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

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Abstract

To evaluate the effect of atmospheric turbulence on a marine ecosystem, high-frequency samplings (two to four times per day) of a mesozooplankton community and the gut pigment of dominant copepods were performed 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 biomass of chlorophyll *a* (chl. *a*) increased, especially for micro-size (> 10 μm) fractions. The zooplankton abundance ranged from 23610 to 56809 ind. m^{-2} and exhibited no clear changes as a result of the SWE. In terms of abundance, calanoid copepods constituted the dominant 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 the 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 the SWE

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

1 Introduction

In marine ecosystems of the western Arctic Ocean, mesozooplankton is 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 are dominated by Arctic copepods. Within Arctic copepods, *Calanus glacialis* is a key species that dominates the zooplankton biomass and commonly occurs in the continental shelf throughout the Arctic Ocean (Conover and Huntley, 1991; Lane et al., 2008). The life cycle of *C. glacialis* is characterized by their growth to C3−C4 at the epipelagic layer during the first summer; then, they descend to a deeper layer and enter diapause, developing to C5 at the epipelagic layer in the second summer before descending down to a deeper layer and moulting to the adult stage (C6) utilizing stored lipids for energy (Longhurst et al., 1984; Ashjian et al., 2003; Falk-Petersen et al., 2009). Concerning seasonal changes, a comparison was made of the zooplankton community between summer and autumn (Llinás et al., 2009) and year-round changes based on a two-week sampling interval at a drifting ice station in the Arctic basin (Ashjian et al., 2003). However, short-term changes in the zooplankton community based on high-frequency samplings (two to four times per day) have not yet been reported.

Recently, a drastic reduction in the area of sea ice has been observed in the Arctic Ocean during summer; 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 the frequency and magnitude of cyclones and a northward shift of their tracks during the 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 the atmospheric turbulence in marine ecosystems in the western Arctic Ocean. From 10 to 25 September 2013, high-frequency samplings/observations were made at a fixed station in the Chukchi Sea and the occurrence of strong wind events (SWE), a vertical flux of nutrients and changes in the 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 the short-term changes of the mesozooplankton community in the Chukchi Sea during autumn based on the high-frequency samplings performed 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 the 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.

2 Materials and Methods

2.1 Field sampling

Zooplankton samplings were obtained at a fixed station in the Chukchi Sea (72º45´N, 168º15´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 µm; Motoda, 1957) and ring net (mouth diameter 80 cm, mesh size 335 µm) from a 49 m depth to the sea surface two to four times per day (total of 47 times), including both day and night. The large mesh size of the NORPAC net (335 µm) may have resulted in a slight underestimation of the smaller zooplankton species and early stages of larger zooplankton species. Zooplankton samples collected with the NORPAC nets were preserved with 5% buffered formalin immediately after being brought on board. The ring net samples were used for copepod gut pigment measurements. For the evaluation of the diel vertical migration (DVM) of the copepods, day and night vertical stratified hauls were taken with closing PCP nets (mouth diameter 45 cm, mesh size 62 µm; Kawamura, 1989) from two layers (0−20 m and 20−49 m) on 14 and 22 September. The samples from the PCP net were preserved with 5% buffered formalin. During the sampling period, there was a horizontal advection of the water mass oscillation caused by tidal waves (Kawaguchi et al., 2015). To minimize the effect of the tidal oscillation, day and night sampling times were set at 12-hour intervals (day: 10:55−11:34, night: 22:27−22:40). The four-time CTD casts at each sampling date confirmed that the hydrography was similar for the day-night sampling period (the CTD data are presented as supplemental material).

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

2.2 Gut pigment

For fresh samples collected using ring nets, 10% v/v soda (saturated CO_2 in water) was added to avoid copepod grazing, gut evacuation and the decomposition of gut pigments. Fresh specimens of *C. glacialis* copepodid stage 5 (C5) were sorted under a stereomicroscope. The sorting of all of the specimens was performed under low temperatures and dim light conditions within one hour. Batches of fifteen specimens were immersed in 6 ml of N,N-dimethylformamide and stored in dark, cold conditions overnight to extract the chlorophyll and phaeopigments. After the extraction of the pigment, the chlorophyll and phaeopigments were measured using a fluorometer (Turner Designs, Inc., 10-AU-005). The chlorophyll and phaeopigments were summed and expressed as gut pigments (ng pigment ind.$^{-1}$) (cf. Mackas and Bohrer, 1976).

The amount gut pigment of *C. glacialis* C5 was higher at night than during the day. Assuming that grazing primarily occurred at night, the grazing rate ($GR_{ind.}$, mg pigment ind.$^{-1}$ day^{-1}) of *C. glacialis* C5 was calculated using the following equation:

$$GR_{ind.} = GP \times k \times T / 10^6, \qquad (1)$$

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 night (mean 13 hours = 780 min during the study period). The grazing impact of *C. glacialis* C5 on micro-size (> 10 μm) chl. *a* (GI, % on chl. *a* biomass day^{-1}) was calculated using 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 the biomass of large-sized (> 10 μm) chl. *a* (mg m^{-2}).

2.3 Zooplankton community

In the laboratory, identification and enumeration by taxa were performed on zooplankton samples collected using NORPAC nets under a stereomicroscope. For the dominant taxa (calanoid copepods), identification was performed at the species and copepodid stage levels. For species identification of calanoid copepods, we referred mostly 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 performed 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 classified 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). The gonad maturation of *C. glacialis* C6F was also classified into three categories: I (immature), II (small oocytes in the ovary or oviduct) and III (large eggs or distended, opaque, filled-in oviducts). For this gonad maturation index, we cited that of *C. hyperboreus* (Hirche and Niehoff, 1996).

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

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

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

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

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

where i is the number of the copepodid stage (1−6 indicates C1−C6) and Ai (ind. m^{-2}) is the abundance of the ith copepodid stage (cf. Marin, 1987).

During the study period, a SWE was observed on approximately 19 to 22 September (Kawaguchi et al., 2015; Nishino et al., 2015). According to Kawaguchi et al. (2015), there were meteorologically and oceanographically distinct periods between 10 and 18 September and 19 and 26 September, represented as terms I and II, respectively. Term II was characterized by longer, stronger northeasterly winds, which continued for several days between 19 and 22 September, the average intensity of which was greater than 13 m s^{-1}. To evaluate the effect of the SWE, the abundances of each zooplankton taxon and species were compared “before the SWE (10−18 September)” and “after the SWE (19−25 September)” using the *U*-test. This statistical analysis was performed using Stat View.

3 Results

3.1 Hydrography and chlorophyll *a*

During the sampling period, the temperature ranged from -1.5 to 3.3ºC and a thermocline was observed at a depth of approximately 25 m (Fig. 2a). Cold water below 0ºC continuously persisted below the thermocline, whereas the temperature above the thermocline decreased from 3.3 to 1.5ºC during the study period (Fig. 2a). The salinity ranged from 31.1 to 32.8, and a halocline was observed at approximately 25 m, which ran parallel to the thermocline (Fig. 2b). The salinity below the halocline was constant (ca. > 32), whereas the 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, the temperature decreased, whereas the salinity increased during the study period (Fig. 2d).

3.2 Zooplankton community

The zooplankton abundance ranged from 23610 to 56809 ind. m^{-2}, and the calanoid copepods and barnacle larvae composed 57% and 31% of the community, respectively (Table 1). For the calanoid copepods, 15 species belonging to nine genera were identified. Among them, *Pseudocalanus* spp. and *C. glacialis* dominated and composed 65% and 30% of the total copepods, respectively. The shannon species diversity and Pielou evenness for the copepods community were 1.87 ± 0.12 and 0.81 ± 0.06, respectively. According to a comparison of time periods before and after the SWE, the total zooplankton abundance, the Shannon species diversity and the Pielou evenness did not change, whereas one calanoid copepod, *Centropages abdominalis*, and the cyclopoid copepods increased after the SWE (Table 1). However, one calanoid copepod, *Metridia pacifica*; appendicularians; barnacle larvae; euphausiids; and gymnosomes (*Clione limacina*) decreased after the SWE.

3.3 *Calanus glacialis*

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

On both 14 and 22 September, the C1−C4 and C5 populations of *C. glacialis* were present mostly 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 approximately half of the C5 population remained in the lower layer both during the day and at night. The lipid accumulation was higher for the C5 population residing in the lower layer. C6F was present at a lower layer throughout the day.

The gut pigment of *C. glacialis* C5 ranged from 0.6 to 12.3 ng pigment $ind.^{-1}$ and showed a significant increase after the SWE (mean values: 2.6 vs. 4.5 ng pigment $ind.^{-1}$, *U*-test, $p < 0.01$) (Fig. 5a). In a comparison between day and night samplings, most dates, except 18 and 23 September, exhibited higher gut pigment levels at night by a factor of two to five times greater than those observed during the day. In both day and night samplings, the gut pigments were correlated with the biomass of chl. *a* ($p < 0.05$) (Fig. 5b).

The population grazing rate of *C. glacialis* C5 ranged from 0.04−0.28 mg pigment m^{-2} day^{-1}, peaking on 20 September (Fig. 6a) and increasing 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 on 18

September and the micro-size chl. *a* (> 10 μm) dominated (54% of the total chl. *a*), especially after the SWE (66%) (Fig. 6b). The grazing impact of *C. glacialis* C5 on the micro-size chl. *a* ranged from 0.5−4.6% chl. *a* biomass 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 large spatial and temporal changes (Springer et al., 1989; Llinás et al., 2009; Matsuno et al., 2011). The 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 a low abundance of small copepods (*Pseudocalanus* spp. and cyclopoids) and a remarkable absence of the Arctic copepod *Metridia longa*. 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 present station is located at a primary stream of water from the Pacific Ocean (Weingartner et al., 2005). The high abundance of the Pacific copepod *M. pacifica* and *Neocalanus* spp. and the absence of the Arctic *M. longa* in this study was thought to be a reflection of the water mass covering the station. For these reasons (less small copepods and high abundance of Pacific copepods), the Shannon species diversity and Pielou evenness in this study (1.87 and 0.81, respectively) are higher than the reported values for the entire Chukchi Sea (1.79 and 0.62, respectively, calculated from Matsuno et al., 2012).

Seasonal characteristics during summer included the dominance of the meroplankton (barnacle and bivalve larvae), which composed 39% of the total zooplankton abundance (Hopcroft et al., 2010). The dominance of barnacle larvae also occurred in this study (Table 1). Benthic 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 settle (Herz, 1933). The abundance of barnacle larvae in this study (mean 10430 ind. m^{-2}) was 13−55% lower than that in summer (19114−79899 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 have ended in the planktonic phase and settled to the sea bottom during the study period (autumn).

Concerning the effect of the SWE, a few taxa and species showed significant changes in abundance (Table 1). Among the dominant species, cyclopoid copepods 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). At ambient temperatures (-1.5 to 3.3ºC), 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 caused by their reproduction within the study period (16 days). 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 the SWE on zooplankton abundance was relatively small because of the longer generation length of the mesozooplankton in this region.

4.2 Population structure of *C. glacialis*

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. 3a) and their *MCS* (mean±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. 3c). 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, immediately before sea-ice melting (Kosobokova, 1999), and reproduces with grazing ice algae and the 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).

The nocturnal ascent DVM, which is related to night-time 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, the DVM was observed for C5 (*U*-test, $p < 0.01$) (Fig. 4). At high-latitude seas, the magnitude of the *Calanus* spp. DVM is known to vary with the season and copepodid stage, and their DVM intensity is greater during spring and autumn when the diel changes in light penetration are large (Falkenhaug et al., 1997). No DVM of *Calanus* spp. was reported for the lipids accumulated in C5 (Falk-Petersen et al., 2008). In the present study, approximately 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 population may have already completed lipid accumulation and ceased DVM in the study period (September), whereas the remaining C5 population with an active DVM may have grazed on phytoplankton in the upper layer during the night and stored lipids in preparation for diapause. These results suggest that the *C. glacialis* population in this study was at the seasonal phase just before entering diapause, and this interpretation corresponded well with their life cycle in this region (Ashjian et al., 2003).

4.3 Grazing of *C. glacialis*

The of *C. glacialis* in the Arctic Ocean is known to exhibit diel changes and higher gut pigment levels at night than during the day (Conover and Huntley, 1991). Higher gut pigment levels at night were also observed in this study (*U*-test, $p < 0.001$) (Fig. 5a). The gut pigments of *C. glacialis* were correlated with the biomass 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).

Concerning the gut pigment measurement, the underestimation by the decomposition of the phytoplankton pigment through the gut passage has been reported (Conover et al., 1986; Head, 1992). This underestimation is reported to be approximately 0.1−10% of grazing (Conover et al., 1986) and varies with light conditions, grazing behaviour and phytoplankton species (Head, 1992). To estimate the grazing impact, data on the gut evacuation rate (k, min^{-1}) are needed (Mauchline, 1998). The gut evacuation rate is known to have a positive correlation with temperature (Dam and Petersen, 1988). From the equation for k and the temperature (T: ºC): $k = 0.00941+0.002575T$ (Mauchline, 1998) and ambient temperature in this study (T: -1.5 to 3.3ºC), k is 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 in 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 grazed on phytoplankton at night, using the C:Chl. *a* ratio (29.9, Sherr et al., 2003), the grazing impact (mg C m^{-2} day^{-1}) of *C. glacialis* C5 was calculated (Table 2). The grazing impact of this study was estimated to be 4.14 mg C m^{-2} day^{-1}. We also estimated the food requirement of *C. glacialis* C5 to support their metabolism under ambient temperatures (Ikeda and Motoda, 1978; Ikeda et al., 2001). The potential contribution of phytoplankton's 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 and that 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. (submitted) 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. From the fatty acid composition, *C. glacialis* is reported to have a strong connection with the microbial food web (Stevens et al., 2004). However, the low abundance of dinoflagellates and ciliates during the study period makes it difficult to assume that they were an important food source for *C. glacialis* in this study. As an alternative explanation, because most *C. glacialis* C5 contained an abundance of lipids in their body (Fig. 3b), they may have entered diapause in the Chukchi Sea during autumn.

5 Conclusions

Throughout this study, short-term changes in the mesozooplankton community and the grazing impact of *C. glacialis* were evaluated in the Chukchi Sea during autumn. During the 16-day sampling/observation period, the zooplankton community exhibited no clear changes related to the SWE and the dominant copepods prepared for diapause (i.e., stored lipids in the pre-adult stage or as adults with immature gonads). However, the feeding intensity of the 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 the mesozooplankton (SWE → nutrient supply from the deep layer → small phytoplankton bloom → copepod feeding) within a short period. These facts suggest that *C. glacialis* may obtain a benefit from an extension of the primary production season with more turbulence and a later freeze date of the Chukchi Sea.

Author contributions

S.N., J.I. and T.K. designed and coordinated this research project. S.N. and J.I. were the 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 laboratory. K.M. and A.Y. wrote the manuscript, with contributions from all of the co-authors.

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Figure captions

Figure 1. Location of the sampling station in the Chukchi Sea from 10 to 25 September 2013. Arrows indicate the major current flows in this region (cf. Grebmeier, 2012).

Figure 2. Temporal changes in the 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.

Figure 3. Temporal changes in the population structure (a), lipid accumulation of C5 (b) and gonad maturation of C6F (c) of *Calanus glacialis* 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. Temporal and diel changes in the gut pigment of *Calanus glacialis* C5 (a), and the relationship between the gut pigment of C5 and chlorophyll *a* biomass (b) at a fixed station in the Chukchi Sea from 10 to 25 September 2013. Dotted and dashed lines indicate regressions for day and night, respectively. The whole regression line is drawn with all of the data from both day and night in panel b. **: $p < 0.01$, *: $p < 0.05$.

Figure 6. Temporal changes in the grazing rate of *Calanus glacialis* C5 (a), integrated size-fractionated chlorophyll *a* (b) and 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.

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. Values are mean±1sd. 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	*U*-test
Population parameters	(10−18 Sep., *n* = 22)	(19−25 Sep., *n* = 25)	
Calanoid copepods			
Acartia longiremis	604±281	542±279	NS
Calanus glacialis	6714±2679	5658±3061	NS
Calanus hyperboreus	0	5±17	NS
Centropages abdominalis	9±23	29±38	*
Eucalanus bungii	6±20	6±19	NS
Eurytemora herdmani	0	2±12	NS
Metridia pacifica	251±150	154±139	*
Microcalanus pygmaeus	6±19	3±14	NS
Neocalanus cristatus	6±19	5±19	NS
Neocalanus flemingeri	46±44	65±79	NS
Neocalanus plumchrus	12±26	15±32	NS
Pseudocalanus acuspes	3393±1239	3254±1651	NS
Pseudocalanus mimus	1194±728	1296±837	NS
Pseudocalanus minutus	2178±768	2387±864	NS
Pseudocalanus newmani	2805±949	2774±1448	NS
Pseudocalanus spp. (C1−C4)	2758±1114	2980±1196	NS
Cyclopoid copepods	511±263	1153±974	**
Poecilostomatoid copepods	0	3±14	NS
Amphipoda	9±24	5±19	NS

Appendicularia	707±413	442±337	*
Barnacle larva	12118±2399	8945±2341	***
Chaetognatha	1281±531	1039±504	NS
Echinodermata larva	31±45	61±79	NS
Eubrachyura zoea	41±60	26±52	NS
Euphausiacea	18±31	3±14	*
Gymnosomata	172±133	84±88	**
Hydrozoa	209±127	205±119	NS
Isopoda	3±14	3±14	NS
Polychaeta	1124±311	1005±435	NS
Thecosomata	16±43	8±30	NS
Total zooplankton	36223±5984	32154±7716	NS
Shannon species diversity	1.85±0.11	1.90±0.11	NS
Pielou evenness	0.80±0.05	0.82±0.06	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 (depth, temp.: *T*, period)	Flux (mg C m^{-2} day^{-1})			Proportion of phytoplankton food (%: B/A)
	Metabolism	Food requirement (ingestion) (A)	Grazing rate on phytoplankton (B)	
Day-lower layer (20−49 m, −0.74ºC, 11 h)	5.64	14.11	−	−
Night-upper layer (0−20 m, 2.31ºC, 13 h)	4.12	10.29	−	−
Night-lower layer (20−49 m, −0.74ºC, 13 h)	3.34	8.34	−	−
Daily-water column	13.10	32.74	4.14	12.6

Dry mass (*DM*: mg $ind.^{-1}$) of *C. glacialis* C5 was 0.654 (Matsuno et al., unpublished data).

Oxygen consumption (μL O_2 $ind.^{-1}$ h^{-1}) = $\exp(-0.399+0.801\times\mathrm{Ln}(DM)+0.069\times T)$ (Ikeda et al., 2001).

Respiratory quotient ([CO_2/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).

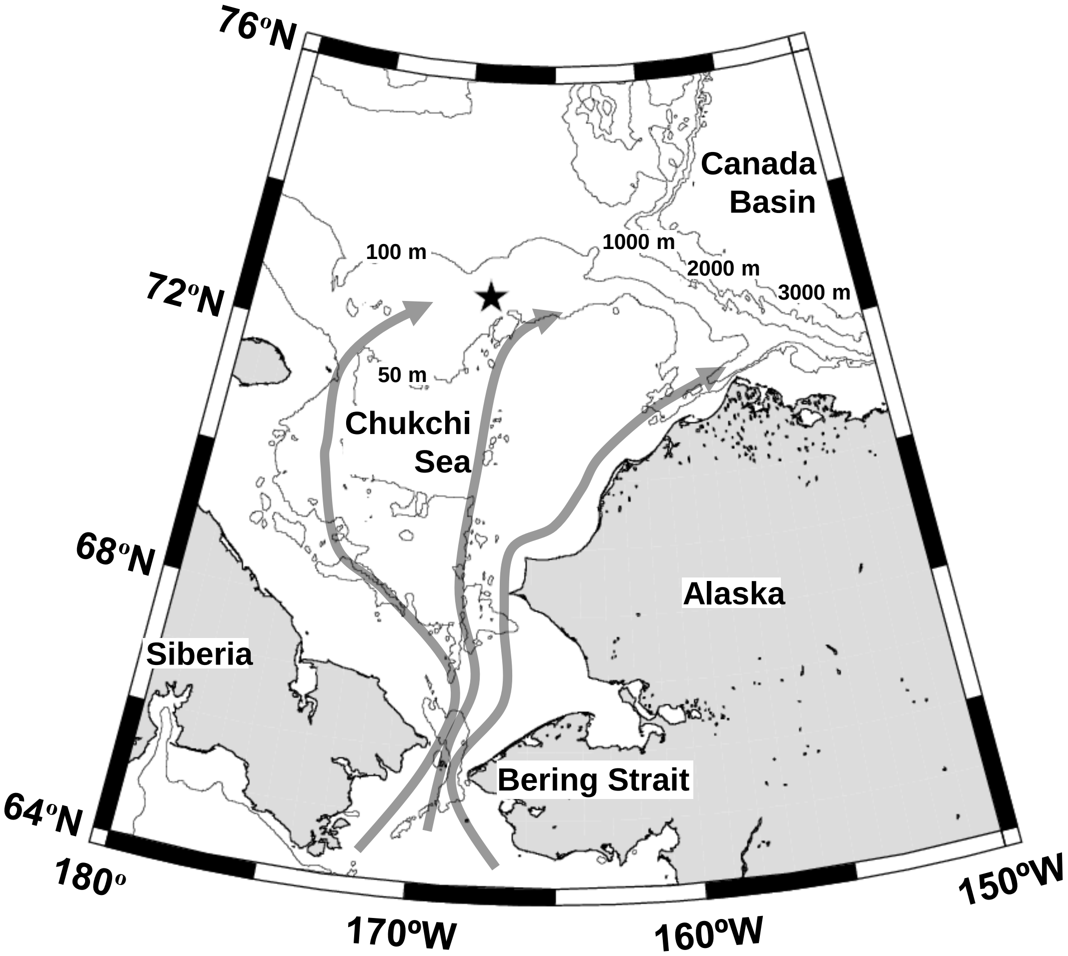


Fig. 1. (Matsuno et al.)

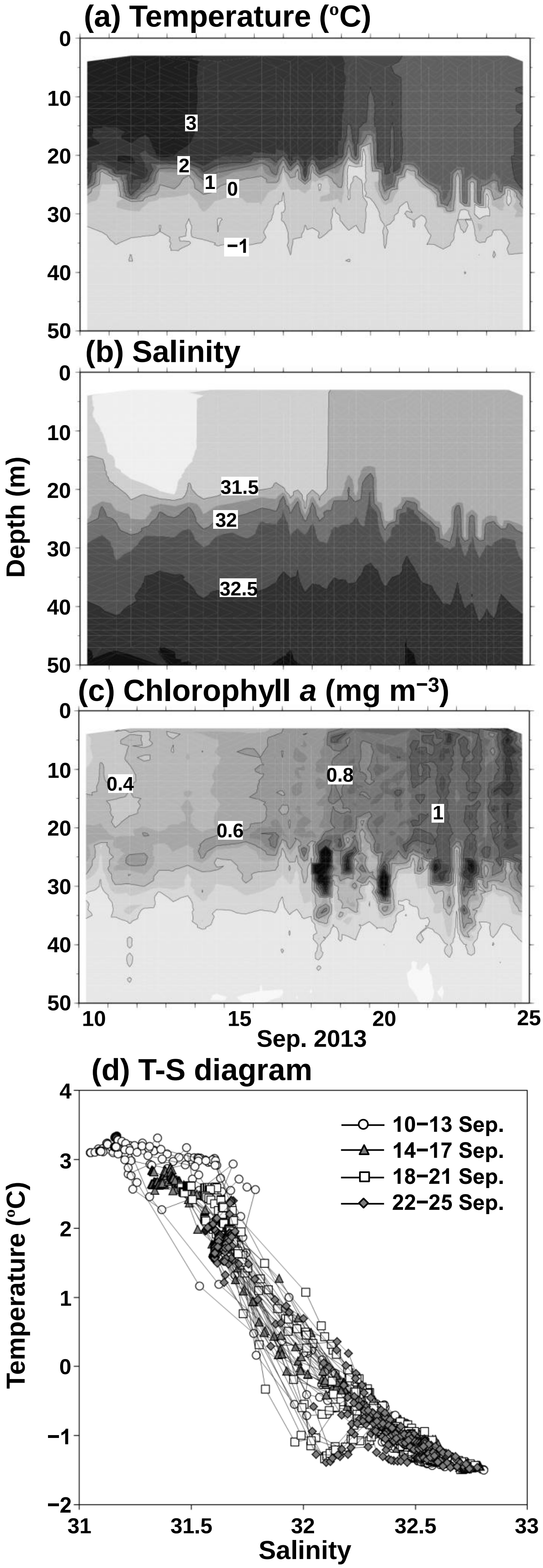
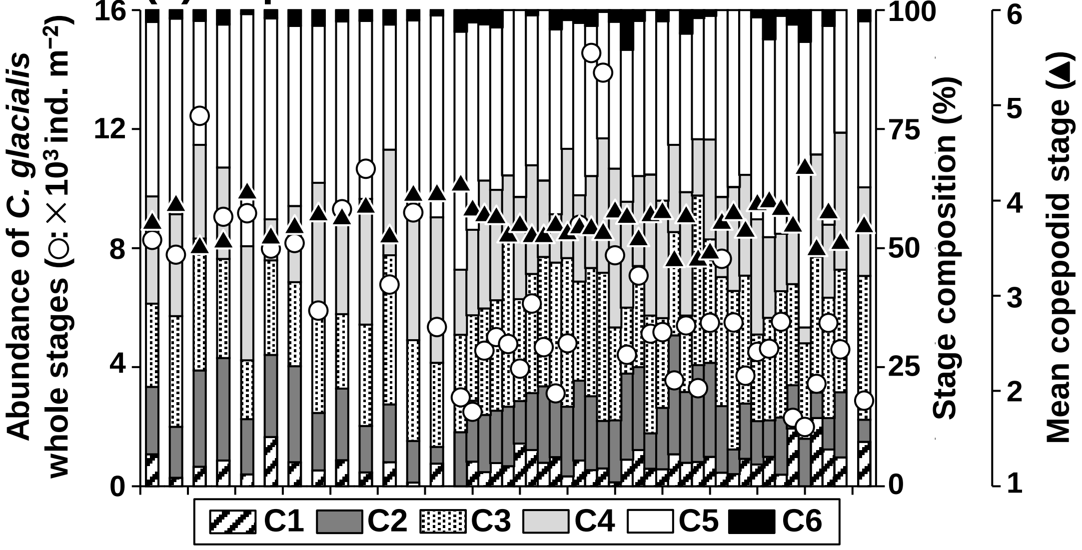
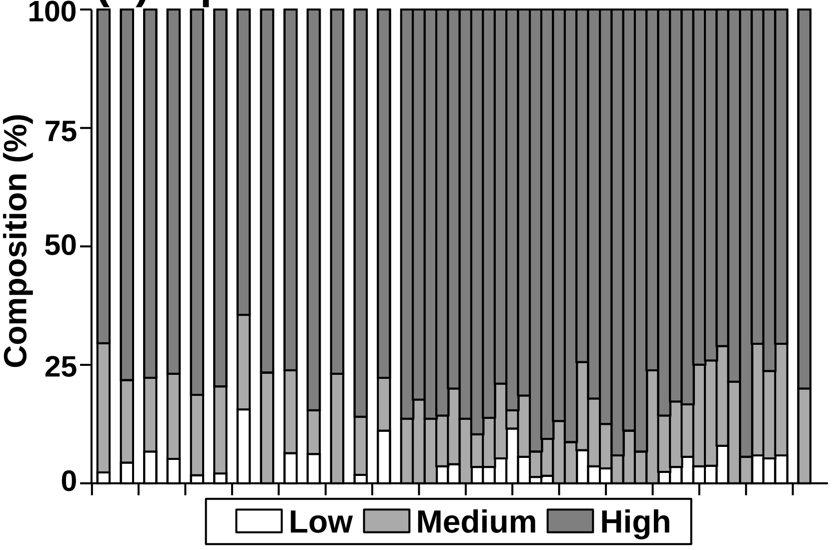


Fig. 2. (Matsuno et al.)

(a) Population structure



(b) Lipid accumulation



(c) Gonad maturation

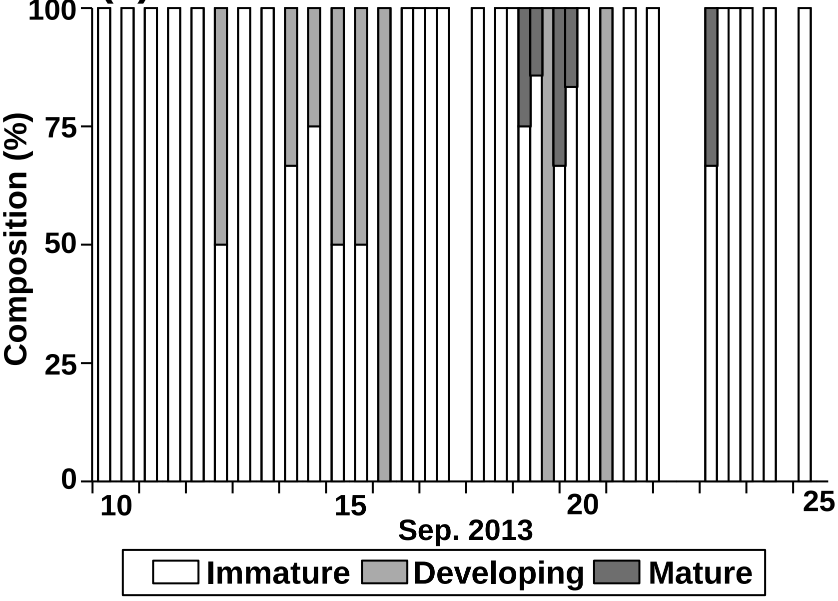
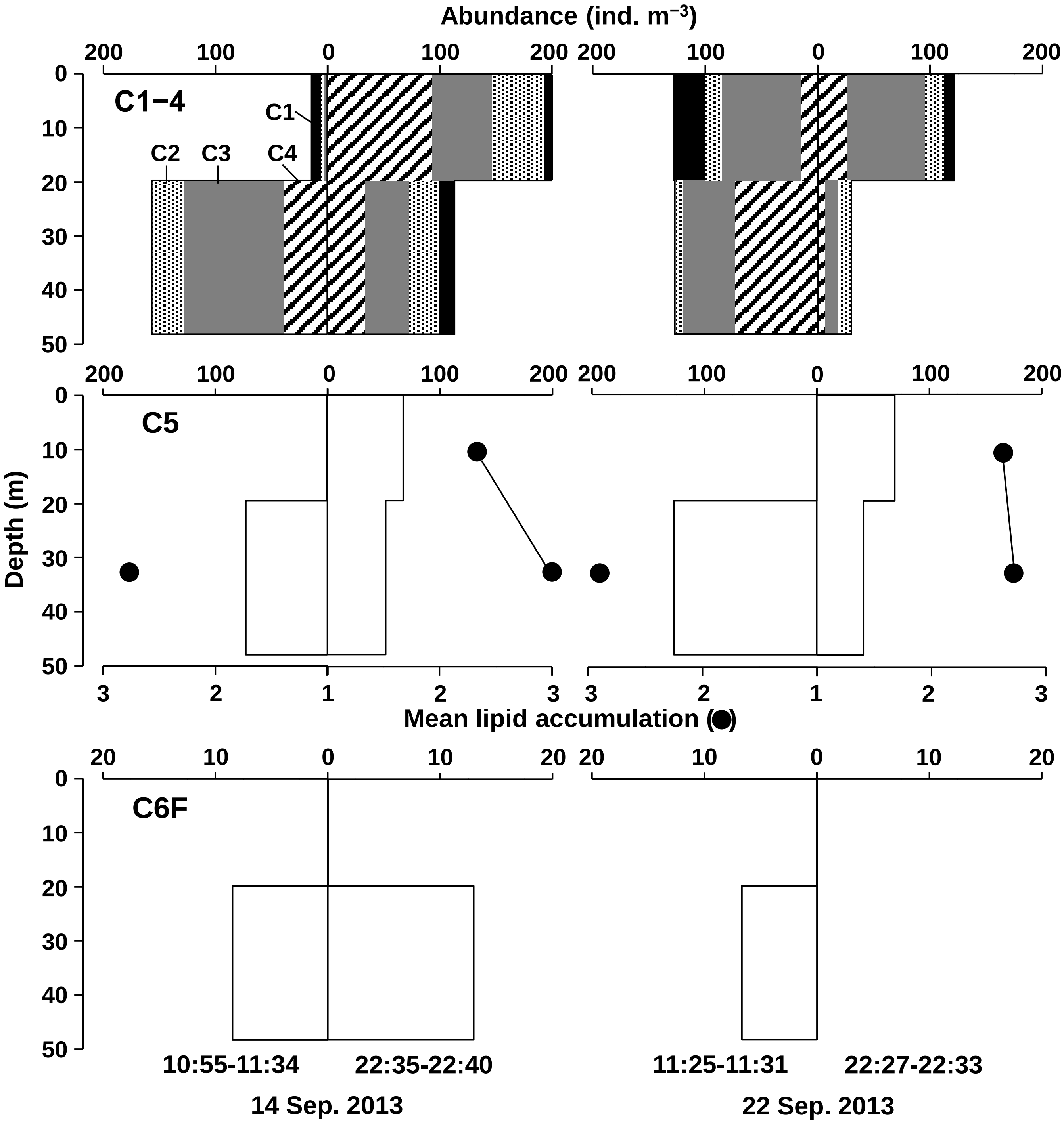


Fig. 3 (Matsuno et al.)



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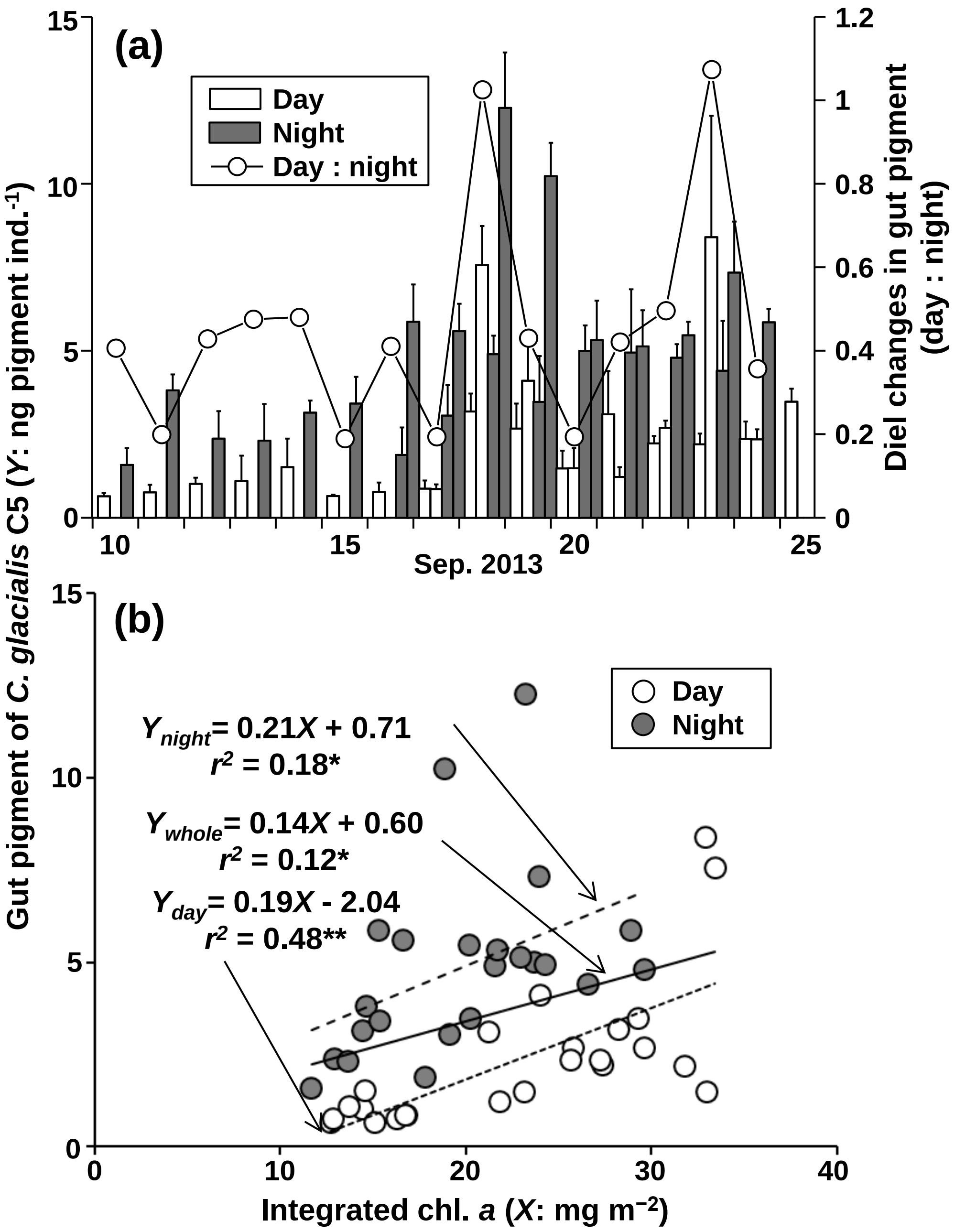

Fig. 5. (Matsuno et al.)

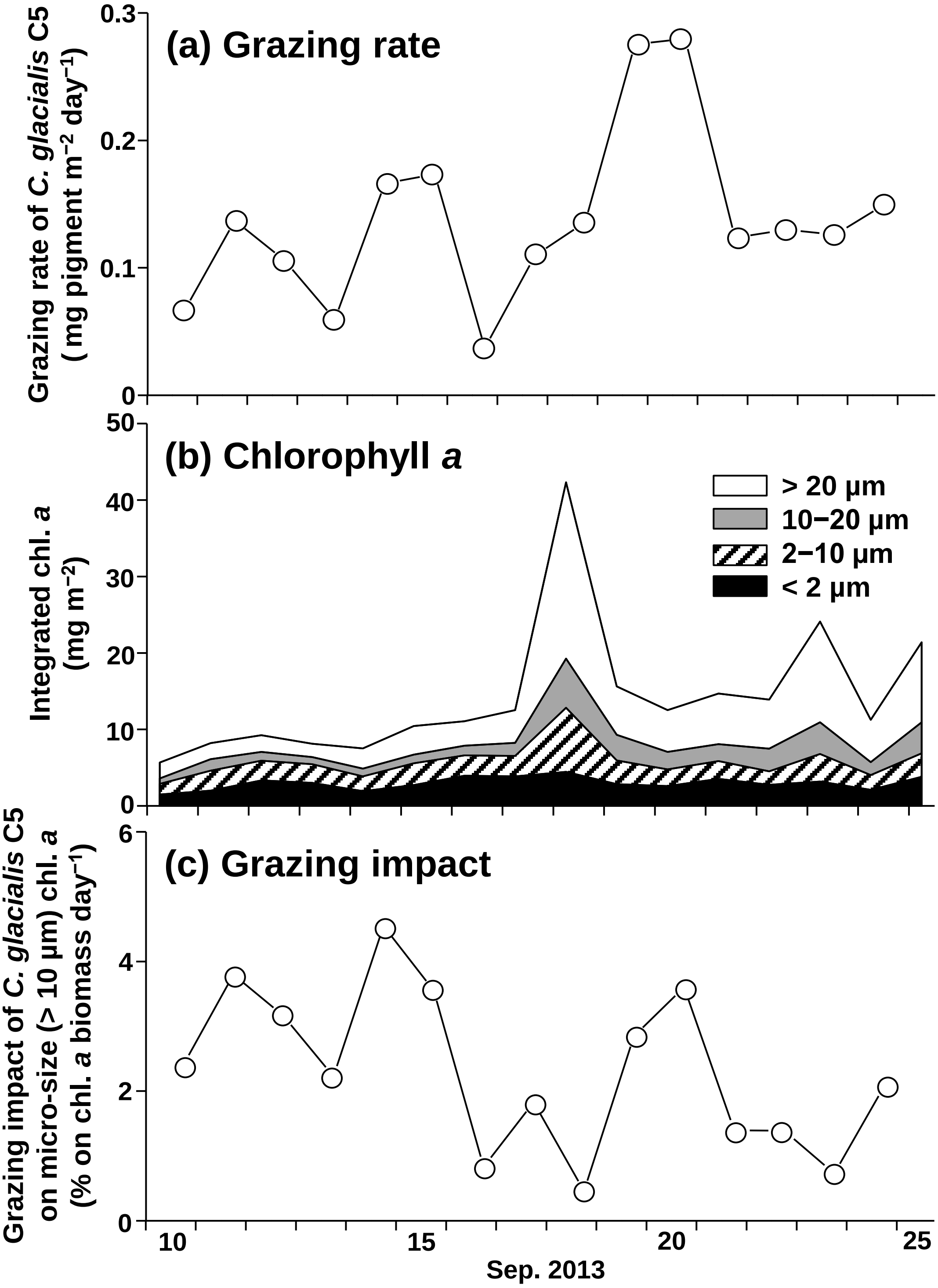

Fig. 6. (Matsuno et al.)