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Short-term changes of the mesozooplankton community

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Short-term changes of the mesozooplankton community and copepod gut pigment in the Chukchi Sea in autumn

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

¹Arctic Environment Research Center, National Institute of Polar Research, 10-3 Midori-cho, Tachikawa, Tokyo 190-8518, Japan

²Laboratory of Marine Biology, Graduate School of Fisheries Sciences, Hokkaido University, 3-1-1 Minato-cho, Hakodate, Hokkaido 041-8611, Japan

³Japan Agency for Marine-Earth Science and Technology, 2-15 Natsushima-cho, Yokosuka, Kanagawa 237-0061, Japan

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

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Abstract

In the Chukchi Sea, due to the recent drastic reduction of sea-ice during the summer, an increasing formation of atmospheric turbulence has been reported. However, the importance and effects of atmospheric turbulence on the marine ecosystem are not fully understood in this region. To evaluate the effect of atmospheric turbulence on the marine ecosystem, high-frequent sampling (two to four times per day) on the mesozooplankton community and the gut pigment of dominant copepods were made at a fixed station in the Chukchi Sea from 10 to 25 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, especially for micro-size ($> 10 \mu\text{m}$) fractions. Zooplankton abundance ranged 23 610–56 809 ind. m^{-2} and exhibited no clear changes with SWE. In terms of abundance, calanoid copepods constituted the most dominated taxa (mean: 57 %), followed by barnacle larvae (31 %). Within the calanoid copepods, small-sized *Pseudocalanus* spp. (65 %) and large-sized *Calanus glacialis* (30 %) dominated. In the population structure of *C. glacialis*, copepodid stage 5 (C5) 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 preparing for seasonal diapause. The gut pigment of *C. glacialis* C5 was higher at night and was correlated with ambient chl *a*, and a significant increase was observed after SWE (2.6 vs. 4.5 ng pigment ind. $^{-1}$). Assuming C:Chl *a* ratio, the grazing impact by *C. glacialis* C5 was estimated to be 4.14 mg C $\text{m}^{-2} \text{day}^{-1}$, which corresponded to 0.5–4.6 % of the standing stock of micro-size phytoplankton. 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 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, temporal phytoplankton bloom, which is enhanced by the atmospheric turbulence (SWE) in autumn, may have a positive effect on copepod nutrition. However, because of the

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relatively long generation length of copepods, a smaller effect was detected for their abundance, population structure, lipid accumulation and gonad maturation within the short-term period (16 days).

1 Introduction

In marine ecosystems of the western Arctic Ocean, mesozooplankton is a secondary producer and an important food 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: i.e., *Calanus glacialis*, *Calanus hyperboreus*, *Metridia longa* and *Pseudocalanus* spp. In the southern Chukchi Sea, large Pacific copepods (e.g., *Calanus marshallae*, *Neocalanus cristatus*, *Neocalanus flemingeri*, *Neocalanus plumchrus*, *Eucalanus bungii* and *Metridia pacifica*) dominated in biomass because of the inflow of Pacific water. Thus, the zooplankton community in this region is greatly governed by water mass formation (Hopcroft et al., 2010; Matsuno et al., 2011, 2012). Concerning seasonal change, a comparison of the zooplankton community between summer and autumn (Llinás et al., 2009) and year-round changes based on the two-week sampling interval at a drifting ice station in the Arctic basin were reported (Ashjian et al., 2003). However, short-term changes in the zooplankton community based on high-frequent sampling (two to four times per day) have 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

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September 2013, high-frequent 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., 2015). 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-frequent samplings made simultaneously by Nishino et al. (2015) and Yokoi et al. (2015). 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., 2015) on the mesozooplankton community in the Chukchi Sea in autumn.

2 Materials and methods

2.1 Field sampling

Zooplankton samplings were conducted at a fixed station in the Chukchi Sea (72°45' N, 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 45 cm, mesh size 335 μ m; Motoda, 1957) and ring net (mouth diameter 80 cm, mesh size 335 μ m) from 49 m depth to the sea surface two to four times per day (total of 47 times) including both day and night. Zooplankton samples collected by NORPAC nets were preserved with 5% buffered formalin 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 night vertical stratified hauls with closing PCP nets (mouth diameter 45 cm, mesh size 62 μ m; Kawamura, 1989) from two layers (0–20 m and 20–49 m) were made on 14 and 22 September. The samples from the PCP net were preserved with 5% buffered formalin.

following equation:

$$GI = GR_{ind.} \times N / \text{Int. chl } a \times 100, \quad (2)$$

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).

2.3 Zooplankton community

In the land laboratory, identification and enumeration with taxa were performed on zooplankton samples collected by NORPAC nets under a stereomicroscope. For dominant taxa (calanoid copepods), identification was made with 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 pro-some 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).

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

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

where i is the number of the copepodid stage (1–6 indicates C1–C6), and A_i (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., 2015). To evaluate the effect of SWE, the abundances of each zooplankton taxon and species were compared between “before SWE (10–18 September)” and “after SWE (19–25 September)” using the U test. This statistical analysis was performed with Stat View.

3 Results

3.1 Hydrography

During the sampling period, the temperature ranged from -1.5 to 3.3 °C, and thermocline was observed at a depth of approximately 25 m (Fig. 2a). Cold water below 0 °C continuously 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 was observed at approximately 25 m, which was parallel to thermocline (Fig. 2b). Salinity 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 after the SWE (Fig. 2c). The T – S diagram showed that the hydrographic conditions in the upper layer changed temporally; thus, temperature decreased while salinity increased during the study period (Fig. 2d).

3.2 Zooplankton community

Zooplankton abundance ranged from 23 610–56 809 ind. m⁻², and calanoid copepods and barnacle larvae composed 57 and 31 % of the community, respectively (Table 1). For calanoid copepods, 15 species belonging to nine genera were identified. Within them, *Pseudocalanus* spp. and *C. glacialis* dominated and composed 65 and 30 % of

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significantly after the SWE (0.11 vs. 0.18 mg pigment $m^{-2} day^{-1}$, U test, $p < 0.05$). During the study period, chl a peaked at 18 September, and micro-size ($> 10 \mu m$) dominated (54 % of total chl a), especially after the SWE (66 %) (Fig. 6b). The grazing impact of *C. glacialis* C5 on micro-size chl a ranged from 0.5–4.6 % on chl a standing stock day^{-1} and was high before the SWE from 10 to 15 September (Fig. 6c).

4 Discussion

4.1 Zooplankton community

The zooplankton community in the Chukchi Sea is known to have greater spatial and temporal changes (Springer et al., 1989; Llinás et al., 2009; Matsuno et al., 2011). According to Matsuno et al. (2012), the calanoid copepod community in the western Arctic Ocean during the autumn could be divided into three groups (Shelf, Slope and Basin) that vary with depth. According to their criteria, a shallower bottom depth and higher temperature and salinity indicate that the zooplankton community in this study corresponded to the Shelf group defined by Matsuno et al. (2012). As characteristics of the Shelf group, high zooplankton abundance (mean: $75\,683$ ind. m^{-2}) and dominance of neritic (*Pseudocalanus* spp. and *Centropages abdominalis*) and Pacific copepods (*Eucalanus bungii*, *Neocalanus cristatus* and *Metridia pacifica*) were reported (Matsuno et al., 2012).

Comparing the above characteristics by Matsuno et al. (2012), the zooplankton abundance of this study was nearly half (mean: $34\,059$ ind. m^{-2}), there was a low abundance of small copepod *Pseudocalanus* spp. and cyclopoid copepods, and no occurrence of Arctic copepod *Metridia longa* was remarkable (Table 1). For the hydrography of this station, Nishino et al. (2015) noted that the upper warm and less saline water was the Pacific Summer water, 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 Arctic Ocean during winter. Geographically, the

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present station was located at a main stream 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 study was thought to be a reflection of the water mass covering the station.

5 Seasonal characteristics during summer included the addition of holoplankton and the dominance of the meroplankton (barnacle and bivalve larvae), which composed 39% of zooplankton abundance (Hopcroft et al., 2010). Dominance of the barnacle larvae also occurred in this study (Table 1). Benthic barnacle adults released their larvae when they met phytoplankton blooms (Crisp, 1962; Clare and Walker, 1986),
10 and their larvae spent two to three weeks at water columns and then settled (Herz, 1933). The abundance of barnacle larvae in this study (mean 10 430 ind. m⁻²) was 13–55% lower than that in summer (19 114–79 899 ind. m⁻², Matsuno et al., 2011). It also should be noted that the abundance of barnacle larvae decreased significantly during the study period (Table 1). These facts suggest that most of the barnacle larvae may
15 have ended the planktonic phase and settled to the sea bottom during the study period (autumn).

Concerning the effect of the SWE, several limited taxa and species showed significant changes in abundance (Table 1). Within them, the decrease of barnacle larvae may have been caused by their seasonal settlement and was not related to the
20 SWE. For dominant species, cyclopoid copepods were increased after the SWE (Table 1). The generation length of cyclopoid copepods was reported to be two to three months in the Arctic Ocean (Dvoretsky and Dvoretsky, 2009). In ambient temperature (–1.5 to 3.3 °C), the egg hatching of this taxon is estimated to be 11–41 days (Nielsen et al., 2002). These facts suggest that the increase of cyclopoid copepods would not be
25 caused by their reproduction within the study period (16 days). As an alternative cause, the horizontal 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 abundance was relatively small because of the longer generation length of mesozooplankton in this region.

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4.2 Population structure of *C. glacialis*

Calanus glacialis is a key species that dominates in the zooplankton biomass and commonly occurs in the continental shelf throughout the Arctic Ocean (Conover and Huntley, 1991; Lane et al., 2008). The generation length of this species is known to vary from one to three years (mostly two years) depending on annual primary productivity in each region (Falk-Petersen et al., 2009). For the life cycle of *C. glacialis*, they grow to C3–C4 at the epipelagic layer during the first summer, then descend to the deep layer and enter diapause, developing to C5 at the epipelagic layer in the second summer, then down to the deep layer and molting to the adult stage (C6) using stored lipid as energy. They reproduce at the epipelagic layer, using the grazed phytoplankton bloom as energy (Longhurst et al., 1984; Ashjian et al., 2003; Falk-Petersen et al., 2009).

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, the population structure of *C. glacialis* was dominated by C5 (Fig. 4a), and their MCS (mean \pm SD: 3.77 ± 0.20) was similar to the reported value for autumn in this region (3.58, Matsuno et al., 2012). Most of the C6F had immature gonads and no ovigerous C6Fs were observed (Fig. 4c). These results corresponded with the year-round observation around the Northwind Abyssal Plain (Ashjian et al., 2003). *Calanus glacialis* C6F is known to occur at 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 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 (diapause).

Nocturnal ascent DVM, which is related to nighttime grazing on phytoplankton, was 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. 3). 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

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and ambient temperature in this study ($T = -1.5$ to 3.3 °C), k would be estimated to be 0.0055 – 0.0179 min^{-1} . This range covers the value 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 , Matsuno et al. unpublished data). These facts suggest that the value applied in this study ($k = 0.017$) was reasonable for *C. glacialis* in this region.

Assuming that half of the C5 population performed nocturnal ascent and grazing on phytoplankton at night, using C : Chl *a* ratio (29.9, Sherr et al., 2003), the grazing impact ($\text{mgCm}^{-2} \text{day}^{-1}$) of *C. glacialis* C5 was calculated (Table 2). The grazing impact of this study was estimated to be 4.14 $\text{mgCm}^{-2} \text{day}^{-1}$, which was lower than the reported value (Tande and Båmstedt, 1985). In the Arctic Ocean, the grazing impact of copepods is greatly affected by the extent of sea-ice, environmental conditions and food 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 be related to the low ambient chl *a* (mean: 14.3 mgm^{-2}) during the study period.

We also estimated the food requirement of *C. glacialis* C5 to support their metabolism under ambient temperature (Ikeda and Motoda, 1978; Ikeda et al., 2001). The proportion of phytoplankton food to food requirements was 12.6% for *C. glacialis* C5 (Table 2). This result indicates that *C. glacialis* C5 could not maintain its population solely on phytoplankton food; other food sources are important. Regarding food for *C. glacialis*, 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 μm) ciliates and dinoflagellates are important food sources during post-bloom. For the microplankton community during the study period, Yokoi et al. (2015) noted that not only diatoms (1.64 – 14.11 cells mL^{-1}) but also dinoflagellates (0.54 – 2.42 cells mL^{-1}) and ciliates (0.14 – 2.76 cells mL^{-1}) were abundant. Thus, as food sources for *C. glacialis*, microzooplankton (dinoflagellates and ciliates) are considered to be important in the Chukchi Sea during autumn.

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5 Conclusions

Throughout this study, short-term changes in the mesozooplankton community and the grazing impact of dominant copepods were evaluated in the Chukchi Sea during autumn. During the 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 pre-adult stage or adults with immature gonads). On the other hand, the feeding intensity of dominant copepods increased with the reflection of the temporal phytoplankton bloom, which was enhanced by the SWE (Nishino et al., 2015). Thus, the temporal phytoplankton bloom caused by the atmospheric turbulence (SWE) during autumn may have had a positive indirect effect on mesozooplankton (SWE → nutrient supply from the deep layer → small phytoplankton bloom → copepod feeding) within a short period. However, because of the relatively long generation length of copepods, a smaller effect was detected for their abundance, population structure, lipid accumulation and gonad maturation within the short-term period.

Author contributions. S. Nishino, J. Inoue, and T. Kikuchi designed and coordinated this research project. S. Nishino and J. Inoue were chief scientists during the MR13-06 cruise of R.V. *Mirai*. K. Matsuno 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. Matsuno and A. Yamaguchi wrote the manuscript with contributions from all co-authors.

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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). Details on the values used in this calculation: dry mass (DM: mg ind.^{-1}) of *C. glacialis* C5 was 0.654 (Matsuno et al., unpublished data). Oxygen consumption ($\mu\text{L O}_2 \text{ ind.}^{-1} \text{ h}^{-1}$) = $\exp(-0.399 + 0.801 \times \ln(\text{DM}) + 0.069 \times T)$ (Ikeda et al., 2001). Respiratory quotient ($[\text{CO}_2/\text{O}_2]$) was assumed to be 0.97 (Gnaiger, 1983). Metabolism was assumed to be 0.4 (40 %) of ingestion (Ikeda and Motoda, 1978). Mean abundance of *C. glacialis* C5 was 2176 ind. m^{-2} during this study period. C : Chl ratio was 29.9 for September in this region (Sherr et al., 2003).

Day/night (depth, temp.: T , period)	Metabolism	Flux ($\text{mg C m}^{-2} \text{ day}^{-1}$)		Proportion of phytoplankton food (%: B/A)
		Food requirement (ingestion) (A)	Grazing rate on phytoplankton (B)	
Day-lower layer (20–49 m, -0.74°C , 11 h)	5.64	14.11	–	–
Night-upper layer (0–20 m, 2.31°C , 13 h)	4.12	10.29	–	–
Night-lower layer (20–49 m, -0.74°C , 13 h)	3.34	8.34	–	–
Daily-water column	13.10	32.74	4.14	12.6

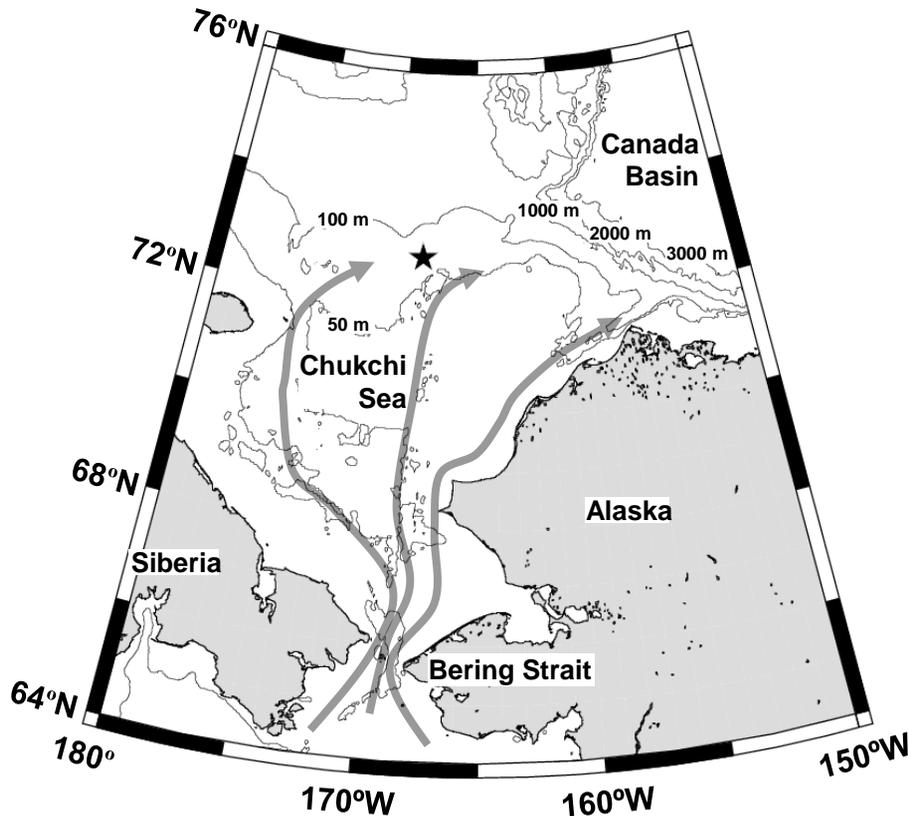


Figure 1. Location of sampling station in the Chukchi Sea from 10 to 25 September 2013. Depth contours (50, 100, 1000, 2000 and 3000 m) are superimposed. Arrows indicate major current flows in this region (cf. Grebmeier, 2012).

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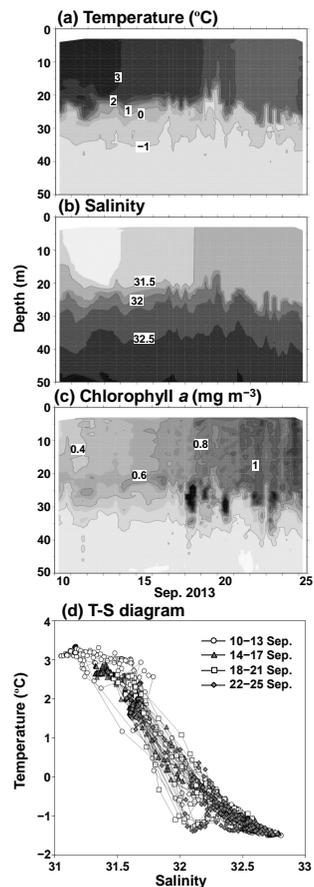


Figure 2. Temporal changes in temperature (a), salinity (b), chlorophyll *a* (c) and *T*–*S* diagram (d) at a fixed-station in the Chukchi Sea from 10 to 25 September 2013.

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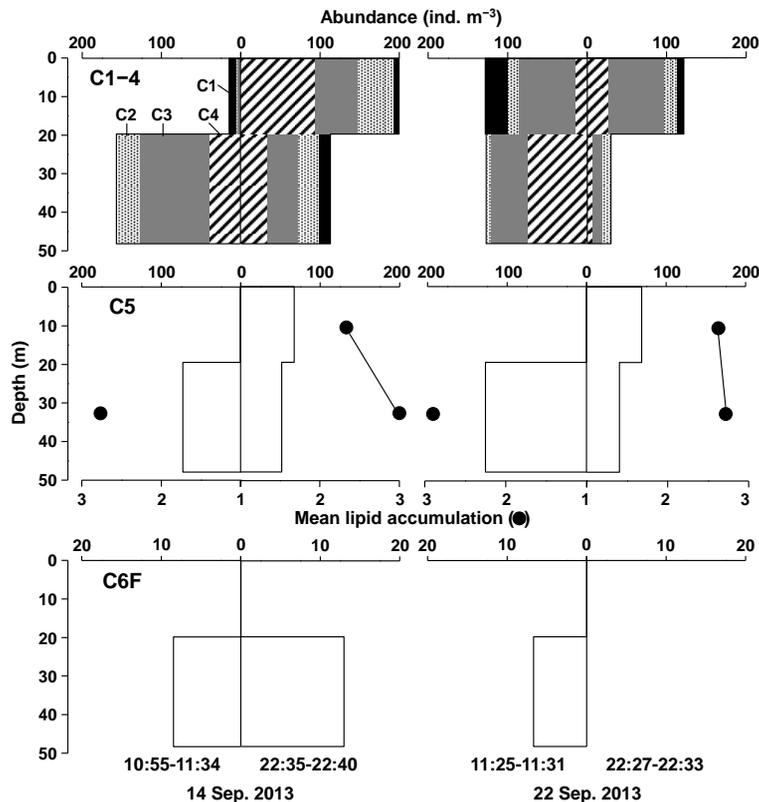


Figure 3. Diel vertical distribution of *Calanus glacialis* at a fixed-station in the Chukchi Sea, 14 and 22 September 2013. For C5, the mean lipid accumulation score (1–3) is also shown. Note that no C6Ms were collected.

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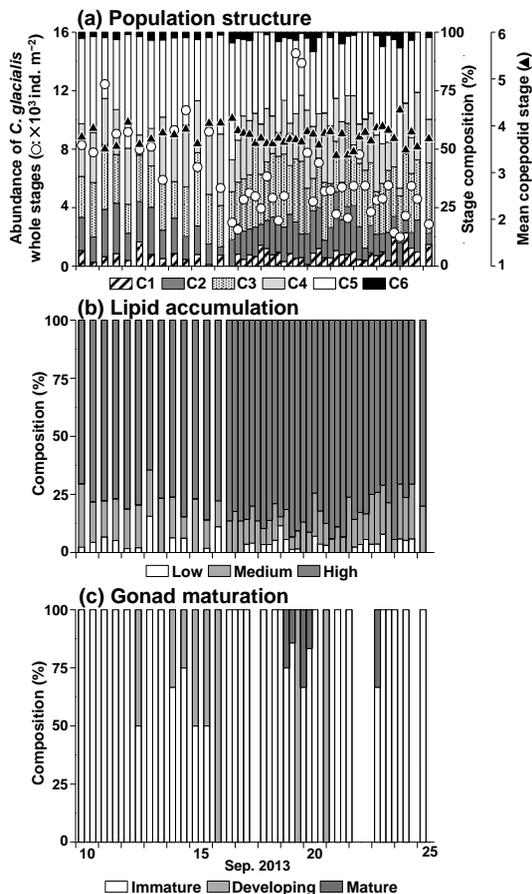


Figure 4. *Calanus glacialis*: temporal changes in the population structure (a), lipid accumulation of C5 (b) and gonad maturation of C6F (c) at a fixed station in the Chukchi Sea from 10 to 25 September 2013.

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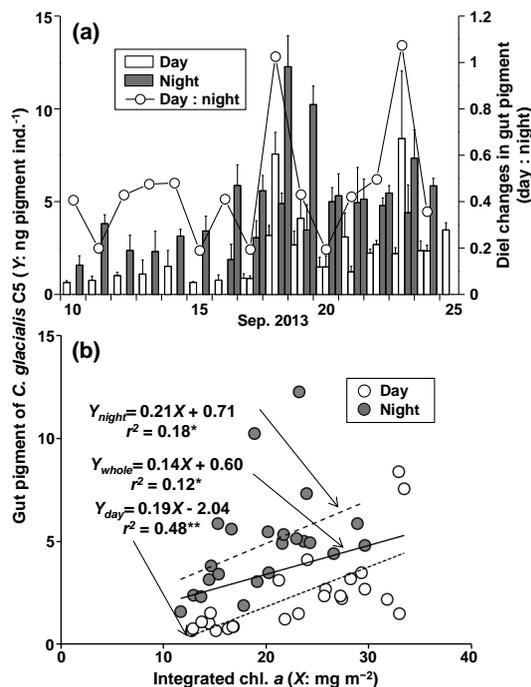


Figure 5. *Calanus glacialis*: temporal and diel changes in the gut pigment of C5 **(a)** at a fixed station in the Chukchi Sea from 10 to 25 September 2013. The relationship between the gut pigment of C5 and standing stock chlorophyll *a* **(b)**. Dotted and dashed lines indicate regressions for day and night, respectively. For **(b)**, “whole” indicates including all data, both day and night. ****** $p < 0.01$, ***** $p < 0.05$.

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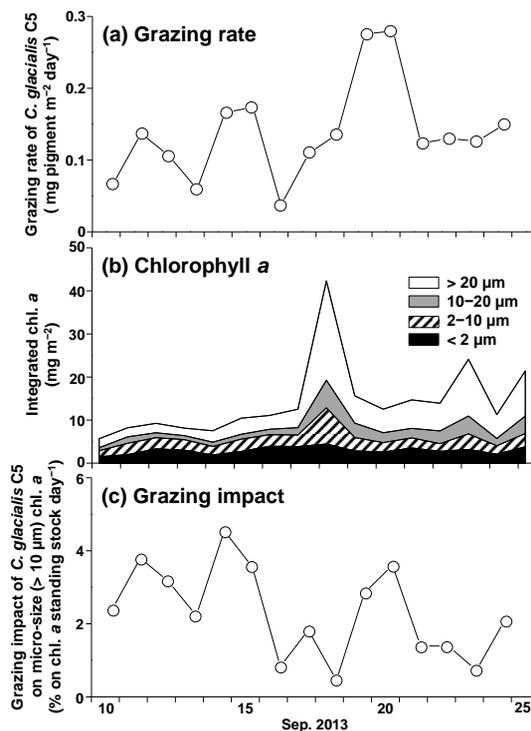


Figure 6. Temporal changes in the grazing rate of *Calanus glacialis* C5 **(a)**, integrated size-fractionated chlorophyll *a* **(b)** and the grazing impact of *C. glacialis* C5 on micro-phytoplankton (> 10 μm) **(c)** at a fixed station in the Chukchi Sea from 10 to 25 September 2013.

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