Phytoplankton and microzooplankton population dynamics along the western area from the North Pacific to the Bering Sea in summer

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Abstract

Phytoplankton growth and microzooplankton grazing are two critical processes in marine food webs, but they remain understudied in the vast area of the subarctic western Pacific and the Bering Sea. In this study, we measured the phytoplankton growth and microzooplankton grazing rates via the dilution technique to demonstrate their spatial patterns and investigate underlying mechanisms driving the planktonic food web dynamics in these less-explored regions. Our results showed that the phytoplankton growth in these regions was determined by nutrient availability and temperature. In the high nutrient, low chlorophyll regions, iron availability was the primary factor limiting phytoplankton growth. In contrast, phytoplankton growth in the Gulf of Anadyr and Kamchatka Strait was mainly limited by inorganic nitrogen exhausted by the summer blooms. Also, we found that microzooplankton grazing rate was affected by both temperature and prey availability, highlighting the positive effect of temperature. Strong top-down control on phytoplankton by microzooplankton was observed in the Gulf of Anadyr and Kamchatka Strait, indicating a active microbial food web with high turnover rates. In contrast, the decoupling of phytoplankton growth and microzooplankton grazing in the HNLC regions illustrates a weak role of microzooplankton in the marine food web. These results indicated different food web structures in the areas with and without riverine iron input. By revealing the roles of temperature and nutrient or prey availability in regulating the spatial variability of plankton rates, we expect that the plankton will respond differently to ocean warming between the HNLC and coastal regions of the western subarctic Pacific due to different nutrient conditions. Our study contributes to understanding how marine plankton will respond to the projected ocean warming and sea ice declines at high latitudes.

Introduction

Marine phytoplankton contribute about half of global primary production with less than 1% of the Earth's photosynthetic biomass (Field et al. 1998). The fates of marine primary production are critical to carbon export and global biogeochemical cycling, among which grazing by microzooplankton is a major pathway (Steinberg and Landry 2017). Microzooplankton (<200 μm in size), including ciliates, heterotrophic or mixotrophic dinoflagellates, and metazoan nauplii, are key trophic links of the marine food web and play essential roles in nutrient regeneration. They consume about 59–75% of daily primary production on a global scale (Calbet and Landry 2004). Nevertheless, more accurate quantification of the role of microzooplankton in the food web entails more empirical estimates of microzooplankton grazing activities in various spaces and times (Schmoker et al. 2013). For instance, microzooplankton grazing accounts for about 60% of primary production loss in high latitude seas where the primary production is relatively high (Calbet and Landry 2004). However, this estimate is primarily based on intensive studies in the eastern subarctic North Pacific (e.g., Gulf of Alaska: Strom et al. 2001; eastern Bering Sea: Sherr et al. 2013; Stoecker et al. 2014a; eastern North Pacific: Landry et al. 1993; McNair et al. 2021). There were few estimates in the vast area along the western North Pacific and the western Bering Sea, and the magnitude of microzooplankton grazing on phytoplankton in these regions remains unknown.

The subarctic Pacific is at the end of the global ocean conveyor belt (Broecker et al. 1991), and it is characterized as one of the high-nutrient, low-chlorophyll (HNLC) regions, where the surface macronutrient concentrations are persistently high while the phytoplankton biomass is relatively low (Boyd et al. 2004). The Bering Sea is connected to the subarctic Pacific through ocean circulations. The Alaskan Stream enters the Bering Sea through several Aleutian passes, such as Near Strait, and joins the anti-clockwise Bering Sea Gyre and the

Bering Slope Current. At the same time, an outflow with East Kamchatka Current through the Kamchatka Strait is balanced with the inflows (Aydin and Mueter 2007). As such, the oceanic part of the Bering Sea is hydrographically recognized as an entity with the subarctic Pacific and presents the characteristic of HNLC as well (Banse and English 1999; Nishioka et al. 2021). In the HNLC regions, iron (Fe) limitation is traditionally recognized as the major factor controlling low primary production (Miller et al. 1991). The top-down control from microzooplankton grazing on phytoplankton has been argued as another critical mechanism in maintaining the relatively low phytoplankton biomass (Landry et al. 1993; Strom et al. 2001). As the small phytoplankton are less affected by the Fe limitation, they could be under strong top-down control by microzooplankton herbivory, leading to low phytoplankton biomass in the eastern subarctic Pacific, where small phytoplankton are dominant (Miller et al. 1991).

In contrast to the HNLC basin, the coastal regions of the Bering Sea are highly productive, especially during spring and summer blooms (Banse and English 1999). Although the diatom-dominated primary production during blooms may be more efficiently grazed by mesozooplankton (Hunt Jr. et al. 2011), studies in the eastern Bering Sea have observed significant microzooplankton grazing on spring blooms (Sherr et al. 2013). Nevertheless, the magnitude of microzooplankton grazing in the western Bering Sea (e.g., the Gulf of Anadyr) remains unexplored, which could be different from the eastern area due to distinct hydro-physical processes (Khen et al. 2013). Therefore, we need to measure microzooplankton grazing rates in these regions to further understand the plankton dynamics at high latitudes.

In addition to the magnitude of microzooplankton grazing, understanding what factors drive the spatial and temporal variability of such food web processes is equally important, particularly in the rapidly changing ocean. Recent observations have documented a

significant increase in sea-surface temperature accompanied by a decrease in sea ice in the subarctic Pacific and the western Bering Sea during the past decades (Max et al. 2014; Frey et al. 2022). A recent study also found early retreat and delayed arrival of sea ice in the northern Bering Sea, resulting in warmer surface temperatures in summer (Stabeno et al. 2019). The substantial warming may impact the marine food web as temperature is crucial in determining metabolic rates. Some studies have pointed out that enhanced phytoplankton blooms at high latitudes occur partially because the low temperature constrains the zooplankton grazing activities (Rose and Caron 2007), which may open a 'loophole' for the explosion of phytoplankton (Irigoien et al. 2005). The ongoing warming may enhance the microzooplankton herbivory on phytoplankton (Chen et al. 2012), affecting the timing and extent of high-latitude phytoplankton blooms (Archer et al. 2000; Sherr et al. 2013). More empirical evidence is needed to understand the relationship between temperature and plankton rates at high latitudes. Moreover, other factors such as prey concentration and quality also play a role in determining the microzooplankton grazing activities (Hansen et al. 1997; Chen et al. 2012).

In this study, we measured the phytoplankton growth rate and microzooplankton grazing rate via the dilution approach (Landry and Hassett 1982) along the western area of the subarctic North Pacific and the Bering Sea in the summer of 2018. The study region spans a latitude of 10° and is scarcely studied on plankton dynamics. We aim to 1) quantify the magnitude of microzooplankton grazing rate in such less studied regions; 2) demonstrate the spatial patterns of phytoplankton growth rate and microzooplankton grazing rate; 3) identify the determining factors driving the spatial variability of these planktonic food web processes.

Materials and Methods

Study area and environmental parameters measurement

123 The study was conducted in the western subarctic Pacific Ocean and the western
124 Bering Sea during the cruise aboard the R/V *Professor Multanovskiy* (belonging to the Far
125 Eastern Hydrometeorological Research Institute, Russia) in summer from July to September
126 2018. The total 33 stations where we conducted dilution experiments were roughly divided
127 into three water masses according to their locations (Fig. 1). As the Aleutian Arc is the
128 boundary between the North Pacific and the Bering Sea, we treated the stations off the Pacific
129 side of the Kamchatka Peninsula and the Kamchatka Strait as a group of western North
130 Pacific (WNP). We also grouped the stations located in the western Bering Sea basin (WBS)
131 and the stations located in the Gulf of Anadyr (GoA).

132 Hydrographic data, including temperature and salinity, were obtained at each station
133 by an SBE-911 plus CTD sensor (Sea-Bird Electronics). The incident photosynthetic active
134 radiation (PAR) was measured continuously by an LI-190SB PAR sensor (LI-COR Inc.). The
135 inorganic macronutrient concentrations, including DIN (dissolved inorganic nitrogen, i.e.,
136 NO_3^-+NO_2^- and NH_4^+), PO_4^{3-}(P), and $Si(OH)_4$ (Si), were measured using an autoanalyzer
137 (QuAAtro, BL TEC Co. Ltd.) which were quality-controlled using KANSO reference
138 material (KANSO Co.). The samples for determining dissolved Fe concentration were
139 collected and measured by an FIA chemiluminescence detection system. The details in the
140 sampling and measurement of macronutrients and dissolved Fe were in Nishioka et al. (2020,
141 2021).

142 ***Phytoplankton and microzooplankton biomass and community measurements***

143 The phytoplankton biomass was represented by chlorophyll *a* (Chl *a*) concentration,
144 and the size structure of the algal community was characterized by size-fractionated Chl *a*
145 analysis. Aliquots of 250 mL or 500 mL seawater were sequentially filtered through 20 μm
146 polycarbonate membrane filters (GVS Corporation) and GF/F glass fiber filters under a low
147 vacuum. The phytoplankton retained on 20 μm and GF/F filters (nominal pore size: 0.7 μm)

were defined as micro and nano+pico phytoplankton, respectively (Sieburth et al. 1978). All filters were soaked in 6 mL N, N-dimethylformamide (DMF) at -20°C in the darkness for 24h, and the Chl *a* concentration was measured onboard by a Turner Design fluorometer (10-AU, Turner Designs; Welschmeyer 1994; Kobari et al. 2007).

The biomass and community composition of microzooplankton were measured from the Lugol's-preserved samples. Aliquots of 250 mL seawater were preserved with 6 mL acidic Lugol's solution. The samples were stored in amber bottles at room temperature onboard and 4 °C in the laboratory. When analyzing, ten to twenty mL samples were settled by Utermöhl chambers for more than 24 hours and observed entirely using an inverted microscope (Olympus IX51) at 200× magnification. The coastal samples from high Chl *a* environments were diluted (3 to 5 fold) before the settling procedure. All ciliates (aloricate-ciliate and Tintinnids), heterotrophic and mixotrophic dinoflagellates, and metazoan nauplii (<200 μm) were enumerated and taken pictures for dimensions measurements. The cell volumes were calculated by the width and length measured by SPOT software (version3.5) after assigning appropriate geometrical shapes. The biovolumes were then converted into carbon content (μg C L^{-1}) by the empirical conversion factors of each microzooplankton category (Table S1).

Dilution experimental setup

Dilution experiments were conducted at each station to estimate the phytoplankton growth rate and mortality rate due to microzooplankton grazing (Landry and Hassett 1982). Seawater samples were collected using acid-cleaned 12 L X-Niskin sampling bottles attached to an SBE-911 plus or SBE-32 rosette multi-sampler system (CTD-CMS system; Sea Bird Electronics, Inc.) or an acid-washed plastic bucket. The particle-free seawater was prepared by filtering the natural seawater through a 0.2 μm filter capsule (Pall Corporation) by gravity and added to the clean polycarbonate bottles (1.2 L) to the pre-designed volumes. The bottles

were filled to the full capacity with natural seawater pre-screened with a 200 μm mesh to remove mesozooplankton. Five dilution treatments with the percentages of natural seawater (i.e., the dilution factors) as 10, 25, 50, 75, and 100% were set up at each station. 10% and 100% of these treatments were established in duplicated bottles, while others were in one bottle. Inorganic nutrients were added to all bottles to ensure that nutrients did not limit phytoplankton growth. The final nutrient concentrations in the bottles were 18 μmol L^{-1} $NaNO_3$, 2 μmol $L^{-1}NH_4Cl$, 20 μmol L^{-1} Na_2SiO_3, and 1.25 μmol L^{-1} KH_2PO_4. Another two bottles filled with pre-screened natural seawater without nutrient addition were prepared as controls. All bottles were tightly capped and incubated for 24 h in an on-deck incubator. The light intensity was simulated by covering bottles with neutral screens, and the temperature was controlled by a thermo-controller (EYELA CTP-3000). The subsamples for determining size-fractionated Chl *a* were taken from the initial natural seawater and each bottle after incubating and measured as described above. Before each experiment, all polycarbonate bottles, carboys, tubing, and filter capsules were acid-washed using 10% HCl and rinsed with distilled water, followed by *in situ* seawater.

Phytoplankton growth rate and grazing mortality rate estimate

The phytoplankton in each bottle was assumed to grow exponentially with the net growth rate as k (d^{-1}) = (1/t) ln(P_t/dP_0), where P_0 and P_t were the phytoplankton biomass represented by Chl *a* concentration before and after incubation, d is the dilution factor (the percentages of natural seawater) of each bottle, P_0 was obtained by multiplying d with initial Chl *a* concentration of *in situ* unfiltered seawater, t is the incubation time (1 day). The growth rate with nutrient enrichment (μ_n; d^{-1}) and grazing mortality rate (m; d^{-1}) of phytoplankton were derived from the linear regression of net growth rate k against dilution factor d. The instantaneous phytoplankton growth rate (μ_0; d^{-1}) was calculated as the sum of the mortality

rate and the net growth rate in the control bottle without nutrient enrichment (i.e., $\mu_0 = m+k_{control}$).

When saturated grazing was observed (i.e., the net growth rates of least-diluted bottles were leveling off; Gallegos 1989), the μ_n and m were estimated following Chen et al. (2009). Briefly, the Chl *a* concentrations between initial natural seawater (P_0) and the least diluted bottle after incubation (P_1) were compared to judge whether the saturated grazing occurred under *in situ* conditions or arose from the nutrient enrichments. If $P_1 > P_0$, this means that phytoplankton do not reach the level for grazing saturation under *in situ* conditions, and the m equals the slope of the regression plots within the non-saturation range. By contrast, $P_1 < P_0$ means that saturated grazing has already occurred under *in situ* conditions. In this case, the m was assumed to be the same in the treatments with and without nutrient enrichments and calculated as $m = \mu_n - k_{n100\%}$, where $k_{n100\%}$ is the net growth rate of 100% bottles with nutrient enrichments, and μ_n was calculated from the intercept of the regression curve within the non-saturation range. For the experiments with a positive slope of linear regression curve (negative grazing rate) that was not significantly different from 0, the m was set to 0, and the μ_n and μ_0 were calculated as the average $k_{n100\%}$ and $k_{control}$, respectively (Chen et al. 2009).

The phytoplankton nutrient limitation index was calculated as μ_0/μ_n, which indicates whether the *in situ* nutrients limited the phytoplankton growth (Landry et al. 1995). The lower index indicates more severe nutrient limitation on phytoplankton growth. The impact of microzooplankton grazing on phytoplankton as the percentage of primary production consumed was calculated as %PP consumed = $m/\mu_0 \times 100\%$ (Calbet and Landry 2004).

Statistical analysis

To investigate the potential factors affecting the phytoplankton growth and microzooplankton grazing rates, Spearman's rank-order correlation analysis was applied to examine the relationships among physical (temperature, salinity, and PAR), chemical (DIN,

P, Si, and DIN:P), and biological (log-transformed Chl *a*, size-fractionated Chl *a*, log-transformed microzooplankton biomass, μ_n, μ_0, m, biomass-specific grazing rate m/B_z, and the growth and grazing mortality rates of two size fractions) parameters. Chl *a* concentration and microzooplankton biomass were log-transformed to ensure a normal distribution. To further explore whether microzooplankton grazing and biomass-specific grazing rate are affected by Chl *a* and temperature, we also used multiple linear regression with these two factors as explanatory variables.

Compiling the data of dilution experiments in the subarctic North Pacific and the Bering Sea

To further understand the plankton population dynamic in the subarctic North Pacific and the Bering Sea, we searched the published data of dilution experiments conducted in the surface water of these regions and compiled a dataset on plankton rates and the corresponding environmental parameters (e.g., temperature, NO_3 concentration, and PAR). We then compared our study regions with other regions based on this dataset (Table S3). In addition, we used the General Additive Models (GAMs, Wood 2006), which employed nonparametric smooth functions to describe the effects of environmental factors, to explore the underlying mechanisms determining phytoplankton growth and microzooplankton grazing at high latitudes (Supplementary Information).

All analyses were implemented using R in version 4.1.2 (R Core Team, 2021). The GAMs were conducted via R function "*gam*" in the package "*mgcv*" (Wood 2006). The multiple linear regression was performed with the R function "*lm*", and the partial regression plots were created by "*avPlots*" in the package "*car*" (Fox and Weisberg, 2019). The figures were created in R using "*ggplot2*" (Wickham 2016) and "*oceanmap*" (Bauer 2020) packages and the Ocean Data View (Schlitzer 2013).

Results

We have conducted the experiments from the area east of Kamchatka Peninsula to the Gulf of Anadyr (Fig. 1). The hydrological and biogeochemical properties varied across the three regions (i.e., WNP, WBS, and GoA; Fig. 2), which influences the population dynamics of phytoplankton and microzooplankton in these regions (Figs. 3, 4).

Western North Pacific (WNP)

In the WNP, the inorganic macronutrient concentrations, including DIN, P, and Si, at the stations located off the Pacific side of the Kamchatka Peninsula (St. C04, B03, and B06) were relatively high, while the dissolved Fe was extremely low (Fig. 2, Table S2). At these stations, the average Chl *a* concentration was 0.78 ± 0.37 μg L^{-1} (mean ± sd, the same below unless otherwise indicated). The phytoplankton community was dominated by nano+pico phytoplankton (Fig. 3). By contrast, the macronutrients were low in the Kamchatka Strait, whereas the dissolved Fe was higher (ranges = 0.06 – 0.57 nM) than that at other stations in the WNP (ranges = 0.05 – 0.28 nM, Fig. 2). The Chl *a* concentration was also higher in the Strait (1.37 ± 0.85 μg L^{-1}), with the size community dominated by nano+pico phytoplankton (Fig. 3). The high dissolved Fe and Chl *a* concentrations in the Strait could result from the freshwater inputs indicated by the slightly lower sea surface salinity (Fig. 2b).

The average phytoplankton growth rate in the WNP was 0.30 ± 0.23 d^{-1} ranging from 0.04 to 0.74 d^{-1}, which was insignificantly different from those of micro-and nano+pico phytoplankton ($F_{2,17}$ = 0.06; p = 0.94; Figs. 4, 5a). The growth rate was significantly stimulated by macronutrient enrichments, especially at the stations in the Kamchatka Strait, with an average macronutrient-enriched growth rate of 0.78 ± 0.44 d^{-1} ($F_{1,12}$ = 6.52; $p < 0.05$; Figs. 4, 5a).

Microzooplankton biomass ranged from 15 μgL^{-1} to 60 μgL^{-1}, with more contribution by heterotrophic or mixotrophic dinoflagellates (Fig. 3). No significant difference was

observed among the grazing mortality rate of the total phytoplankton community and the two size groups ($F_{2,17}$ = 0.06; p = 0.84; Figs. 4, 5d). The average 82% ± 73% (0~221%) primary production was consumed by microzooplankton in this area, where a high %PP consumed was observed in the Kamchatka Strait (Table 1).

Western Bering Sea basin (WBS)

The WBS includes the Kamchatka basin and Aleutian Basin, where the hydrological and nutrient conditions were relatively stable and similar to the Kamchatka basin on the Pacific side (Fig. 2). The average DIN, P, and Si concentrations (9.2 μM, 1.0 μM, and 25.5 μM, respectively) were between those found for WNP and GoA, and the dissolved Fe concentration was very low (Fig. 2). Such conditions led to low Chl *a* concentration (0.8 ± 0.27 μgL^{-1}) with major contributions by nano+pico phytoplankton (79.4% ± 6.6%, Fig. 3). Based on the results of pigment analysis in the same expedition, the haptophytes, pelagophytes, and chlorophytes were the major groups of the phytoplankton community (Fig. 3 in Waga et al. 2022). The growth rates of total phytoplankton and the two size groups (> 20 μm and < 20 μm) were not different from each other with average values of 0.30 ± 0.15 d^{-1}, 0.34 ± 0.21 d^{-1}, and 0.26 ± 0.18 d^{-1}, respectively ($F_{2,74}$ = 1.9; p = 0.16; Figs. 4, 5b). Adding macronutrients did not boost their growth rate ($F_{1,74}$ = 3.324; p = 0.07; Figs. 4, 5b). As such, the μ_0/μ_n was about one at most stations (Fig. S1), indicating that the phytoplankton growth was not limited by the macronutrient in this area.

Microzooplankton biomass ranged from 14 to 93 μg C L^{-1} (Fig. 3), and their average grazing rates on the total phytoplankton community were 0.07 ± 0.07 d^{-1}, which were relatively low compared with WNP and GoA (Figs. 4, 5d). At some stations, no microzooplankton grazing were observed (Fig. 4, Table 1). This low grazing pressure was more frequently observed on micro-phytoplankton in this area (Table 1). The percentage of

296 primary production consumed by microzooplankton (0 to 86%) was also lower than WNP
297 and GoA (Table 1).

298 ***Gulf of Anadyr (GoA)***

299 The hydrological properties and nutrient conditions in the GoA were very different
300 from the other two regions. The temperature in the GoA (8.9 ± 0.8 °C) was lower than that in
301 the WNP and WBS (Fig. 2a). The sea surface salinity varied from 28.5 at St. I01 to 32.7 at St.
302 H03, signifying freshwater inputs to the Gulf (Fig. 2b). In contrast to WNP and WBS, the
303 inorganic macronutrient concentrations were extremely low in the GoA, where the DIN and P
304 were depleted at some stations, such as H03 and H05 (Fig. 2c, d). The Si was also low with
305 an average concentration of 5.9 μM (Fig. 2e). In contrast, the dissolved Fe concentration was
306 relatively high, with an average concentration of 3.03 ± 1.59 nM (Fig. 2f). Under such
307 conditions, the Chl *a* concentration was also high (2.84 ± 2.23 μgL^{-1}), ranging from 0.46 μgL^{-1}
308 at St. I07 to 7.7 μgL^{-1} at St. H01 (Fig. 3). The nano+pico phytoplankton were the dominant
309 size fractions at most stations in the GoA (74.8% ± 26%), whereas the micro-phytoplankton
310 dominated the phytoplankton communities at St. H01 (67.8%) and I03 (76.9%). At these two
311 stations, abundant diatoms (mainly *Pseudo-nitzschia*) were observed (Fig. S3). The
312 microzooplankton biomass ranged from 20.4 to 103 μgL^{-1}, with the highest value at St. H01
313 (Fig. 3).

314 In these macronutrient-depleted regions, the growth rates were negative at most
315 stations except H01, I03, and I05 (Fig. 4). Adding macronutrients significantly drove the
316 growth rates to increase to positive values with the average macronutrient-enriched growth
317 rate of 0.28 ± 0.14 d^{-1} ($F_{1,18} = 11.74$, $p < 0.01$; Fig. 5c). The μ_0/μ_n was less than 0.5 (Fig. S1),
318 signifying a severe nutrient limitation in this region. The average grazing mortality rate of the
319 total phytoplankton community was 0.20 ± 0.27 d^{-1}, which was also not different from the
320 grazing mortality rate of the micro and nano+pico phytoplankton ($F_{2,27} = 0.16$, $p = 0.85$; Fig.

5d). In the GoA, the percentage of primary production consumed by microzooplankton was not calculated at the stations where the phytoplankton growth rates were negative, but for the stations H03, I03, and I05, the values were 183%, 103% and 119%, respectively (Table 1).

Potential environmental variables affecting plankton population dynamics

The growth rates of the phytoplankton community and nano+pico size group were strongly positively correlated with the macronutrients but negatively correlated with the dissolved Fe (Fig. 6), as the growth rate was low in the macronutrient-depleted but Fe-rich GoA (Fig. 4). The growth rates were also positively correlated with temperature (Fig. 6). While the micro-phytoplankton growth rate was positively correlated with macronutrients but not temperature (Fig. 6). No significant relationship was observed between phytoplankton growth and grazing mortality rate (Fig. 6).

Microzooplankton grazing rate was positively correlated with Chl *a* and microzooplankton biomass (Fig. 6). No significant correlations were observed between grazing rates and physical and chemical parameters, including temperature (Fig. 6). However, the relationship between temperature and grazing rate could be masked by the correlation with Chl *a*. We then conducted multiple linear regression analyses that used both Chl *a* and temperature as explanatory variables to predict the grazing rates. The effect of temperature on grazing rates was significant ($t = 2.14$, $p < 0.05$ for phytoplankton community; $t = 3.40$, $p < 0.01$ for nano+pico size group; Fig. 7), suggesting that microzooplankton grazing rate increased with increasing temperature in the study regions. Considering the effect of grazer biomass, we calculated the biomass-specific grazing rate (normalized to microzooplankton biomass, m/B_z) and conducted the multiple linear regression analysis. The result showed that m/B_z also increased with increasing Chl *a* and temperature (Fig. 7).

Based on the GAMs analysis on the compiled dataset of the plankton rates in the subarctic North Pacific and the Bering Sea, including the Chukchi sea, the phytoplankton

346 growth rate was affected by temperature ($p < 0.05$; Fig. 8), NO_3 concentration ($p < 0.001$;
347 Fig. 8), and *PAR* ($p < 0.001$; Fig. 8), which explained 23.6% variability of the growth rate.
348 The temperature explained the 9.09 % variability of microzooplankton grazing rate ($p <$
349 0.001; Fig. 8), whereas the effect of Chl *a* on microzooplankton grazing rate was not
350 significant ($p = 0.09$; Fig. 8).
351
352 **Discussion**
353 The subarctic Pacific and the Bering Sea cover a large area at high latitudes in the
354 northern hemisphere, and their offshore region is one of the HNLC regions. This region is
355 undergoing substantial warming and changes in winter sea ice concentration and is sensitive
356 to climate changes (Stabeno et al. 2019; Max et al. 2014). Such changes could strongly
357 impact the planktonic food web structure and function, which, however, remains
358 understudied in this region. Our study filled gaps of *in situ* data on phytoplankton growth and
359 grazing mortality rates in the less-explored western regions of the subarctic Pacific and the
360 Bering Sea and revealed their distinct spatial patterns. Moreover, we compiled the
361 corresponding data in the subarctic Pacific and the Bering Sea, including the Chukchi Sea, to
362 further identify the pivotal environmental variables driving the spatial variability of plankton
363 population dynamics, which is conducive to our understanding of the impact of
364 environmental changes on planktonic ecosystems at high latitudes.
365 ***Phytoplankton growth rates: effects of nutrient availability and temperature***
366 The phytoplankton growth rate varied among stations, with a sharp contrast observed
367 between two different types of environments, i.e., Fe-limited HNLC regions and Fe-rich Gulf
368 and Strait regions. This contrast was shaped by the impact of nutrient availability.
369 In the HNLC areas, including the offshore stations in the WNP (St. C04, B03, and
370 B06) and WBS, the phytoplankton growth rate was not limited by macronutrients as the

371 macronutrients enrichment did not significantly promote their growth (Figs. 4, 5). The
372 phytoplankton growth rate in the offshore stations of WNP was slightly higher than that in
373 the eastern North Pacific (Rivkin et al. 1999). No published data on phytoplankton growth
374 rates are available in the western Bering Sea, but extensive studies have been conducted in
375 the eastern Bering Sea (Fig. 8), where no macronutrient limitation was observed for
376 phytoplankton growth as we found in western regions (Liu et al. 2002; Olson and Strom
377 2002). These results collectively show that macronutrients were not limited for phytoplankton
378 growth in the HNLC areas. However, dissolved Fe availability may limit the phytoplankton
379 growth rate as it was extremely low in these regions (Fig. 2).
380 In contrast, the phytoplankton assemblages in the Kamchatka Strait and GoA suffered
381 from severe macronutrient limitations in August. The growth rates were negative at most
382 stations in the GoA and dramatically boosted by the enrichment of macronutrients (Figs. 4,
383 5). As the macronutrients, especially Si, were deprived, whereas the biomass (i.e., Chl *a*) was
384 very high, this area was experiencing the summer diatom bloom at its late or post phases. At
385 St. H01 and I03, the bloom was in the late phase as we detected positive growth rates and
386 observed highly abundant diatoms (mainly *Pseudo-nitzschia*) (Fig. S3). Conversely, at other
387 stations, the diatoms should have bloomed and probably been grazed by microzooplankton as
388 the bloom proceeded. In this post-bloom period, the phytoplankton community has been
389 reshaped, in which diatoms comprised a small proportion but haptophytes and cryptophytes
390 were the major phytoplankton groups (the results from the same expedition; Fig. 3 in Waga et
391 al. 2022). The blooms in the Kamchatka Strait were initiated by the Fe-rich freshwater input
392 from the Kamchatka Peninsula to the Strait, and its influence expanded to adjacent coastal
393 waters (Nishioka et al. 2021). In the GoA, the mixing of macronutrient-rich oceanic waters
394 and the Fe-rich freshwater from the Anadyr River boosted the growth of phytoplankton and

fostered the spring-summer bloom (Sorokin, 1999), fueling the higher trophic levels of the food web.

Our study captured the dynamic features of plankton in the late- or post-phase of the bloom initiated by Fe input, as well as the features in the relatively stable HNLC waters where Fe was limited. These results revealed that the effect of macronutrients on phytoplankton growth in our study regions was mediated by Fe availability. Throughout the subarctic North Pacific, the Bering Sea, and the Chukchi Sea, the effect of macronutrients on phytoplankton growth was also significant, whereas the growth rate tended to level off at high nitrogen concentrations (Fig. 8), indicating that the effect of Fe availability overrides macronutrients in the HNLC regions. As such, both macronutrients and micronutrients are critical drivers of phytoplankton growth at high latitudes.

In addition to nutrient availability, temperature also influences phytoplankton growth. In our study region, temperature was significantly positively correlated with phytoplankton growth rate (Fig. 6). The results of the compiled dataset further confirmed the significant effect of temperature on phytoplankton growth (Fig. 8). Consequently, the low temperature contributed to the low phytoplankton growth rate in the GoA. When adding macronutrients to satisfy the phytoplankton growth, the macronutrient-enriched phytoplankton growth rates in the GoA were still much lower than that in the Kamchatka Strait where the temperature was higher (Figs. 4, 5). Despite the low growth rate, massive algal blooms frequently occur in the GoA partially because the low-temperature constraint on the zooplankton grazers might be more severe (Rose and Caron 2007), which opens a ‘loophole’ for the explosion of phytoplankton (Irigoien et al. 2005). Nevertheless, more investigation is still needed to understand the role of temperature in shaping algal blooms and plankton dynamics at high latitudes.

Microzooplankton grazing rate: bottom-up controls of prey availability and temperature

The microzooplankton grazing rates in the WNP (0.18 ± 0.12 d^{-1}) were almost identical to the previous estimates in the same regions (Liu et al. 2002) and similar to those in the eastern North Pacific (Rivkin et al. 1999; McNair et al. 2021). In the WBS, the grazing rate (0.07 ± 0.07 d^{-1}) was lower than in the WNP and the southeastern Bering Sea (Olson and Strom 2002). The lower grazing rate in the WBS can be attributed to the low Chl *a* concentration and possibly poor food quality stemming from the limited Fe concentration in the HNLC regions (Strom and Fredrickson 2008). Conversely, higher microzooplankton grazing rates were observed at high Chl *a* stations of GoA and Kamchatka Strait. Therefore, the prey availability represented by Chl *a*, along with food quality, should be regarded as the critical factors that determine microzooplankton grazing activities (Fig. 6).

In addition, the prey availability affects the grazing activities of individual grazers as the m/B_z positively correlated with Chl *a* concentration (Fig. 6). The m/B_z can be considered as the per capita clearance rate of grazers, which usually decreases with increasing prey concentration based on the functional responses, especially the Ivlev and Holling II functions (Holling 1959; Ivlev 1975; Chen et al. 2012). However, the m/B_z increased with increasing Chl *a* in our study regions (Fig. 7). This pattern can be explained by the increasing part of the Holling III function that is unimodal with a peak at low prey concentrations (Liu et al. 2021). Furthermore, it is also likely due to a shift of community composition towards more active grazers when Chl *a* increased. When expanding the dataset to the whole subarctic North Pacific, the Bering Sea, and the Chukchi Sea, the effect of Chl *a* concentration on grazing rate was insignificant (Fig. 8), which was also observed in other (sub)arctic waters (e.g., Lawrence and Mender-Deuer 2012). The results imply that other factors (e.g., prey quality and grazer selectivity), in addition to prey concentration, may affect the microzooplankton grazing rates at high latitudes.

Temperature is another vital factor affecting microzooplankton grazing (Chen et al. 2012; Liu et al. 2019). However, some studies found no relationship or an inverse relationship between temperature and microzooplankton grazing (Verity 1986; Menden-Deuer et al. 2018; Lavrentyev et al. 2019; Marrec et al. 2021). However, the temperature effect could be confounded by prey concentration or predator biomass with the consequence of no or negative correlations (e.g., Fig. 6). In our study, we used multiple linear regression analysis to consider both effects of temperature and prey concentration and found a positive correlation between temperature and microzooplankton community herbivory as well as the individual clearance rate (i.e., m/B_z; Fig. 7). Likewise, temperature positively influenced the microzooplankton grazing rate in the subarctic and polar regions based on GAM including the effect of prey concentration (Fig. 8). As such, in the warmer ocean, the grazing activities of microzooplankton on primary production will be enhanced by warming with more energy and material transferred to the higher trophic levels. It has been found that the temperature sensitivity of microzooplankton growth and grazing is much higher than phytoplankton (Chen et al. 2012). Rose and Caron (2007) attributed the algae blooms in cold waters to the stronger low-temperature constraint of microzooplankton over phytoplankton. Similarly, rising temperature enhances microzooplankton herbivory to a greater extent than phytoplankton growth elevates, which may accelerate the blooming progress and change the food web dynamics in high-latitude oceans. Nevertheless, the effect of temperature on predator-prey interaction and food web dynamics is more complex than the clear temperature dependence of plankton (Synodinos et al. 2021). For example, although the temperature sensitivity of per capita grazing rate of microzooplankton can be greater than that of phytoplankton growth rate, the biomass of microzooplankton will also depend on temperature, which may actually lead to a temperature independent grazing rate of the whole

468 microzooplankton community. More investigations are imperative to unveil the impact of
469 projected ocean warming on the high-latitude marine food web and ecosystems.

470 ***The balance between phytoplankton growth and microzooplankton grazing with***
471 ***implications of food web structure***

472 The grazing activities of microzooplankton were more active with greater grazing
473 pressure on phytoplankton in the Fe-rich Kamchatka Strait and GoA, which was assessed by
474 the m/μ_0 calculated as %PP consumed (Calbet and Landry 2004). The low (<100%) and high
475 (>100%) %PP consumed indicate the decoupling of growth and grazing with weak and strong
476 grazing pressure from microzooplankton, respectively. In the GoA, although the negative
477 growth rates at most stations make the estimation of %PP consumed difficult, the
478 average %PP consumed of the three stations with positive growth rates (H05, I03, I05) was
479 high (Fig. 8), indicating a strong grazing pressure on phytoplankton from microzooplankton.
480 At these stations, the phytoplankton communities were dominated by large phytoplankton (>
481 20 μm, mainly diatoms; Figs. 3; S3), which had been thought to be primarily consumed by
482 mesozooplankton such as copepods. Nevertheless, our results confirmed that the grazing
483 impacts from microzooplankton were as or more significant as mesozooplankton on large
484 diatoms. It has been increasingly recognized that heterotrophic dinoflagellates were voracious
485 predators on diatoms (Sherr and Sherr 2007). Ciliates have been found to prey on large-sized
486 diatoms in the eastern Bering Sea (Sherr et al. 2013). Therefore, both heterotrophic
487 dinoflagellates and ciliates are important predators on large phytoplankton such as diatoms.
488 In addition, the top-down control of microzooplankton grazing on phytoplankton was also
489 substantial in the Kamchatka Strait, where the average %PP consumed was 139% (Fig. 8).
490 Collectively, the Fe-rich freshwater input drove the rapid growth of phytoplankton, followed
491 by vigorous grazing activities, which made the planktonic food web more active.

By contrast, the %PP consumed at the offshore stations of WNP and WBS was relatively low, with an average of 40% and 35%, respectively, indicating a decoupling between phytoplankton growth and microzooplankton grazing and relatively weak grazing pressure from microzooplankton (Fig. S2). Such decoupling has also been observed in other HNLC regions (e.g., eastern Bering Sea basin; Fig. 8). In these regions, phytoplankton growth rate exceeded microzooplankton grazing, whereas the phytoplankton biomass did not accumulate as Chl *a* concentration was low. One possible explanation is a possible trophic cascade arising from the exclusion of higher trophic levels in the incubation bottles. The microzooplankton were released from grazing pressure by mesozooplankton that were removed artificially, which in turn enhanced microzooplankton predation on nanoflagellates and relieved the grazing of heterotrophic nanoflagellates on small phytoplankton (Marrec et al. 2021). In the current study, we conducted the same treatment at all stations, however, the decoupling between growth and grazing in the HNLC regions suggested that the trophic cascade was more severe and the protistan predatory chains could be longer. The role of heterotrophic nanoflagellates in consuming small phytoplankton could be more significant in the Fe-limited HNLC regions than in the Fe-rich Strait and Gulf.

In addition, the mixotrophs in plankton communities may also cause the growth-grazing imbalance. The mixotrophs may use their inherent or acquired phototrophy to supplement the energy demands when suffering from low food concentration and poor food quality, which reduces their grazing activities and results in low microzooplankton grazing rates (Stoecker et al. 2017). It has been found that the Chl *a* of mixotrophic ciliates was sometimes higher than 50% of total Chl *a* in the eastern Bering Sea, implying a significant role of mixotrophs in plankton communities at high latitudes (Stoecker et al. 2014b). Nevertheless, it remains a challenge to quantify the proportion of mixotrophs in the plankton community and their impact on the grazing rate estimates (Stoecker et al. 2017).

The balance between phytoplankton growth and microzooplankton grazing illustrates the role of microzooplankton in marine food webs with implications for the planktonic food web structure (Calbet and Landry 2004). In the more stable and Fe-limited HNLC regions, the decoupling between growth rate and grazing rate with low %PP consumed suggests a more complicated food web structure involving nanoflagellates and mixotrophs. By contrast, in the GoA and Kamchatka Strait, the Fe input via freshwater discharges not only triggered the rapid growth of phytoplankton but also enhanced the grazing activities of microzooplankton, driving the microbial food web more active with high turnover rates. Microzooplankton in these regions is a crucial vehicle for transferring organic matter and energy to the higher trophic levels. In fact, the strong top-down control of microzooplankton was observed more frequently in the coastal regions with high phytoplankton biomass at high latitudes (Fig. 8). For instance, high %PP consumed values in the southeastern Bering Sea occurred during phytoplankton blooms (Strom et al. 2008). As such, in these regions, the role of microzooplankton is more significant, with more contributions to the energy transfer from primary production to higher trophic levels.

Concluding remarks and perspectives

Our results revealed the variability in spatial patterns of phytoplankton growth and grazing mortality rates and the potential mechanisms driving such spatial variability in the less-explored western area of the subarctic Pacific and the Bering Sea. In the HNLC regions, the phytoplankton growth rate was relatively low and presumably limited by Fe availability, while the mortality due to microzooplankton grazing was also low, resulting in weak top-down controls on phytoplankton. By contrast, in the Gulf of Anadyr and Kamchatka Strait, where freshwater input brought a large amount of Fe, phytoplankton growth was limited by macronutrients (mainly N limitation) under the late-bloom or past-bloom conditions, together with strong top-down control by microzooplankton grazing. Collectively, in high-latitude

543 waters, phytoplankton growth was determined by temperature, nutrient availability, and light
544 intensity. Particularly, in the HNLC regions, the effect of macronutrients was mediated by Fe
545 availability, and the blooms could be stimulated by Fe input, accomplished by more active
546 microzooplankton herbivory. Through multiple linear regression analysis, we also identified
547 the effect of temperature and prey availability on microzooplankton grazing rate at high
548 latitudes. These insights into the crucial environmental variables driving the variability of
549 plankton population dynamics advance our understanding of how plankton will respond to
550 environmental changes.

551 The subarctic and polar regions are already under substantial warming. In the HNLC
552 regions, warming enhances the stratification of water column (Behrenfeld et al. 2006).
553 Without an additional Fe source, phytoplankton community will grow slowly and be
554 dominated by small phytoplankton, along with less active microzooplankton grazing, which
555 will result in a reduction of carbon sequestration capacity and fisheries production. While in
556 the Gulfs and Straits with Fe-rich freshwater input, the early retreat of sea ice and warmer sea
557 surface temperature may bring forward phytoplankton blooms and enhance
558 microzooplankton herbivory, leading to an increase in energy transfer to higher trophic
559 levels, shifts in food web structures, and accelerating carbon cycling in high-latitude waters.
560

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577 **References**

578 Archer, S. D., P. G. Verity, and J. Stefels. 2000. Impact of microzooplankton on the
579 progression and fate of the spring bloom in fjords of northern Norway. Aquat. Microb.
580 Ecol. **22**(1): 27-42. doi:10.3354/ame022027

581 Aydin, K., and F. Mueter. 2007. The Bering Sea - A dynamic food web perspective. Deep-
582 Sea Res. Part II Top. Stud. Oceanogr. **54**: 2501-2525. doi:10.1016/j.dsr2.2007.08.022

583 Banse, K. and D. C. English. 1999. Comparing phytoplankton seasonality in the eastern and
584 western subarctic Pacific and the western Bering Sea. Prog. Oceanogr., **43**(2-4): 235-
585 288. doi: 10.1016/S0079-6611(99)00010-5

586 Bauer, Robert. K. 2020. *oceanmap: A Plotting Toolbox for 2D Oceanographic Data.*
587 https://cran.r-project.org/web/packages/oceanmap/oceanmap.pdf

588 Behrenfeld, M. J., R. T. O'Malley, D. A. Siegel, C. R. McClain, J. L. Sarmiento, G. C.
589 Feldman, A. J. Milligan, P. G. Falkowski, R. M. Letelier, and E. S. Boss. 2006.
590 Climate-driven trends in contemporary ocean productivity. Nature 444:752-755.

591 Boyd, P.W. and others. 2004. The decline and fate of an iron-induced subarctic
592 phytoplankton bloom. Nature **428**: 549–553. doi: 10.1038/nature02437

593 Broecker, W.S. 1991. The great ocean conveyor. Oceanogr. **4** (2): 79–89. doi:
594 10.1063/1.41925

595 Calbet, A., and M. R. Landry. 2004. Phytoplankton growth, microzooplankton grazing, and
596 carbon cycling in marine systems. Limnol. Oceanogr. **49**: 51-57. doi:
597 10.4319/lo.2004.49.1.0051

598 Chen, B., H. Liu, M. R. Landry, M. Chen, J. Sun, L. Shek, X. H. Chen, and P. J. Harrison.
599 2009. Estuarine nutrient loading affects phytoplankton growth and microzooplankton
600 grazing at two contrasting sites in Hong Kong coastal waters. Mar. Ecol. Prog. Ser.
601 **379**: 77-90. doi:10.3354/meps07888

602 Chen, B., M. R. Landry, B. Huang, and H. Liu. 2012. Does warming enhance the effect of
603 microzooplankton grazing on marine phytoplankton in the ocean? Limnol. Oceanogr.
604 **57**: 519-526. doi:10.4319/lo.2012.57.2.0519
605 Connell, P. E., C. Michel, G. Meisterhans, K. R. Arrigo, and D. A. Caron 2018.
606 Phytoplankton and bacterial dynamics on the Chukchi Sea Shelf during the spring-
607 summer transition. Mar. Ecol. Prog. Ser. **602**: 49-62. doi: 10.3354/meps12692
608 Field, C. B., M. J. Behrenfeld, J. T. Randerson, and P. Falkowski. 1998. Primary production of
609 the biosphere: Integrating terrestrial and oceanic components. Science **281:** 237-240. doi:
610 10.1126/science.281.5374.237
611 Fox J, Weisberg S (2019). *An R Companion to Applied Regression*, Third edition. Sage,
612 Thousand Oaks CA. https://socialsciences.mcmaster.ca/jfox/Books/Companion/.
613 Frey, K. E., J. Clement Kinney, L. V. Stock, and R. Osinski. 2022. Observations of declining
614 primary productivity in the western Bering Strait. Oceanography, doi:
615 10.5670/oceanog.2022.123.
616 Gallegos, C. L. 1989. Microzooplankton Grazing on Phytoplankton in the Rhode River,
617 Maryland - Nonlinear Feeding Kinetics. Mar. Ecol. Prog. Ser. **57**: 23-33.
618 doi:10.3354/meps057023
619 Hansen, P. J., P. K. Bjørnsen, and B. W. Hansen. 1997. Zooplankton grazing and growth:
620 Scaling within the 2-2000-µm body size range. Limnol. Oceanogr. **42**: 687-704.
621 Holling, C. S. 1959. The components of predation as revealed by a study of small-mammal
622 predation of the European pine sawfly. Can. Entomol. **91**: 293-320. doi:
623 10.4039/Ent91293-5
624 Hunt Jr, G. L., K. O. Coyle, L. B. Eisner, E.V. Farley, R. A. Heintz, F. Mueter, J. M. Napp, J.
625 E. Overland, P. H. Ressler, S. Salo, and P. J. Stabeno. 2011. Climate impacts on eastern

626 Bering Sea foodwebs: a synthesis of new data and an assessment of the Oscillating
627 Control Hypothesis. ICES J. Mar. SCI. **68**(6): 1230-1243. doi: 10.1093/icesjms/fsr036
628 Irigoien, X., K. Flynn, and R. Harris. 2005. Phytoplankton blooms: a 'loophole'in
629 microzooplankton grazing impact? J. Plankton Res. **27**:313-321. doi:
630 10.1093/plankt/fbi011
631 Ivlev, V. S. 1975. Experimental ecology of the feeding of fishes. Yale University Press. J.
632 Oceanogr. **58**: 259–264. doi: 10.1023/A:1015857624562
633 Johansson, M., E. Gorokhova, and U. Larsson. 2004. Annual variability in ciliate community
634 structure, potential prey and predators in the open northern Baltic Sea proper. J.
635 Plankton Res. **26**: 67-80.
636 Khen, G.V., E.O. Basyuk, N.S. Vanin, and V.I. Matveev. 2013. Hydrography and biological
637 resources in the western Bering Sea. Deep-Sea Res. Part II Top. Stud. Oceanogr. **94**:
638 106-120.
639 Kobari, T., Kobari, Y., & Koga, S. 2007. Possible underestimation of Chlorophyll *a*
640 measurements for subtropical phytoplankton community by the pigment extraction and
641 the fluorometric determination. South Pacific Studies. 28: 1-8.
642 Landry, M. R., B. C. Monger, and K. E. Selph. 1993. Time-dependency of microzooplankton
643 grazing and phytoplankton growth in the subarctic Pacific. Prog. Oceanogr. **32**: 205-
644 222. doi: 10.1016/0079-6611(93)90014-5
645 Landry, M. R., J. Constantinou, J. Kirshtein. 1995. Microzooplankton grazing in the central
646 equatorial Pacific during February and August, 1992. Deep-Sea Res. Part II Top. Stud.
647 Oceanogr. **42**: 657–671. doi: 10.1016/0967-0645(95)00024-K
648 Landry, M., and R. Hassett. 1982. Estimating the grazing impact of marine micro-
649 zooplankton. Mar. Biol. **67**: 283–288, doi:10.1007/BF00397668

650 Lavrentyev, P. J., G. Franzè, and F. B. Moore. 2019. Microzooplankton distribution and
651 dynamics in the Eastern Fram Strait and the Arctic Ocean in May and August 2014.
652 Front. Mar. Sci. 6: 264. doi:10.3389/fmars.2019.00264
653 Lawrence, C., and S. Menden-Deuer. 2012. Drivers of protistan grazing pressure: Seasonal
654 signals of plankton community composition and environmental conditions. Mar. Ecol.
655 Prog. Ser. **459**: 39–52. doi:10.3354/meps09771
656 Leising, A.W., R. Horner, J. J. Pierson, J. Postel, and C. Halsband-Lenk. 2005 The balance
657 between microzooplankton grazing and phytoplankton growth in a highly productive
658 estuarine fjord. *Prog. Oceanogr.* **67**: 366–383. doi: 10.1016/j.pocean.2005.09.007
659 Liu, H., K. Suzuki, and T. Saino. 2002. Phytoplankton growth, and microzooplankton grazing
660 in the subarctic Pacific Ocean and the Bering Sea during summer 1999. Deep Sea Res. I
661 **49**: 363–375. doi: 10.1016/S0967-0637(01)00056-5
662 Liu, H., K. Suzuki, J. Nishioka, R. Sohrin, and T. Nakatsuka. 2009. Phytoplankton growth
663 and microzooplankton grazing in the Sea of Okhotsk during late summer of 2006. Deep
664 Sea Res. I **56**(4): 561–570. doi: 10.1016/j.dsr.2008.12.003
665 Liu, K., B. Chen, L. Zheng, S. Su, B. Huang, M. Chen, and H. Liu. 2021. What controls
666 microzooplankton biomass and herbivory rate across marginal seas of China? Limnol.
667 Oceanogr. **66**: 61-75. doi: 10.1002/lno.11588
668 Marrec, P., H. McNair, G. Franzè, F. Morison, J. P. Strock, and S. Menden-Deuer. 2021.
669 Seasonal variability in planktonic food web structure and function of the Northeast US
670 Shelf. Limnol. Oceanogr. **66**: 1440-1458. doi: 10.1002/lno.11696
671 Max, L., L. Belz, R. Tiedemann, K. Fahl, D. Nürnberg, and J. R. Riethdorf. 2014. Rapid
672 shifts in subarctic Pacific climate between 138 and 70 ka. Geology **42**(10): 899-902.
673 doi: 10.1130/G35879.1

McNair, H.M., F. Morison, J. R. Graff, T. A. Rynearson, and S. Menden-Deuer. 2021. Microzooplankton grazing constrains pathways of carbon export in the subarctic North Pacific. Limnol. Oceanogr. **66**(7): 2697-2711.

Menden-Deuer, S., C. Lawrence, and G. Franzè. 2018. Herbivorous protist growth and grazing rates at in situ and artificially elevated temperatures during an Arctic phytoplankton spring bloom. PeerJ 6: e5264. doi:10.7717/peerj.5264

Miller, C. B., B. W. Frost, P. A. Wheeler, M. R. Landry, N. Welschmeyer, and T. M. Powell. 1991. Ecological dynamics in the sub-arctic Pacific, a possibly iron-limited ecosystem. Limnol. Oceanogr. **36**: 1600–1615. doi: 10.4319/lo.1991.36.8.1600

Nishioka, J., T. Hirawake, D. Nomura, Y. Yamashita, K. Ono, A. Murayama, A. Shcherbinin, Y. N. Volkov, H. Mitsudera, N. Ebuchi, and M. Wakatsuchi. 2021. Iron and nutrient dynamics along the East Kamchatka Current, western Bering Sea Basin and Gulf of Anadyr. Prog. Oceanogr. **198**: 102662. doi: 10.1016/j.pocean.2021.102662

Nishioka, J., H. Obata, H. Ogawa, K. Ono, Y. Yamashita, K. J. Lee, S. Takeda, I. Yasuda. 2020. Sub-polar marginal seas fuel the North Pacific through the intermediate water at the termination of the global ocean circulation. Proc. Natl. Acad. Sci. **117** (23): 12665–12673. doi: 10.1073/pnas.2000658117.

Olson, M. B., and S. L. Strom. 2002. Phytoplankton growth, microzooplankton herbivory and community structure in the southeast Bering Sea: insight into the formation and temporal persistence of an Emiliania huxleyi bloom. Deep-Sea Res. Part II Top. Stud. Oceanogr. **49**: 5969-5990. doi: 10.1016/S0967-0645(02)00329-6

R Core Team. 2021. R: A language and environment for statistical computing. Vienna, Austria: R Foundation for Statistical Computing. Available from https://www.r-project.org

Rivkin, R. B., J. N. Putland, M. R. Anderson, and D. Deibel. 1999. Microzooplankton bacterivory and herbivory in the NE subarctic Pacific. Deep-Sea Res. Part II Top. Stud. Oceanogr. **46**: 2579-2618. doi: 10.1016/S0967-0645(99)00077-6

Rose, J. M., and D. A. Caron. 2007. Does low temperature constrain the growth rates of heterotrophic protists? Evidence and implications for algal blooms in cold waters. Limnol. Oceanogr. **52**: 886-895. doi: 10.4319/lo.2007.52.2.0886

Schmoker, C., S. Hernandez-Leon, and A. Calbet. 2013. Microzooplankton grazing in the oceans: impacts, data variability, knowledge gaps and future directions. J. Plankton Res. **35**: 691-706. doi: 10.1093/plankt/fbt023

Sherr, E. B., and B. F. Sherr. 2007. Heterotrophic dinoflagellates: a significant component of microzooplankton biomass and major grazers of diatoms in the sea. Mar. Ecol. Prog. Ser. **352**: 187-197. doi: 10.3354/meps07161

Sherr, E. B., B. F. Sherr, and C. Ross. 2013. Microzooplankton grazing impact in the Bering Sea during spring sea ice conditions. Deep-Sea Res. Part II Top. Stud. Oceanogr. **94**: 57-67. doi: 10.1016/j.dsr2.2013.03.019

Sieburth, J. M., V. Smetacek, and J. Lenz. 1978. Pelagic ecosystem structure: heterotrophic compartments of the plankton and their relationship to plankton size fractions. Limnol. Oceanogr. **23**: 1256-1263. doi: 10.4319/lo.1978.23.6.1256

Sorokin, Y. I. 1999. Data on primary production in the Bering Sea and adjacent Northern Pacific. J. Plankton Res. **21**(4): 615-636. doi:10.1093/plankt/21.4.615

Stabeno, P. J., S. W. Bell, N. A. Bond, D. G.Kimmel, C. W. Mordy, and M. E. Sullivan. 2019. Distributed biological observatory region 1: physics, chemistry and plankton in the northern Bering Sea. Deep-Sea Res. Part II Top. Stud. Oceanogr. **162**: 8-21. doi: 10.1016/j.dsr2.2018.11.006

722 Steinberg, D. K., and M. R. Landry. 2017. Zooplankton and the Ocean Carbon Cycle. Ann.
723 Rev. Mar. Sci. **9**: 413-444. doi: 10.1146/annurev-marine-010814-015924
724 Stoecker, D. K., A. Weigel, and J. I. Goes. 2014a. Microzooplankton grazing in the Eastern
725 Bering Sea in summer. Deep-Sea Res. Part II Top. Stud. Oceanogr. **109**: 145-156. doi:
726 10.1016/j.dsr2.2013.09.017
727 Stoecker, D. K., P. J. Hansen, D. A. Caron, and A. Mitra. 2017. Mixotrophy in the marine
728 plankton. Ann. Rev. Mar. Sci. **9**: 311–335. doi:10.1146/annurev-marine-010816-
729 060617
730 Stoecker, D. K., A. C. Weigel, D. A. Stockwell, and M. W. Lomas 2014b. Microzooplankton:
731 Abundance, biomass and contribution to chlorophyll in the Eastern Bering Sea in
732 summer. Deep-Sea Res. Part II Top. Stud. Oceanogr. **109**: 134-144. doi:
733 10.1016/j.dsr2.2013.09.007
734 Strom, S. L., and K. A. Fredrickson. 2008. Intense stratification leads to phytoplankton
735 nutrient limitation and reduced microzooplankton grazing in the southeastern Bering
736 Sea. Deep-Sea Res. Part II Top. Stud. Oceanogr. **55**: 1761-1774. doi:
737 10.1016/j.dsr2.2008.04.008
738 Strom, S. L., M. A. Brainard, J. L. Holmes, and M. B. Olson. 2001. Phytoplankton blooms
739 are strongly impacted by microzooplankton grazing in coastal North Pacific Waters.
740 Mar. Biol., **138**: 355-368. doi: 10.1007/s002270000461
741 Strom, S. L., E. L. Macri, and M. B. Olson. 2007. Microzooplankton grazing in the coastal
742 Gulf of Alaska: Variations in top-down control of phytoplankton. Limnol. Oceanogr.,
743 52: 1480-1494. doi: 10.4319/lo.2007.52.4.1480
744 Strom, S. L., and N. A. Welschemeyer. 1991. Pigment-Specific Rates of Phytoplankton
745 Growth and Microzooplankton Grazing in the Subarctic Pacific Ocean. Limnol.
746 Oceanogr. **36**: 50-63. doi: 10.1093/plankt/fbl051

747 Verity, P. 1986. Grazing of phototrophic nanoplankton by microzooplankton in Narragansett
748 Bay. Mar. Ecol. Prog. Ser. 29: 105–115. doi:10.3354/meps029105
749 Waga, H., A. Fujiwara, T. Hirawake, K. Suzuki, K. Yoshida, H. Abe, and D. Nomura. 2022.
750 Primary productivity and phytoplankton community structure in surface waters of the
751 western subarctic Pacific and the Bering Sea during summer with reference to bloom
752 stages. Prog. Oceanogr. doi: 10.1016/j.pocean.2021.102738.
753 Welschmeyer, N. A. 1994. Fluorometric Analysis of Chlorophyll-a in the Presence of
754 Chlorophyll-B and Pheopigments. Limnol. Oceanogr. **39**: 1985-1992. doi:
755 10.4319/lo.1994.39.8.1985
756 Wickham H (2016). ggplot2: Elegant Graphics for Data Analysis. Springer-Verlag New
757 York. ISBN 978-3-319-24277-4, https://ggplot2.tidyverse.org
758 Wood, S. N. 2006. Generalized additive models: An introduction with R. Chapman and Hall.
759 Yang, E. J., H. K. Ha, and S. H. Kang. 2015. Microzooplankton community structure and
760 grazing impact on major phytoplankton in the Chukchi sea and the western Canada
761 basin, Arctic ocean. Deep-Sea Res. Part II Top. Stud. Oceanogr. **120**: 91-102. doi:
762 10.1016/j.dsr2.2014.05.020
763

764 **Figure legends**

765 **Fig. 1** Map of experimental stations. The rectangles show three study regions (from below to
766 top): Western North Pacific (WNP), Western Bering Sea Basin (WBS), and the Gulf of
767 Anadyr (GoA).

768

769 **Fig. 2** Spatial distributions of (a) sea surface temperature (SST, °C); (b) sea surface salinity;
770 (c) total dissolved inorganic nitrogen concentration (DIN, including NO_3^-, NO_2^-, and NH_4^+,
771 μmol L^{-1}); (d) PO_4^{3-} concentration (P, μmol L^{-1}); (e) $Si(OH)_4$ concentration (μmol L^{-1}); (f)
772 dissolved Fe concentration at the depth of 10 m (D-Fe, nmol L^{-1}).

773

774 **Fig. 3** The spatial patterns of plankton in the study regions: (a) Chl *a* concentration (μg L^{-1});
775 (b) microzooplankton abundance (cell ml^{-1}); and (c) microzooplankton biomass (μg C L^{-1}).
776 The community composition of (d) phytoplankton; (e) microzooplankton abundance, and (f)
777 microzooplankton biomass. The phytoplankton community includes microphytoplankton
778 (Chl *a* > 20 μm) and nano+pico phytoplankton (Chl *a* < 20 μm), and the microzooplankton
779 consist of three categories: dinoflagellates, tintinnids, and aloricate-ciliates. The
780 dinoflagellates include the heterotrophic and mixotrophic dinoflagellates.

781

782 **Fig. 4** Spatial variations of growth rate and mortality rate due to microzooplankton grazing of
783 micro-phytoplankton (Chl *a* > 20 μm) (a, d), nano+phytoplankton (Chl *a* < 20 μm) (b, e), and
784 total phytoplankton community (c, f).

785

786 **Fig. 5** Boxplots of nutrient enriched growth rate (μ_n, d^{-1}), instantaneous growth rate (μ_0, d^{-1}),
787 of phytoplankton community and the two size groups (micro, nano+pico-phytoplankton) in
788 the three regions: (a) Western North Pacific; (b) Western Bering Sea basin, and (c) Gulf of

789 Anadyr (GoA). (d) Boxplot of microzooplankton grazing rate (m, d^{-1}) on phytoplankton
790 community and the two size groups in the three regions. The asterisk indicates whether the
791 effect of adding macronutrients was significant (one-way ANOVA; *$p < 0.05$; **$p < 0.01$;
792 ***$p < 0.001$).
793
794 **Fig. 6** Correlation matrix among physical (Temp, Sal, PAR), chemical (DIN, P, Si, DIN:P,
795 DFe), and biological (log-transformed Chl *a*: lnChla, size-fractionated Chl *a*, log-transformed
796 microzooplankton biomass: lnBz, phytoplankton growth rate: μ_0, and microzooplankton
797 grazing rates: *m,* and biomass-specific grazing rate m/Bz) parameters. %Chla represents the
798 percentage of size fractions (indicated by micro and nano+pico in parentheses) account for
799 the total Chl *a* concentration. The colour and colour intensities indicate the direction (green =
800 negative, purple = positive) and magnitude of Spearman's rank-order correlation coefficient,
801 respectively. The asterisks showing the significant levels of the correlations (*$p < 0.05$; **$p <$
802 0.01; ***$p < 0.001$).
803
804 **Fig. 7** The partial relationship between microzooplankton grazing rate (m) and Chl *a*
805 concentration (a), and temperature (b). The black dots are the total phytoplankton, and the
806 blue open dots are the nano+pico phytoplankton. The partial relationship between biomass-
807 specific grazing rate (m/B_z) and Chl *a* (c) and temperature (d).
808
809 **Fig. 8** (a) The percentage of primary production consumed by microzooplankton (%PP
810 consumed) in the subarctic North Pacific, the Bering Sea, and the Chukchi Sea (45°N -
811 80 °N) based on a compiled dataset including the studies: [1] Landry et al. (1993); [2] Leising
812 et al. (2005); [3] Liu et al. (2002); [4] Liu et al. (2009); [5] Menden-Deuer and Fredrickson
813 (2010); [6] Olson and Strom (2002); [7] Rivkin et al. (1999); [8] Sherr et al. (2009); [9]

814 Strom and Welschmeyer (1991); [10] Strom et al. (2001); [11] Strom et al. (2007); [12]
815 Strom et al. (2008); [13] Yang et al. (2014); [14] Sherr et al. (2013); [15] Connell et al.
816 (2018); [16] this study. Partial effects of (b) temperature, (c) ln(NO_3), and (d) *PAR* on relative
817 phytoplankton growth rate (μ_0). Partial effects of (e) temperature and (f) ln (*Chl*) on relative
818 microzooplankton grazing rate (*m*) based on the compile dataset. The black dots are the data
819 from the abovementioned studies and the red dots are the data of this study. Shaded areas
820 denote 95% confidential intervals.