind.} = GP \times k \times T / 10^{\circ},$$
 (1)

where *GP* is the individual gut pigment at night (ng pigment ind.⁻¹), *k* is the gut evacuation rate (0.017 min⁻¹, Tande and Båmstedt, 1985), and *T* is the length of the nighttime (mean 13 hours = 780 min during study period). The grazing impact of *C. glacialis* C5 on micro-size (> 10 µm) chl. *a* (*GI*, % on chl. *a* standing stock day⁻¹) was calculated by the following equation: $GI = GR_{ind.} \times N / Int. chl. a \times 100,$ (2)

where *N* is the abundance of *C. glacialis* C5 (ind. m^{-2}), and *Int. chl. a* is standing stock of large-sized (> 10 µm) chl. *a* (mg m⁻²).

25 **2.3 Zooplankton community**

In the land laboratory, identification and enumeration by taxa were performed on zooplankton samples collected by NORPAC nets under a stereomicroscope. For dominant taxa (calanoid copepods), identification was made to species and copepodid stage levels. For species identification of calanoid copepods, we referred mainly to Brodsky (1967) and Frost (1974) for *Calanus* spp., Miller (1988) for *Neocalanus* spp. and Frost (1989) for *Pseudocalanus* spp.
 For *Pseudocalanus* spp., species identification was made only for late copepodid stage C5
 females/males (C5F/M) and C6F/M, and their early copepodid stages (C1–C4) were treated
 as *Pseudocalanus* spp.

For the evaluation of the DVM of large dominant copepods, we enumerated *C*. *glacialis* from PCP net samples. For *C. glacialis*, the lipid accumulation of C5 was scored into three categories: I (the oil droplet length (ODL) was 0–4% of the prosome length (PL)), II (ODL was 4–40% of PL) and III (ODL was > 40% of PL). Gonad maturation of *C*. *glacialis* C6F was also scored into three categories: I (immature), II (small oocytes in the ovary or oviduct) and III (large eggs or distended opaque filled-in oviduct). For this gonad maturation index, we cited those for *C. hyperboreus* (Hirche and Niehoff, 1996).

12

A species diversity index
$$(H')$$
 in each sample was calculated using the equation:

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

where *n* is the abundance (ind. m^{-2}) of *ith* species and *Ni* is the abundance (ind. m^{-2}) of total calanoid copepods in the sample (Shannon and Weaver, 1949). Pielou evenness (*J*) was also calculated using the equation:

17 $J'=H'/\ln(s)$

18 where *s* is total number of observed species in the community (Pielou, 1966).

19 From NORPAC net samples, the mean copepodid stage (*MCS*) of *C. glacialis* was20 calculated from the following equation:

21
$$MCS = \frac{\sum_{i=1}^{6} i \times Ai}{\sum_{i=1}^{6} Ai},$$
 (3)

where *i* is the number of the copepodid stage (1–6 indicates C1–C6), and Ai (ind. m⁻²) is the abundance of the *i*th copepodid stage (cf. Marin, 1987).

During the study period, SWE was observed from 18 to 19 September (Nishino et al., 25 2015). To evaluate the effect of SWE, the abundances of each zooplankton taxon and species 26 were compared between "before SWE (10–18 September)" and "after SWE (19–25 27 September)" using the *U*-test. This statistical analysis was performed with Stat View.

1 3 Results

2 3.1 Hydrography and chlorophyll a

During the sampling period, the temperature ranged from -1.5° C to 3.3° C, and thermocline 3 4 was observed at a depth of approximately 25 m (Fig. 2a). Cold water below 0°C continuously 5 occurred below thermocline, whereas the temperature above thermocline decreased from 3.3 to 1.5°C during the study period (Fig. 2a). Salinity ranged from 31.1 to 32.8, and halocline 6 7 was observed at approximately 25 m, which was parallel to thermocline (Fig. 2b). Salinity 8 below halocline was constant ca. > 32, whereas salinity in the upper layer increased from 31.1 to 31.6 throughout the study period. Chl. *a* ranged from 0.08 to 3.25 mg m⁻³ and increased 9 after the SWE (Fig. 2c). The T-S diagram showed that the hydrographic conditions in the 10 11 upper layer changed temporally; thus, temperature decreased while salinity increased during 12 the study period (Fig. 2d).

13 **3.2 Zooplankton community**

Zooplankton abundance ranged from 23610 to 56809 ind. m^{-2} , and calanoid copepods and 14 barnacle larvae composed 57% and 31% of the community, respectively (Table 1). For 15 calanoid copepods, 15 species belonging to nine genera were identified. Within them, 16 17 Pseudocalanus spp. and C. glacialis dominated and composed 65% and 30% of the total 18 copepods, respectively. Shannon species diversity and Pielou evenness for the copepods 19 commutive were 1.87 ± 0.12 and 0.81 ± 0.06 , respectively. According to a comparison of time 20 periods before and after the SWE, the total zooplankton abundance, the Shannon species 21 diversity and the Pielou evenness did not change, whereas one calanoid copepod Centropages 22 abdominalis and cyclopoid copepods increased after the SWE (Table 1). On the other hand, 23 one calanoid copepod Metridia pacifica, appendicularians, barnacle larvae, euphausiids and gymnosomes (Clione limacina) decreased after the SWE. 24

25 3.3 Calanus glacialis

Throughout the study period, the standing stock of *C. glacialis* ranged from 1990 to 14554 ind. m^{-2} , and no significant changes were detected with the SWE (Fig. 3a, Table 1). For the population structure, all copepodid stages (C1 to C6F/M) occurred, and C5 was the most dominant stage (36%) of the population (Fig. 3). The *MCS* did not vary with SWE (Fig. 3a). 1 Throughout the study period, the lipid accumulation of C5 was high (Fig. 3b), and the gonad 2 maturation of C6F was dominated by immature specimens (Fig. 3c). These parameters 3 exhibited no significant change with the SWE (*U*-test, p = 0.285-0.303).

On both 14 and 22 September, the C1–C4 and C5 populations of *C. glacialis* occurred mainly at lower layers (20–49 m) during the daytime, and they migrated to upper layers (0–20 m) at night (Fig. 4). It should be noted that nearly half of C5 remained in the lower layer both day and night. Lipid accumulation was higher for the C5 population residing in the lower layer. C6F occurred at a lower layer throughout the day.

9 The gut pigment of *C. glacialis* C5 ranged from 0.6 to 12.3 ng pigment ind.⁻¹ and 10 showed a significant increase after the SWE (mean values: 2.6 vs 4.5 ng pigment ind.⁻¹, *U*-11 test, p < 0.01) (Fig. 5a). In a comparison between day and night, most dates except 18 and 23 12 September showed high gut pigment levels at night by a factor of two to five times those of 13 the daytime. In both day and night, the gut pigments were correlated with a standing stock of 14 chl. a (p < 0.05) (Fig. 5b).

15 The population grazing rate of *C. glacialis* C5 ranged from 0.04–0.28 mg pigment m⁻² 16 day⁻¹, peaked on 20 September (Fig. 6a) and increased significantly after the SWE (0.11 vs 17 0.18 mg pigment m⁻² day⁻¹, *U*-test, p < 0.05). During the study period, chl. *a* peaked at 18 18 September, and micro-size (> 10 µm) dominated (54% of total chl. *a*), especially after the 19 SWE (66%) (Fig. 6b). The grazing impact of *C. glacialis* C5 on micro-size chl. *a* ranged 10 from 0.5–4.6% on chl. *a* standing stock day⁻¹ and was high before the SWE from 10 to 15 11 September (Fig. 6c).

22

23 4 Discussion

24 **4.1 Zooplankton community**

The zooplankton community in the Chukchi Sea is known to have large spatial and temporal changes (Springer et al., 1989; Llinás et al., 2009; Matsuno et al., 2011). Total zooplankton abundance in this study was approximately half (mean: 34059 ind. m⁻²) the abundance reported by Matsuno et al. (2012) on the Chukchi shelf (mean: 75683 ind. m⁻²), with low abundance of small copepods (*Pseudocalanus* spp. and cyclopoids) and the remarkable absence of the Arctic copepod *Metridia longa*. For the hydrography of this station, Nishino et

1 al. (2015) noted that the upper warm and less saline water was the Pacific Summer water, 2 which was transported to the Arctic Ocean during summer, and the cold saline water of the lower layer was the remnant brine of the Pacific Winter water, which was transported to the 3 4 Arctic Ocean during winter. Geographically, the present station was located at a main stream 5 of the Pacific water (Weingartner et al., 2005). The high abundance of the Pacific copepod M. pacifica and Neocalanus spp. and the lack of the occurrence of the Arctic M. longa in this 6 7 study was thought to be a reflection of the water mass covering the station. Because of these 8 reasons (less small copepods and high abundance of Pacific copepods), the Shannon species 9 diversity and Pielou evenness in this study (1.87 and 0.81) are higher than the reported values 10 for the whole Chukchi Sea (1.79 and 0.62 calculated from Matsuno et al., 2012).

11 Seasonal characteristics during summer included the dominance of the meroplankton 12 (barnacle and bivalve larvae), which composed 39% of zooplankton abundance (Hopcroft et 13 al., 2010). Dominance of the barnacle larvae also occurred in this study (Table 1). Benthic 14 barnacle adults release their larvae when they meet phytoplankton blooms (Crisp, 1962; Clare and Walker, 1986), and their larvae spend two to three weeks in the water column and then 15 settle (Herz, 1933). The abundance of barnacle larvae in this study (mean 10430 ind. m^{-2}) 16 was 13–55% lower than that in summer (19114–79899 ind. m^{-2} , Matsuno et al., 2011). It also 17 18 should be noted that the abundance of barnacle larvae decreased significantly during the study 19 period (Table 1). These facts suggest that most of the barnacle larvae may have ended the 20 planktonic phase and settled to the sea bottom during the study period (autumn).

21 Concerning the effect of the SWE, a few taxa and species showed significant changes 22 in abundance (Table 1). For dominant species, cyclopoid copepods were increased after the 23 SWE (Table 1). The generation length of cyclopoid copepods was reported to be two to three 24 months in the Arctic Ocean (Dvoretsky and Dvoretsky, 2009). In ambient temperature (-1.5 25 to 3.3°C), the egg hatching of this taxon is estimated to be 11–41 days (Nielsen et al., 2002). 26 These facts suggest that the increase of cyclopoid copepods would not be caused by their 27 reproduction within the study period (16 days). As an alternative cause, the horizontal 28 advection of the water mass during the study period, which was reported by Nishino et al. (2015), should be considered. These results suggest that the effect of SWE on zooplankton 29 30 abundance was relatively small because of the longer generation length of mesozooplankton 31 in this region.

1 4.2 Population structure of *C. glacialis*

2 Concerning the population structure, Ashjian et al. (2003) reported that C. glacialis around the Northwind Abyssal Plain was dominated by C5 and C6F in September. In the present study, 3 4 the population structure of C. glacialis was dominated by C5 (Fig. 3a), and their MCS 5 (mean±sd: 3.77±0.20) was similar to the reported value for autumn in this region (3.58, 6 Matsuno et al., 2012). Most of the C6F had immature gonads and no ovigerous C6Fs were 7 observed (Fig. 3c). These results corresponded with the year-round observation around the 8 Northwind Abyssal Plain (Ashjian et al., 2003). Calanus glacialis C6F is known to occur at 9 the epipelagic layer in April, just before sea-ice melting (Kosobokova, 1999), and to reproduce with grazing ice algae and ice-edge bloom (Campbell et al., 2009). Thus, because 10 11 this study period (September) greatly varied with regards to their reproduction period (April), most C6Fs were considered to have immature gonads when residing in the lower layer 12 13 (diapause).

14 Nocturnal ascent DVM, which is related to nighttime grazing on phytoplankton, was 15 reported for C. glacialis in the Arctic Ocean during spring and autumn (Runge and Ingram, 1988; Conover and Huntley, 1991). In this study, DVM was observed for C3, C4 and C5 (Fig. 16 17 4). At high-latitude seas, the magnitude of *Calanus* spp. DVM is known to vary with the season and copepodid stage, and their DVM intensity is greater during spring and autumn 18 19 when the diel changes in light penetration are large (Falkenhaug et al., 1997). No DVM of 20 Calanus spp. was reported for lipid accumulated C5 (Falk-Petersen et al., 2008). In the 21 present study, nearly half of the C5 population, which was characterized as having a large lipid accumulation, remained in the lower layer throughout the day (Fig. 4). The deep C5 22 23 population may have already completed lipid accumulation and ceased DVM in the study period (September), while the remaining C5 population with active DVM may have grazed on 24 25 phytoplankton in the upper layer during the night and stored lipid in preparation for diapause. 26 These results suggest that the C. glacialis population in this study was at the seasonal phase 27 just before entering diapause, and this interpretation corresponded well with their life cycle in 28 this region (Ashjian et al., 2003).

29 4.3 Grazing of C. glacialis

The gut pigment of *C. glacialis* in the Arctic Ocean is known to exhibit diel changes and higher levels at night than in the daytime (Conover and Huntley, 1991). Higher gut pigment levels at night were also observed in this study (*U*-test, p < 0.001) (Fig. 5a). Their gut pigments were correlated with the standing stock of chl. *a* (Fig. 5b) and increased during the high chl. *a* period after the SWE (Fig. 5a). These facts suggest that *C. glacialis* feeding responded to the small phytoplankton bloom, which was enhanced by the nutrient supply and vertical mixing caused by the SWE (Nishino et al., 2015; Yokoi et al., submitted).

5

Concerning gut pigment measurement, underestimation by decomposition of 5 phytoplankton pigment through gut passage has been reported (Conover et al., 1986; Head, 6 7 1992). This underestimation is reported to be ca. 0.1–10% of grazing (Conover et al., 1986) 8 and varies with light conditions, grazing behavior and phytoplankton species (Head, 1992). 9 To estimate the grazing impact, data on the gut evacuation rate (k, \min^{-1}) is needed (Mauchline, 1998). The gut evacuation rate is known to have a positive correlation with 10 11 temperature (Dam and Petersen, 1988). From the equation between k and temperature (T: °C): k = 0.00941 + 0.002575T (Mauchline, 1998) and ambient temperature in this study (T: 12 -1.5 to 3.3°C), k would be estimated to be 0.0055–0.0179 min⁻¹. This range covers the value 13 14 applied in the present study (k = 0.017, Tande and Båmstedt, 1985). The value was also at the range observed by our independent laboratory experiments in September 2010 (0.006–0.041, 15 16 Matsuno et al., unpublished data). These facts suggest that the value applied in this study (k =17 0.017) was reasonable for *C. glacialis* in this region.

Assuming that half of the C5 population performed nocturnal ascent and grazing on 18 19 phytoplankton at night, using C:Chl. a ratio (29.9, Sherr et al., 2003), the grazing impact (mg $C m^{-2} dav^{-1}$) of C. glacialis C5 was calculated (Table 2). The grazing impact of this study 20 was estimated to be 4.14 mg C m^{-2} day⁻¹. In the Arctic Ocean, the grazing impact of 21 22 copepods is greatly affected by the extent of sea-ice, environmental conditions and food 23 concentration (Hirche et al., 1991; Campbell et al., 2009). The low grazing impact of this study may be caused by the low feeding activity of C5 just before their diapause and may also 24 be related to the low ambient chl. a (mean: 14.3 mg m⁻²) during the study period. 25

We also estimated the food requirement of C. glacialis C5 to support their metabolism 26 27 under ambient temperature (Ikeda and Motoda, 1978; Ikeda et al., 2001). The potential 28 contribution of phytoplankton food to food requirements was 12.6% for C. glacialis C5 29 (Table 2). This result indicates that C. glacialis C5 could not maintain its population solely 30 on phytoplankton food; other food sources are important. Regarding food for C. glacialis, 31 Campbell et al. (2009) reported that this species prefers microzooplankton rather than phytoplankton in the Chukchi Sea, and Levinsen et al. (2000) noted that the micro-size (> 10 32 µm) ciliates and dinoflagellates are important food sources during post-bloom. For the 33

10

1 microplankton community during the study period, Yokoi et al. (submitted) noted that not 2 only diatoms $(1.64-14.11 \text{ cells ml}^{-1})$ but also dinoflagellates $(0.54-2.42 \text{ cells ml}^{-1})$ and 3 ciliates $(0.14-2.76 \text{ cells ml}^{-1})$ were abundant. Thus, as food sources for *C. glacialis*, 4 microzooplankton (dinoflagellates and ciliates) are considered to be important in the Chukchi 5 Sea during autumn.

6 **5 Conclusions**

7 Throughout this study, short-term changes in the mesozooplankton community and the 8 grazing impact of C. glacialis were evaluated in the Chukchi Sea during autumn. During the 9 16-day sampling/observation period, the zooplankton community showed no clear changes related to the SWE and dominant copepods prepared for diapause (i.e., stored lipids in the 10 11 pre-adult stage or adults with immature gonads). On the other hand, the feeding intensity of 12 dominant copepods increased with the reflection of the temporal phytoplankton bloom, which 13 was enhanced by the SWE (Nishino et al., 2015). Thus, the temporal phytoplankton bloom 14 caused by the atmospheric turbulence (SWE) during autumn may have had a positive indirect effect on mesozooplankton (SWE \rightarrow nutrient supply from the deep layer \rightarrow small 15 phytoplankton bloom \rightarrow copepod feeding) within a short period. These facts suggest that 16 17 some zooplankton may obtain benefit from an extension of the primary production season with more turbulence and later freeze-up of the Chukchi Sea. 18

19 Author contributions

S.N., J.I. and T.K. designed and coordinated this research project. S.N. and J.I. were chief
scientists during the MR13-06 cruise of R.V. *Mirai*. K.M. collected the zooplankton samples,
measured copepod gut pigments during the cruise and performed species identification and
enumeration of the zooplankton samples in the land laboratory. K.M. and A.Y. wrote the
manuscript with contributions from all co-authors.

25 Acknowledgements

We are grateful to the captain, officers and crew of the R.V. *Mirai* (JAMSTEC), operated by GODI, for their help in the sample collection. This study was supported by the Green Network of Excellence Program's (GRENE Program) Arctic Climate Change Research Project: 'Rapid Change of the Arctic Climate System and its Global Influences.' This study was partially supported by a Grant-in-Aid for Scientific Research (A) (24248032) and a Grant-in-Aid for Scientific Research on Innovative Areas (24110005) from the JSPS.

32

1 References

- Ashjian, C. J., Campbell, R. G., Welch, H. E., Butler, M., and Keuren, D. V.: 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, 2003.
- Ashjian, C. J., Braund, S. R., Campbell, R. G., George, J. C. C., Kruse, J., Maslowski, W.,
 Moore, S. E., Nicolson, C. R., Okkonen, S. R., Sherr, B. F., Sherr, E. B., and Spitz, Y.
 H.: Climate variability, oceanography, bowhead whale distribution, and Iñupiat
 subsistence whaling near Barrow, Alaska, Arctic, 63, 179–194, 2010.
- Brodsky, K. A.: Calanoida of the far-eastern seas and polar basin of the USSR. Israel Program
 Scientific Translation, Jerusalem, 1967.
- Cabe, G. J., Clark, M. P., and Serreze, M. C.: Trends in northern hemisphere surface cyclone
 frequency and intensity, J. Climate, 14, 2763–2768, 2001.
- Campbell, R. G., Sherr, E. B., Ashjian, C. J., Plourde, S., Sherr, B. F., Hill, V., and Stockwell,
 D. A.: Mesozooplankton prey preference and grazing impact in the western Arctic
 Ocean, Deep-Sea Res. II, 56, 1274–1289, 2009.
- Clare, A. S. and Walker, G.: Further studies on the control of the hatching process in *Balanus balanoides* (L), J. Exp. Mar. Biol. Ecol., 97, 295–304, 1986.
- Comiso, J. C., Parkinson, C. L., Gersten, R., and Stock, L.: Accelerated decline in the Arctic
 sea ice cover, Geophys. Res. Lett., 35, L01703. doi: 10.1029/2007GL031972, 2008.
- Conover, R. J. and Huntley, M.: 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, 1991.
- Conover, R. J., Durvasula, R., Roy, S., and Wang, R.: Probable loss of chlorophyll-derived
 pigments during passage through the gut of zooplankton, and some of the
 consequences, Limnol. Oceanogr., 31, 878–887, 1986.
- Crisp, D. J.: Release of larvae by barnacles in response to the available food supply, Anim.
 Behav., 10, 382–383, 1962.
- Dam, H. G. and Peterson, W. T.: The effect of temperature on the gut clearance rate constant
 of planktonic copepods, J. Exp. Mar. Biol. Ecol., 123, 1–14, 1988.

1	Dvoretsky, V. G. and Dvoretsky, A. G.: Life cycle of Oithona similis (Copepoda:
2	Cyclopoida) in Kola Bay (Barents Sea), Mar. Biol., 156, 1433-1446, 2009.
3	Falkenhaug, T., Tande, K. S., and Semenova, T.: Diel, seasonal and ontogenetic variations in
4	the vertical distributions of four marine copepods, Mar. Ecol. Prog. Ser., 149,
5	105–119, 1997.
6	Falk-Petersen, S., Leu, E., Berge, J., Kwasniewski, S., Nygård, H., Røstad, A., Keskinen, E.,
7 8	Thormar, J., von Quillfeldt, C., Wold, A., and Gulliksen, B.: Vertical migration in high Arctic waters during autumn 2004, Deep-Sea Res. II, 55, 2275–2284, 2008.
9 10	Falk-Petersen, S., Mayzaud, P., Kattner, G., and Sargent, J. R.: Lipids and life strategy of Arctic <i>Calanus</i> , Mar. Biol. Res., 5, 18–39, 2009.
11 12	Frost, B. W.: <i>Calanus marshallae</i> , a new species of calanoid copepod closely allied to the sibling species <i>C. finmarchicus</i> and <i>C. glacialis</i> , Mar. Biol., 26, 77–99, 1974.
13 14	Frost, B. W.: A taxonomy of the marine calanoid copepod genus <i>Pseudocalanus</i> , Can. J. Zool., 67, 525–551, 1989.
15 16 17	 Gnaiger, E.: Calculation of energetic and biochemical equivalents of respiratory oxygen consumption, in: Polarographic oxygen sensors, edited by: Gnaiger, E., and Horstner, H., Springer-Verlag, Berlin, 337–345, 1983.
18 19	Grebmeier, J. M.: Shifting patterns of life in the pacific Arctic and sub-Arctic Seas, Annu. Rev. Mar. Sci., 4, 63–78, 2012.
20 21	Head, E. J. H.: Gut pigment accumulation and destruction by arctic copepods <i>in vitro</i> and <i>in situ</i> , Mar. Biol., 112, 583–592, 1992.
22 23	Herz, L. E.: The morphology of the later stages of <i>Balanus crenatus</i> Bruguiere, Biol. Bull., 64, 432–442, 1933.
24 25	Hirche, HJ. and Niehoff, B.: Reproduction of the Arctic copepods <i>Calanus hyperboreus</i> in the Greenland sea-field and laboratory observations, Polar Biol., 16, 209–219, 1996.
26 27 28	 Hirche, HJ., Baumann, M. E. M., Kattner, G., and Gradinger, R.: Plankton distribution and the impact of copepod grazing on primary production in Fram Strait, Greenland Sea, I. Mar. Syst. 2, 477–494, 1991
_0	v. 11101. 0 jou, 2, 1/7 17 1, 1771.

1 2	Hopcroft, R. T., Kosobokova, K. N., and Pinchuk, A. I.: Zooplankton community patterns in the Chukchi Sea during summer 2004, Deep-Sea Res. II, 57, 27–39, 2010.
3 4	Ikeda, T. and Motoda, S.: Estimated zooplankton production and their ammonia excretion in the Kuroshio and adjacent seas, Fish. Bull., 76, 357–367, 1978.
5 6 7	Ikeda, T., Kanno, Y., Ozaki, K., and Shinada, A.: Metabolic rates of epipelagic marine copepods as a function of body mass and temperature, Mar. Biol., 139, 587–596, 2001.
8 9	Kawamura, A.: Fast sinking mouth ring for closing Norpac net, Bull. Japan. Soc. Sci. Fish., 55, 1121, 1989.
10 11	Kosobokova, K. N.: The reproduction cycle and life history of the Arctic copepod <i>Calanus glacialis</i> in the White Sea, Polar Biol., 22, 254–263, 1999.
12 13 14	Lane, P. V. Z., Llinás, L., Smith, S. L., and Pilz, D.: Zooplankton distribution in the western Arctic during summer 2002: Hydrographic habitats and implications for food chain dynamics, J. Mar. Syst., 70, 97–133, 2008.
15 16 17	Levinsen, H., Turner, J. T., Nielsen, T. G., and Hansen, B. W.: On the trophic coupling between protists and copepods in arctic marine ecosystem, Mar. Ecol. Prog. Ser., 204, 65–77, 2000.
18 19	Llinás, L., Pickart, R. S., Mathis, J. T., and Smith, S. L.: Zooplankton inside an Arctic Ocean cold-core eddy: probable origin and fate, Deep-Sea Res. II, 56, 1290–1304, 2009.
20 21	Longhurst, A., Sameoto, D., and Herman, A.: Vertical distribution of Arctic zooplankton in summer: eastern Canadian archipelago, J. Plankton Res., 6, 137–168, 1984.
22 23 24	Lowry, L. F., Sheffield, G., and George, C.: Bowhead whale feeding in the Alaskan Beaufort Sea, based on stomach contents analyses. J. Cetacean Res. Manage., 6, 215–223, 2004.
25 26	Mackas, D. and Bohrer, R.: Fluorescence analysis of zooplankton gut contents and an investigation of diel feeding patterns. J. Exp. Mar. Biol. Ecol., 25, 77–85, 1976.
27 28	Marin, V.: The oceanographic structure of eastern Scotia Sea-IV. Distribution of copepod species in relation to hydrography in 1981, Deep-Sea Res. A, 34, 105–121, 1987.

- Markus, T., Stroeve, J. C., and Miller, J.: Recent changes in Arctic sea ice melt onset,
 freezeup, and melt season length. J. Geophys. Res., 114, C12024. doi:
 10.1029/2009JC005436, 2009.
- Matsuno, K., Yamaguchi, A., Hirawake, T., and Imai, I.: Year-toyear changes of the
 mesozooplankton community in the Chukchi Sea during summers of 1991, 1992 and
 2007, 2008. Polar Biol., 34, 1349–1360, 2011.
- Matsuno, K., Yamaguchi, A., Shimada, K., and Imai, I.: Horizontal distribution of calanoid
 copepods in the western Arctic Ocean during the summer of 2008. Polar Sci., 6,
 105–119, 2012.
- 10 Mauchline, J.: The biology of calanoid copepods, Adv. Mar. Biol., 33, 1–660, 1998.
- Miller, C. B.: *Neocalanus flemingeri*, a new species of calanidae (copepoda: calanoida) from
 the subarctic Pacific Ocean, with a comparative redescription of *Neocalanus plumchrus* (Marukawa) 1921, Prog. Oceanog., 20, 223–273, 1988.
- 14 Motoda, S.: North Pacific standard plankton net, Inf. Bull. Planktol. Jpn., 4, 13–15, 1957.
- Nielsen, T. G., Møller, E. F., Satapoomin, S., Ringuette, M., and Hopcroft, R. R.: Egg
 hatching rate of the cyclopoid copepod *Oithona similis* in arctic and temperate waters,
 Mar. Ecol. Prog. Ser., 236, 301–306, 2002.
- Nishino, S., Kawaguchi, Y., Inoue, J., Hirawake, T., Fujiwara, A., Futsuki, R., Onodera, J.,
 and Aoyama, M.: Nutrient supply and biological response to wind-induced mixing,
 inertial motion, internal waves, and currents in the northern Chukchi Sea, J. Geophys.
 Res. C, 120, 1975–1992, 2015.
- Pielou, E. C.: The measurement of diversity in different types of biological collections. J.
 Theor. Biol., 13, 131–144, 1966.
- Runge, J. A. and Ingram, R. G.: Underice grazing by planktonic, calanoid copepods in
 relation to a bloom of ice microalgae in southeastern Hudson Bay, Limnol.
 Oceanogr., 33, 280–286, 1988.
- Sepp, M. and Jaagus, J. Changes in the activity and tracks of Arctic cyclones, Climate Change,
 105, 577–595, 2011.
- Serreze, M. C., Walsh, J. E., Chapin III, F. S., Osterkamp, T., Dyurgerov, M., Romanovsky,
 V., Oechel, W. C., Morison, J., Zhang, T., and Barry, R. G. Observational evidence

1	of recent change in the northern high-latitude environment, Climate Change, 46
2	159–207, 2000.

- Shannon, C. E., and Weaver, W.: The Mathematical Theory of Communication. The
 University of Illinois Press, Urbana, 1949.
- Sherr, E. B., Sherr, B. F., Wheeler, P. A., and Thompson, K.: 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, 2003.
- 8 Springer, A. M., McRoy, C. P., and Turco, K. R.: The paradox of pelagic food web in the
 9 northern Bering Sea-II. Zooplankton communities. Cont. Shelf Res., 9, 359–386,
 10 1989.
- Stroeve, J., Holland, M. M., Meier, W., Scambos, T., and Serreze, M.: Arctic sea ice decline:
 Faster than forecast. Geophys. Res. Lett., 34, L09501. doi: 10.1029/2007GL029703,
 2007.
- Tande, K. S. and Bámstedt, U.: Grazing rates of the copepods *Calanus glacialis* and *C. finmarchicus* in arctic waters of the Barents Sea, Mar. Biol., 87, 251–258, 1985.
- Weingartner, T., Aagaard, K., Woodgate, R., Danielson, S., Sasaki, Y., and Cavalieri, D.:
 Circulation on the north central Chukchi Sea shelf, Deep-Sea Res. II, 52, 3150–3174,
 2005.
- Yokoi, N., Matsuno, K., Ichinomiya, M., Yamaguchi, A., Nishino, S., Onodera, J., Inoue, J.,
 and Kikuchi, T.: Short-term changes of microplankton community in the Chukchi
 Sea during autumn: Consequence of strong wind event, Biogeosciences, submitted.
- Zhang, X., Walsh, J. E., Zhang, J., Bhatt, U. S., and Ikeda, M.: Climatology and interannual
 variability of Arctic cyclone activity: 1948–2002, J. Climate, 17, 2300–2317, 2004.
- 24

1 Figure captions

- Figure 1. Location of sampling station in the Chukchi Sea from 10 to 25 September 2013.
 Arrows indicate major current flows in this region (cf. Grebmeier, 2012).
- 4 Figure 2. Temporal changes in temperature (a), salinity (b), chlorophyll *a* (c) and T-S
 5 diagram (d) at a fixed-station in the Chukchi Sea from 10 to 25 September 2013.
- Figure 3. *Calanus glacialis*: temporal changes in the population structure (a), lipid
 accumulation of C5 (b) and gonad maturation of C6F (c) at a fixed station in the
 Chukchi Sea from 10 to 25 September 2013.
- Figure 4. Diel vertical distribution of *Calanus glacialis* at a fixed-station in the Chukchi Sea,
 14 and 22 September 2013. For C5, the mean lipid accumulation score (1–3) is also
 shown. Note that no C6Ms were collected.
- Figure 5. *Calanus glacialis*: temporal and diel changes in the gut pigment of C5 (a) at a fixed station in the Chukchi Sea from 10 to 25 September 2013. The relationship between the gut pigment of C5 and standing stock chlorophyll *a* (b). Dotted and dashed lines indicate regressions for day and night, respectively. For (b), "whole" indicates including all data, both day and night. **: p < 0.01, *: p < 0.05.
- 17Figure 6. Temporal changes in the grazing rate of Calanus glacialis C5 (a), integrated size-18fractionated chlorophyll a (b) and the grazing impact of C. glacialis C5 on micro-19phytoplankton (> 10 µm) (c) at a fixed station in the Chukchi Sea from 10 to 2520September 2013.
- 21

Table 1. List of mesozooplankton taxa and calanoid copepod species and their mean abundances (ind. m⁻²) at a fixed station in the Chukchi Sea from 10 to 18 September, before the strong wind event (SWE), and 19–25 September (after the SWE), 2013.
For calanoid copepods, Shannon species diversity and Pielou evenness were calculated. Differences between the two periods (before vs. after the SWE) were tested with the *U*-test. *: p < 0.05, **: p < 0.01, ***: p < 0.0001, NS: not significant.

Species/taxa	Before SWE	After SWE	II to st
Community parameters	(10-18 Sep.)	(19-25 Sep.)	U-test
Calanoid copepods			
Acartia longiremis	604	542	NS
Calanus glacialis	6714	5658	NS
Calanus hyperboreus	0	5	NS
Centropages abdominalis	9	29	*
Eucalanus bungii	6	6	NS
Eurytemora herdmani	0	2	NS
Metridia pacifica	251	154	*
Microcalanus pygmaeus	6	3	NS
Neocalanus cristatus	6	5	NS
Neocalanus flemingeri	46	65	NS
Neocalanus plumchrus	12	15	NS
Pseudocalanus acuspes	3393	3254	NS
Pseudocalanus mimus	1194	1296	NS
Pseudocalanus minutus	2178	2387	NS
Pseudocalanus newmani	2805	2774	NS
Pseudocalanus spp. (C1–C4)	2758	2980	NS
Cyclopoid copepods	511	1153	**
Poecilostomatoid copepods	0	3	NS
Amphipoda	9	5	NS
Appendicularia	707	442	*

Barnacle larva	12118	8945	***
Chaetognatha	1281	1039	NS
Echinodermata larva	31	61	NS
Eubrachyura zoea	41	26	NS
Euphausiacea	18	3	*
Gymnosomata	172	84	**
Hydrozoa	209	205	NS
Isopoda	3	3	NS
Polychaeta	1124	1005	NS
Thecosomata	16	8	NS
Total zooplankton	36223	32154	NS
Shannon species diversity	1.85	1.90	NS
Pielou evenness	0.80	0.82	NS

Table 2. *Calanus glacialis*: Comparison of food requirements (ingestion) and grazing rate on
phytoplankton and the proportion of phytoplankton food in the Chukchi Sea from 10
to 25 September 2013. Food requirements were calculated from the metabolism,
which was estimated by the body mass, temperature (Ikeda et al., 2001), respiratory
quotient (Gnaiger, 1983) and individual carbon budget (Ikeda and Motoda, 1978).
For details on the values used in this calculation, see the footnotes.

Day/night		Flux (mg C m^{-2} da	Proportion of phytoplankton	
(depth, temp.: <i>T</i> , period)	Metabolism	Food requirement (ingestion) (A)	Grazing rate on phytoplankton (B)	food (%: B/A)
Day-lower layer	5.64	14.11	_	_
(20–49 m, –0.74°C, 11 h)				
Night-upper layer	4.12	10.29	-	_
(0–20 m, 2.31°C, 13 h)				
Night-lower layer	3.34	8.34	_	-
(20–49 m, –0.74°C, 13 h)				
Daily-water column	13.10	32.74	4.14	12.6

7 Dry mass (*DM*: mg ind.⁻¹) of *C. glacialis* C5 was 0.654 (Matsuno et al., unpublished data).

8 Oxygen consumption (μ L O₂ ind.⁻¹ h⁻¹) = exp(-0.399+0.801×Ln(*DM*)+0.069×*T*)) (Ikeda et al.,

9 2001).

10 Respiratory quotient ([CO₂/O₂]) was assumed to be 0.97 (Gnaiger, 1983).

11 Metabolism was assumed to be 0.4 (40%) of ingestion (Ikeda and Motoda, 1978).

12 Mean abundance of *C. glacialis* C5 was 2176 ind. m^{-2} during this study period.

13 C:Chl ratio was 29.9 for September in this region (Sherr et al., 2003).





Fig. 2. (Matsuno et al.)









Fig. 6. (Matsuno et al.)