Author’s response to Dr. G. Darnis

We are grateful to your comments and useful suggestions that improved our manuscript greatly. As described below, we have revised our manuscript. Please note that the expression in black colored letters are the ones provided by you whereas those in red are our replies.

Specific comments

Title

Could it better reflect the changes related to the strong wind event that occurred during the field work? On the other hand, I understand that the chosen title fits with that of a companion paper addressing the case of microplankton community during the same field campaign.

Answer: We changed the title to “Short-term changes of the mesozooplankton community and copepod gut pigment in the Chukchi Sea in autumn: Reflection of strong wind event” (marked manuscript p1 L1-3).

Abstract

The abstract is too wordy. The content could be synthesized, and multiple uses of words limited. A lot of results reported but few conclusions in comparison.

Answer: We shortened the abstract (marked manuscript p1 L16-p2 L14).

Line 6: Change “high-frequent” to “high-frequency”, here and elsewhere in the text.

Answer: We changed to “high-frequency” through the manuscript (marked manuscript p1 L20, p3 L4, L12, L19).

Line 12: “dominant” and not “most dominated”

Answer: We changed to “dominant” (marked manuscript p1 L26).

Line 20: If you decide to keep this part add the value of the C:Chl a ratio, although I don’t think that this is necessary to mention in the abstract the assumption of this ratio in the calculation of the estimate.

Answer: We deleted “Assuming C:Chl. a ratio” (marked manuscript p2 L4).

Introduction

More emphasis should be put on *Calanus glacialis* in the Introduction since it is clearly the dominant species in terms of biomass and one focus of the study with the gut content analysis. My suggestion is to move one paragraph on this species from the Discussion to the Introduction.

Answer: We moved one paragraph of *C. glacialis* from Discussion to Introduction (marked manuscript p2 L20-26).

Line 6. Mesozooplankton are secondary producers everywhere. This trivial statement can be removed.

Answer: We deleted "is a secondary producer and" (marked manuscript p2 L17).

Line 11: "dominate" and not "dominated"

Answer: We deleted this part owing above change (marked manuscript p2 L30).

Line 13: Maybe "origin" would be better here than "formation"

Answer: We deleted this part owing above change (marked manuscript p2 L31).

Materials and methods

Page 6, line 6: replace "with" by "of"

Answer: We changed to "by" (marked manuscript p5 L7).

Page 6, line 8: replace "with" by "to"

Answer: We changed to "to" (marked manuscript p5 L9).

Results

For section 3.1, I am not sure that "Hydrography" is the right title since chl *a*, a biological feature, is described there also. Description of vertical distribution of chl *a* (Figure 2c) could be relevant for the study.

Answer: We changed the title as "Hydrography and chlorophyll *a*" (marked manuscript p6 L11).

Section 3.3 on *Calanus glacialis* I would start by describing population structure instead of DVM right away. Swap the paragraphs.

Answer: We swapped the paragraphs (marked manuscript p7 L7-18). Owing this change in text, Figs. 3 and 4 are also swapped (Figs. 3 and 4).

Detail the composition of the population by giving the percentage of other stages than

CV. Mention that the young copepodites abundances are underestimated due to the coarse mesh net used.

Answer: Concerning underestimation of small zooplankton, we added short note in Materials and methods (marked manuscript p4 L1-2).

Page 8, line 16: “their population” by “the population”

Answer: We changed to “the population” (marked manuscript p7 L10).

Discussion

Page 9, line 8: Greater spatial and temporal change than what? I did not get the meaning of the sentence. It should be clarified. In fact, the whole paragraph needs to be rewritten as it’s difficult to differentiate what’s comes from this study and what are Matsuno et al (2012) findings.

Answer: We changed the word from “greater” to “large” (marked manuscript p8 L11). Concerning comparison with Matsuno et al. (2012), we rewrote this part (marked manuscript p8 L12-28).

The structure of the sentences should be simpler and more direct. Most sentences should start simply with the subject for sake of clarity. As an example: “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).” could well be: “Total zooplankton abundance in this study was approximately half (mean: 34 059 ind.m^{-2}) the abundance reported by Matsuno et al. (2012) on the Chukchi shelf (mean: 75 683 ind.m-2), with low abundance of small copepods (*Pseudocalanus* spp. and cyclopoids) and the remarkable absence of the Arctic copepod *Metridia longa*.”

Answer: We changed the sentence following referee’s comment (marked manuscript p8 L12-16).

Page 10, line 5: Again, this sentence is not clear. What does the addition of holoplankton mean?

Answer: We deleted the sentence “the addition of holoplankton and” (marked manuscript p9 L10).

Page 10, line 8-11: “Benthic barnacle adults released their larvae when they met phytoplankton blooms (Crisp, 1962; Clare and Walker, 1986), and their larvae spent two to three weeks at water columns and then settled (Herz, 1933).” If this is usual behavior on the part of adult barnacles, present tense should be used. Furthermore, replace “at water columns” by “in the water column”.

Answer: We changed to “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).” (marked manuscript p9 L13-15).

Page 10, line 17: replace “several limited” by “a few”

Answer: We changed to “a few” (marked manuscript p9 L21).

Page 10, line 18: this issue has been already addressed in the previous paragraph.

Answer: We deleted the sentence on barnacle larvae (marked manuscript p9 L22-23).

Section 4.2 Population structure of Calanus glacialis

The first paragraph belongs to the Introduction section. It’s a description of the status and life cycle of this important arctic shelf copepod, which is a focus of the work.

Answer: We moved this paragraph into Introduction (marked manuscript p10 L2-11).

Page 13, line 9-11. What is the value measured by Tande and Bamstedt (1985)? Why make this comparison with the situation in the Barents Sea in spring-summer if it’s not interpreted further. Wouldn’t it be more relevant to try a comparison with grazing impacts estimated by Campbell et al (2009) for roughly the same region? At least conclusions of this study should be better addressed in the present work.

Answer: We deleted sentence comparing with Tande and Bamstedt (1985) (marked manuscript p11 L31-32).

Page 13, line 18. Change “proportion” for “potential contribution”

Answer: We changed to “potential contribution” (marked manuscript p12 L6-7).

Conclusion

Page 14, line 3. In fact, grazing impacts was only estimated for the dominant stage of *C. glacialis*, excluding other dominant copepods such as *Pseudocalanus*. The sentence should be changed accordingly.

Answer: We changed from “dominant copepods” to “*C. glacialis*” (marked manuscript p12 L20).

Page 14, line 12. This conclusion is rather trivial. We certainly could not expect metazoan plankton demography to respond so fast to a short surge in phytoplankton stock. However, it would be particularly interesting to speculate on the cumulative effects of late summer-early autumn strong winds in a region more and more impacted by the reduction in sea ice cover. Could some zooplankton benefit from an extension of the primary production season with more turbulence and later freeze-up of the Chukchi Sea?

Answer: Yes, the case is expected. Owing to comment, we added short note on this issue at end of the conclusion (marked manuscript p12 L29-31).

Tables

Table 2. Some information given in the legend for the calculations should be moved to the Materials and methods section.

Answer: Since this Table 2 is only cited in Discussion (note that not in Results), we remained that the legend of this Table as it was.

Figure 1. No need to mention in the legend that the depth contours are superimposed since it’s obvious.

Answer: We deleted the sentence (marked manuscript p19 L3).

Author's response to Dr. V. Dvoretsky

We are grateful to your comments and useful suggestions that improved our manuscript greatly. As described below, we have revised our manuscript. Please note that the expression in black colored letters are the ones provided by you whereas those in red are our replies.

Specific comments.

Abstract L 11. 'ranged 23 610–56 809 ind.m^{-2}' replace by 'ranged from 23 610 to 56 809 ind.m^{-2}'

Answer: We changed to "ranged from 23 610 to 56 809 ind. m^{-2}" (marked manuscript p1 L24-25).

Results L 21 'ranged 23 610–56 809 ind.m^{-2}' replace by 'ranged from 23 610 to 56 809 ind.m^{-2}'

Answer: We changed to "ranged from 23 610 to 56 809 ind. m^{-2}" (marked manuscript p6 L23).

Methods

In general, methods are good described. Therefore I suggest to mention that NORPAC nets (mouth diameter 45 cm, mesh size 335 μm) are rather coarse to quantitatively catch smaller zooplankton forms (e.g. Pseudocalanus spp. C1-4, Cyclopoida, the youngest stages of other copepods) and there may be some underestimations of these zooplankton taxa.

Amswer: We added short note on the underestimation of small copepods in the Materials and Methods (marked manuscript p4 L1-2).

Results

I recommend calculating the Shannon diversity index and the Pielou evenness of the zooplankton communities. These indices may give interesting information on the shortterm dynamics of zooplankton structure in the Chukchi Sea. Estimated zooplankton biodiversity should be described in the Results in detail, and therefore compared (if possible) with previous studies in the Discussion section.

Answer: We calculated both Shannon species diversity index and Pielou evenness and compared with the reported values in this region (marked manuscript p5 L22-28, p6 L27-28, p7 L1-2, p9 L5-8).

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

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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-frequency~~t~~ 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 μm) fractions. Zooplankton abundance ranged from 23610 to ~~–~~56809 ind. m^{-2} and exhibited no clear changes with SWE. In terms of abundance, calanoid copepods constituted the ~~most~~ dominant~~ed~~ 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, t~~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 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 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. Within the Arctic copepods, *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). 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 (Longhurst et al., 1984; Ashjian et al., 2003; Falk-Petersen et al., 2009).~~: 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-frequency~~t~~ 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 September 2013, high-frequency~~t~~ 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~~in press~~; Yokoi et al., submitted~~in preparation~~). 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~~t~~ samplings made simultaneously by Nishino et al. (2015~~in press~~) and Yokoi et al. (submitted~~in preparation~~). We estimated the grazing impact of dominant copepods based on their gut pigments and evaluated the effect of SWE (Nishino et al., 2015~~in press~~) and short-term changes of microplankton assemblages (Yokoi et al., submitted~~in preparation~~) on the mesozooplankton community in the Chukchi Sea in autumn.

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2 Materials and Methods

2.1 Field sampling

Zooplankton samplings were conducted 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~~in press~~). 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 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 NORPAC net (335 µm) may induce somewhat underestimation of smaller zooplankton species and early stages of larger zooplankton species. 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 µm; 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.

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,N-dimethylformamide and measured with a fluorometer (Turner Designs, Inc., 10-AU-005).

2.2 Gut pigment

For fresh samples collected by ring nets, 10% v/v soda (saturated CO_2 in water) was added to avoid copepod grazing, gut evacuation and decomposition of gut pigment. Fresh specimens 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 conditions overnight to extract chlorophyll and phaeopigments. After the extraction of pigment, the chlorophyll and phaeopigments were measured with a fluorometer (Turner Designs, Inc., 10-AU-005). Chlorophyll and phaeopigments were summed and expressed as gut pigments (ng pigment ind.$^{-1}$) (cf. Mackas and Bohrer, 1976).

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

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

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:

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

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 by~~with~~ taxa were performed on zooplankton samples collected by NORPAC nets under a stereomicroscope. For dominant taxa (calanoid copepods), identification was made to~~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 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).

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:

$$J´ = H´/\ln(s)$$

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

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

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

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, SWE was observed from 18 to 19 September (Nishino et al., 2015~~in press~~). 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 and chlorophyll *a*

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During the sampling period, the temperature ranged from −1.5°C 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 23610~~–~~ to 56809 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 the total copepods, respectively. Shannon species diversity and Pielou evenness for the copepods commuity 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 cyclopoid copepods increased after the SWE (Table 1). On the other hand, 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 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). 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 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~~3~~). 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.

~~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. 4a, Table 1). For the population structure, all copepodid stages (C1 to C6F/M) occurred, and C5 was the most dominant stage (36%) of their population (Fig. 4). The *MCS* did not vary with SWE (Fig. 4a). Throughout the study period, the lipid accumulation of C5 was high (Fig. 4b), and the gonad maturation of C6F was dominated by immature specimens (Fig. 4c). These parameters exhibited no significant change with the SWE (*U*-test, $p = 0.285–0.303$).~~

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, most dates except 18 and 23 September showed high gut pigment levels at night by a factor of two to five times those of the daytime. In both day and night, the gut pigments were correlated with a standing stock 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}, peaked on 20 September (Fig. 6a) and increased 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 µm) 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~~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*. ~~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: 75683 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: 34059 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~~in press~~) 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

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transported to the Arctic Ocean during winter. Geographically, the 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. Because of 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) are higher than the reported values for the whole Chukchi Sea (1.79 and 0.62 calculated from Matsuno et al., 2012).

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 release~~d~~ their larvae when they meet phytoplankton blooms (Crisp, 1962; Clare and Walker, 1986), and their larvae spend~~t~~ two to three weeks ~~at~~in the water column~~s~~ and then settle~~d~~ (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 the planktonic phase and settled to the sea bottom during the study period (autumn).

Concerning the effect of the SWE, ~~several limited~~ a few 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 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 3.3ºC), 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). As an alternative cause, the horizontal advection of the water mass during the study period, which was reported by Nishino et al. (2015~~in press~~), 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.

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. 3~~4~~a), 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. 3~~4~~c). 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. 4~~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 spring and autumn when the diel changes in light penetration are large (Falkenhaug et al., 1997). No DVM of *Calanus* spp. was reported for lipid accumulated C5 (Falk-Petersen et al., 2008). In the 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~~3~~). The deep C5 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 phytoplankton in the upper layer during the night and stored lipid 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 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~~in press~~; Yokoi et al., submitted~~in preparation~~).

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Concerning gut pigment measurement, underestimation by decomposition of phytoplankton pigment through gut passage has been reported (Conover et al., 1986; Head, 1992). This underestimation is reported to be ca. 0.1−10% of grazing (Conover et al., 1986) and varies with light conditions, grazing behavior and phytoplankton species (Head, 1992). 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 temperature (Dam and Petersen, 1988). From the equation between k and temperature (T: ºC): $k = 0.00941+0.002575T$ (Mauchline, 1998) and ambient temperature in this study (T: −1.5 to 3.3ºC), 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 (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}~~, 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 mg m^{-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 potential contribution ~~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. (submitted~~in preparation~~) 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.

5 Conclusions

Throughout this study, short-term changes in the mesozooplankton community and the grazing impact of *C. glacialis* ~~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~~in press~~). 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. These facts suggest that some zooplankton may obtain benefit from an extension of the primary production season with more turbulence and later freeze-up of the Chukchi Sea.~~However, because of the relatively long generation length of copepods, a smaller effect was detected for their abundance, population structure, lipid accumulation and gonad~~

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~~maturation within the short-term period.~~

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.

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Figure captions

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).

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.

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. ~~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 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.~~*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 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. **: $p < 0.01$, *: $p < 0.05$.

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.

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 Community parameters	Before SWE (10–18 Sep.)	After SWE (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

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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). 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×Ln(*DM*)+0.069×*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).

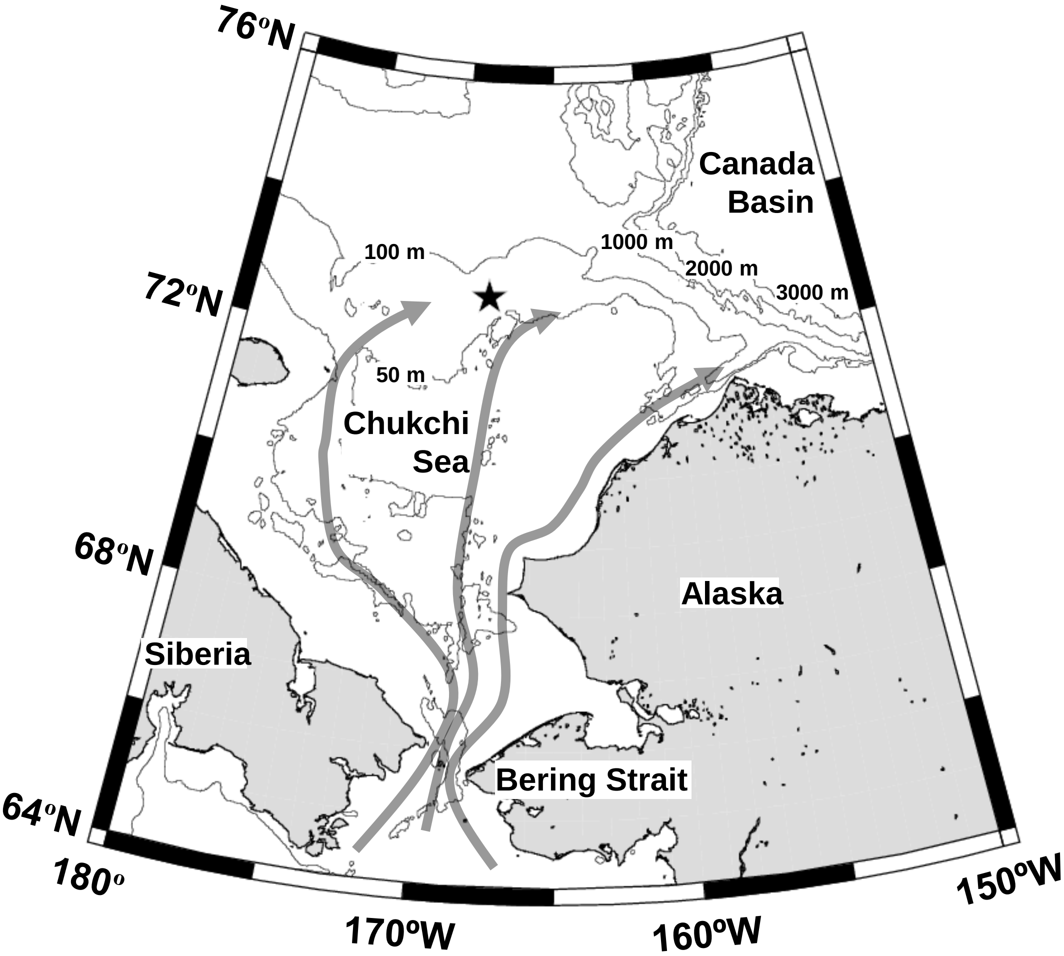
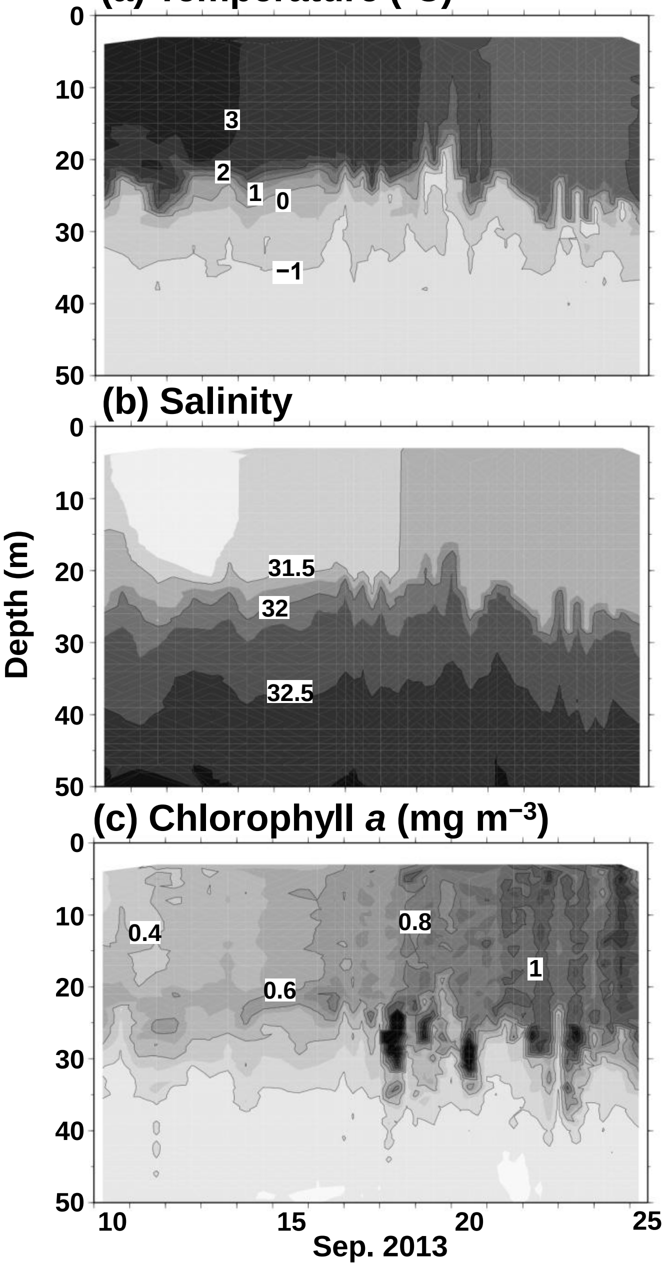


Fig. 1. (Matsuno et al.)


(a) Temperature (^{o}C)

(b) Salinity

(c) Chlorophyll *a* (mg m^{-3})

(d) T-S diagram

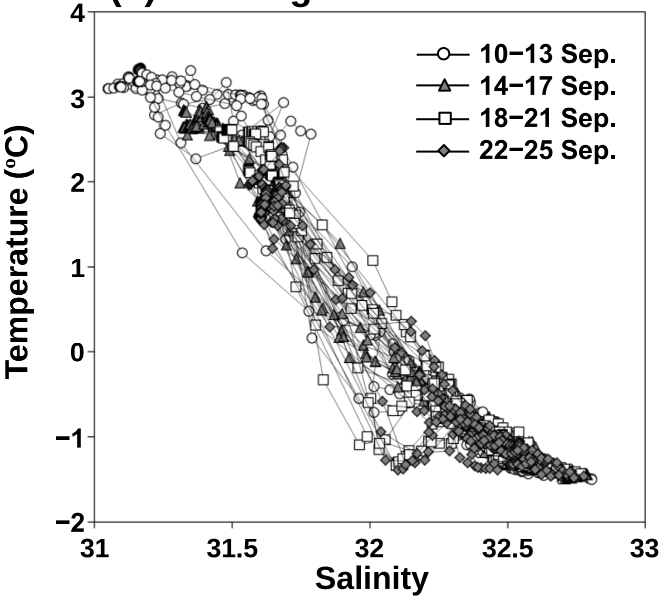
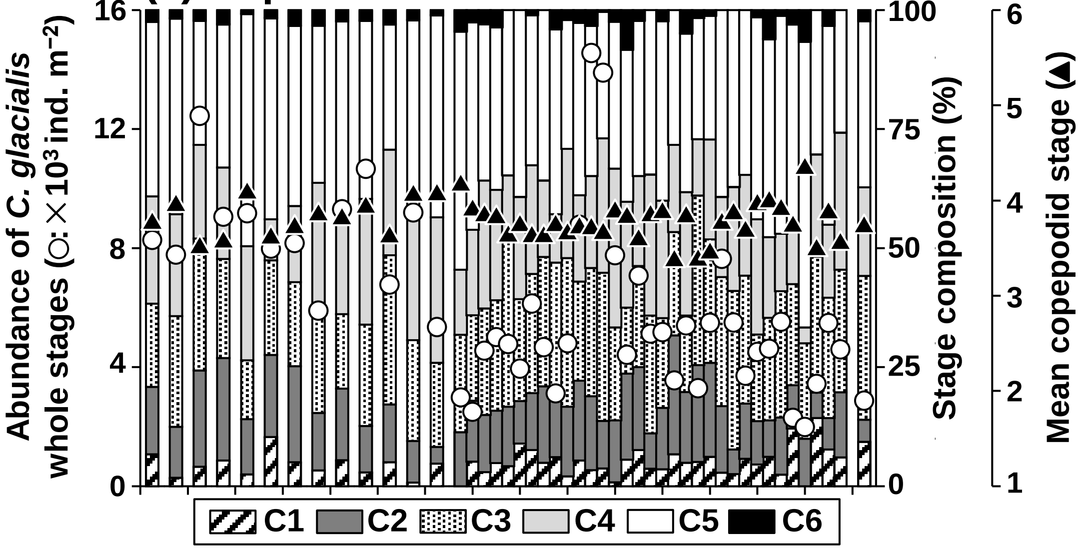
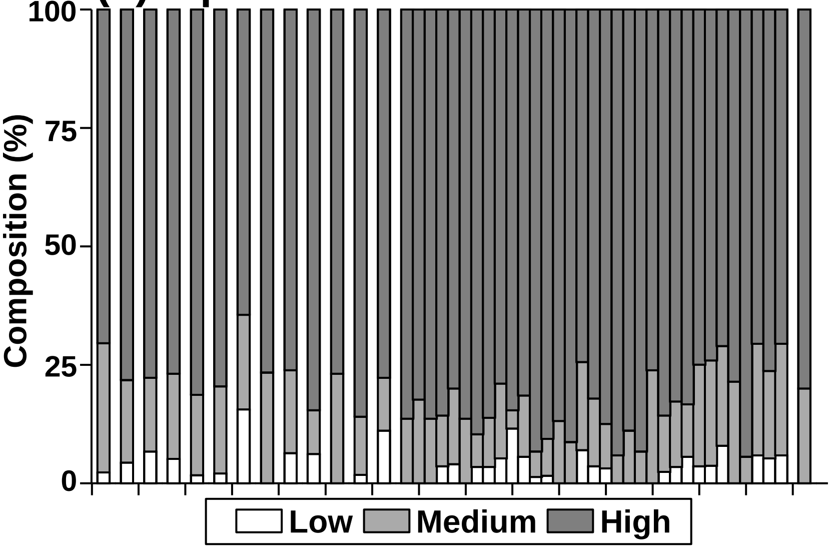


Fig. 2. (Matsuno et al.)

(a) Population structure



(b) Lipid accumulation



(c) Gonad maturation

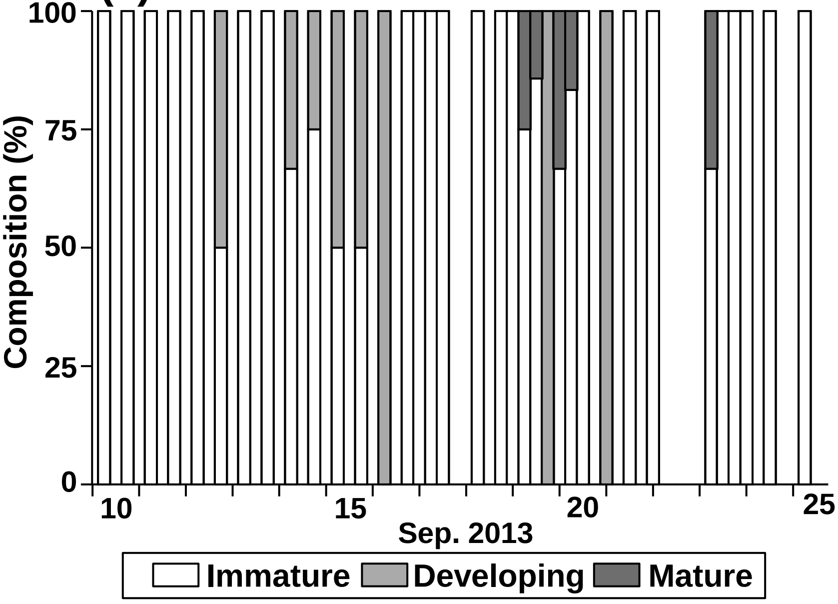


Fig. 3 (Matsuno et al.)

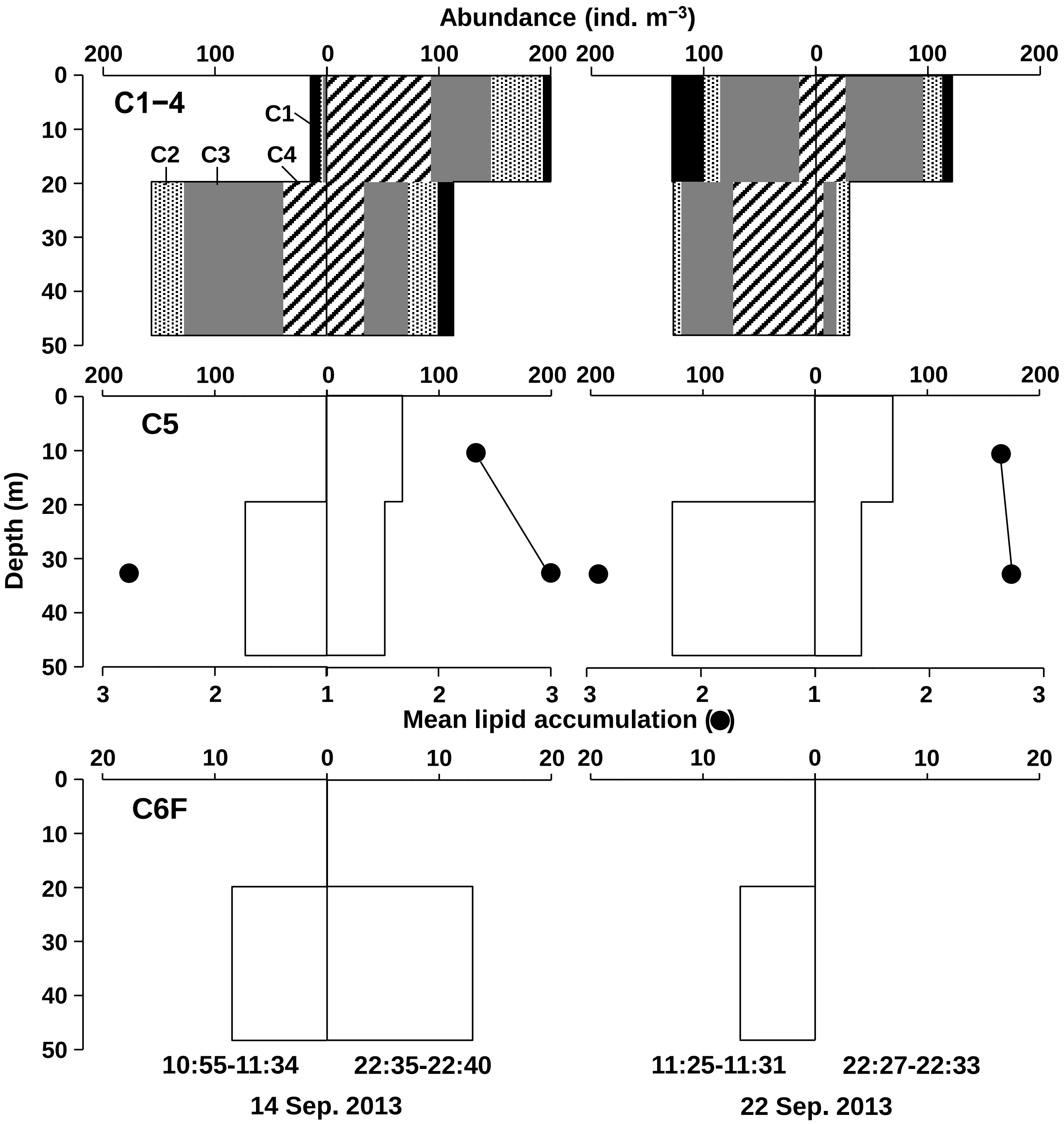


Fig. 4. (Matsuno et al.)

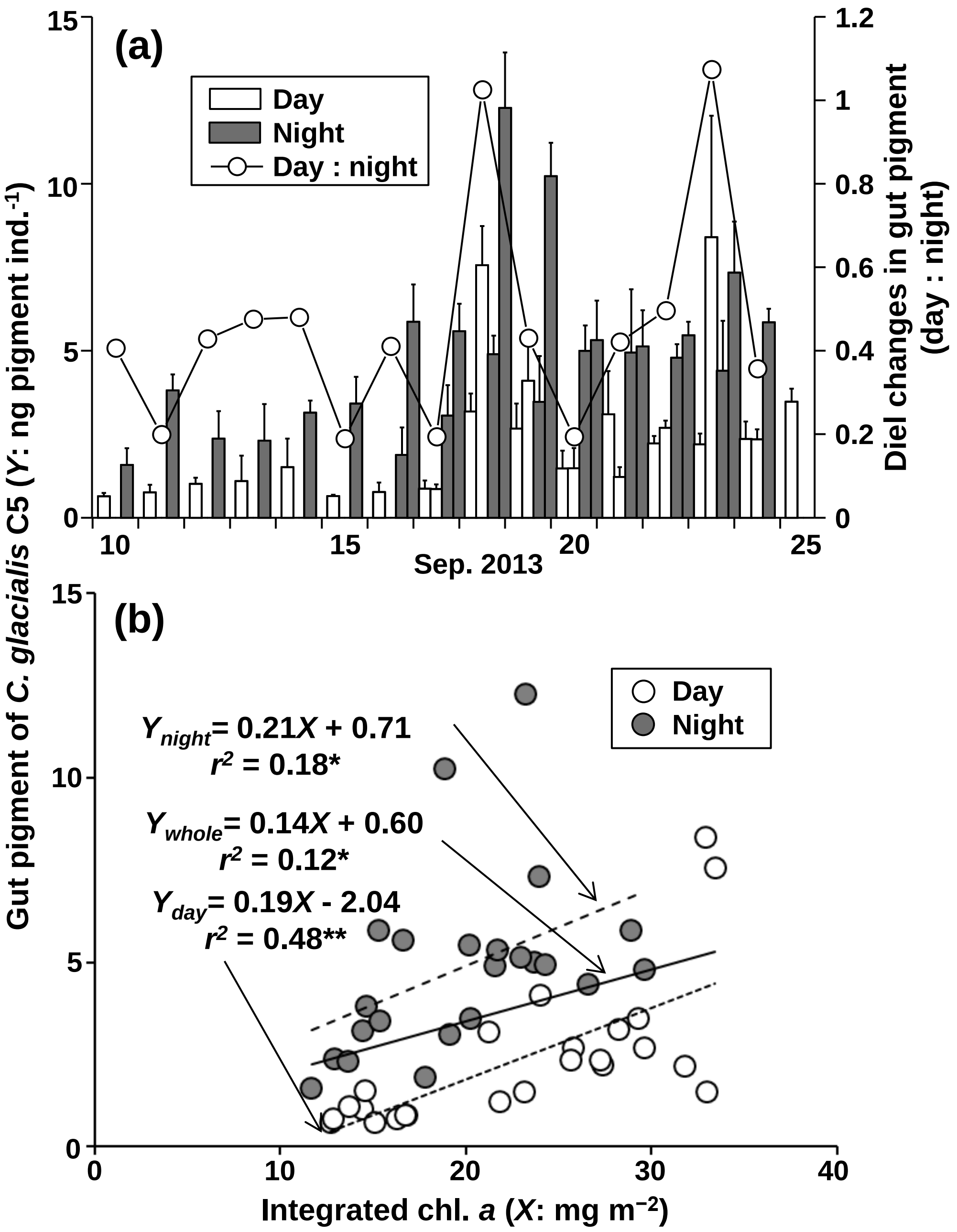


Fig. 5. (Matsuno et al.)

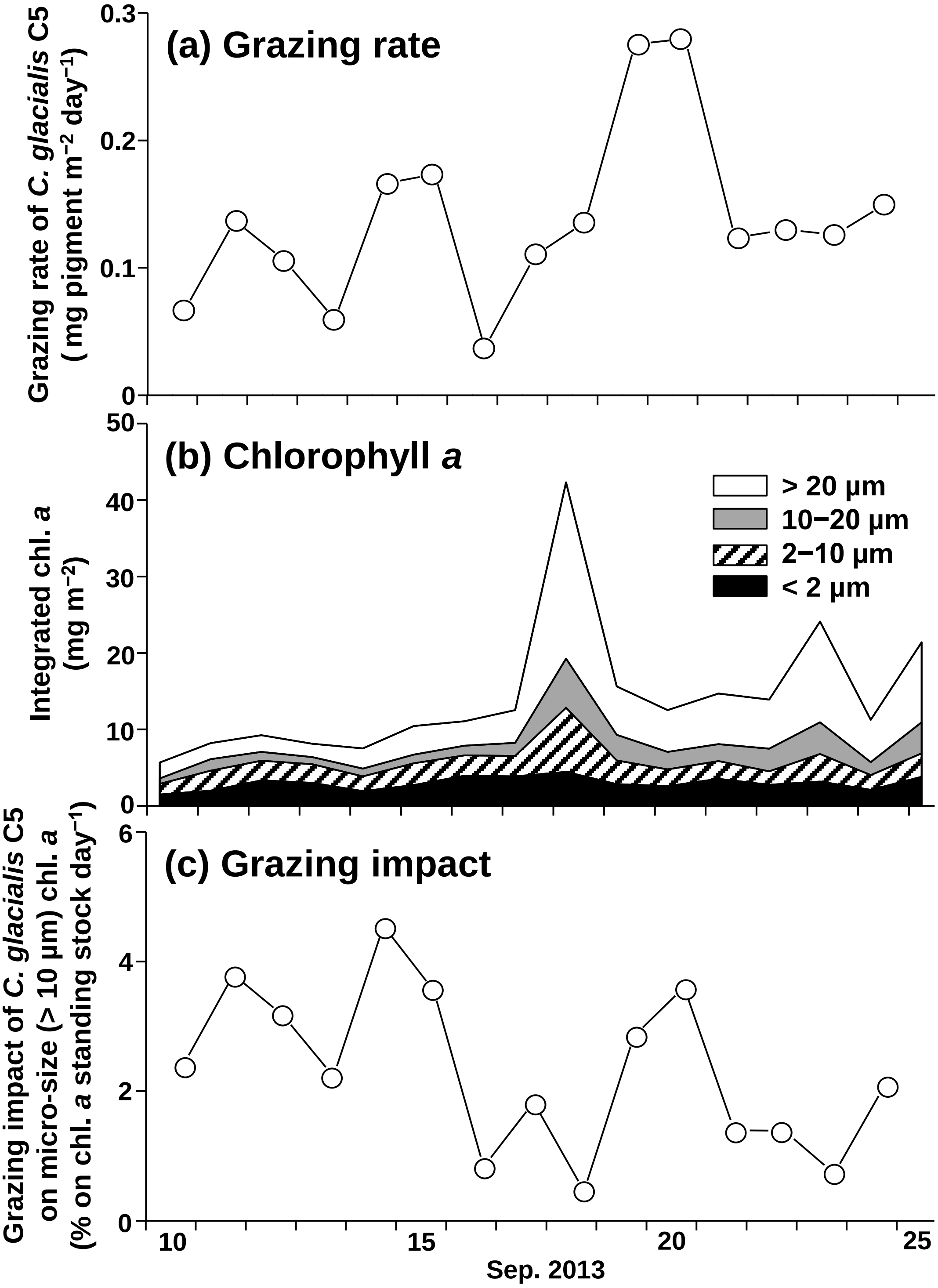


Fig. 6. (Matsuno et al.)