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RESEARCH ARTICLE

Warming enhances protozooplankton top-down control and nutrient competition

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Abstract

Protozooplankton regulate microbial food webs through top-down control and nutrient cycling, yet their grazing impacts under ocean warming, particularly in subsurface chlorophyll maximum (SCM) layers, remain poorly understood. This study investigated spatial and seasonal variability in protozooplankton grazing in the northern East China Sea, influenced by Tsushima Warm Current (TWC) intrusion and stratification. Thirty in situ dilution experiments were conducted in surface and SCM layers to quantify grazing impacts on dominant diatoms and dinoflagellates across natural temperature gradients. Light limitation was excluded ($Zm/Zeu < 1$), and nutrients were enriched to isolate temperature effects. Grazing impact increased with temperature up to 29°C at the surface and 27°C in the SCM, indicating intensified top-down control even during extreme heat events. Grazing pressure was generally lower on bloom-forming species and in coastal waters, facilitating bloom development. In the SCM layer, elevated grazing rates coincided with high phytoplankton growth under conditions of moderate light availability and nutrient-replete conditions, suggesting rapid turnover and strong trophic interactions. Higher carbon biomass of ciliates and mixotrophic dinoflagellates in the SCM layer also indicated active grazing and nutrient competition with phytoplankton, supported by the lack of significant differences in growth rates between nutrient–enriched and depleted treatments. These findings reveal that warming-driven shifts in protozooplankton grazing and mixotroph-phytoplankton interactions may reshape bloom dynamics and nutrient flows in stratified marine ecosystems. This study highlights the critical role of top-down processes in regulating phytoplankton blooms and provides insights into microbial food web responses under future ocean warming scenarios.

Microbial food webs play a critical role in the biogeochemical cycles and ecosystem functioning within a changing marine environment (Sarmento et al. 2010; Caron and Hutchins 2013; Sánchez et al. 2024). Protozooplankton, including ciliates and heterotrophic dinoflagellates, are important mediators for energy transfer to upper trophic levels and for nutrient regeneration within microbial food webs (Yang et al. 2010). While bottom-up factors such as temperature, nutrient availability, and light regulate plankton bloom dynamics, grazing pressure plays a concurrent and significant role in shaping plankton communities, particularly across regions with varying primary productivity and bloom formation types (Calbet and Landry 2004; Kang et al. 2015; Liu et al. 2023). Seasonal variations in protozooplankton follow phytoplankton dynamics, and the carbon acquisition of protozooplankton can be up to 83% of daily primary production on the continental shelf (Yang et al. 2008).

Heterotrophic growth is more sensitive to warming than phototrophic growth and may lead to an increase in grazing activity in phagotrophs as ocean temperatures rise (Gillooly et al. 2001). Grazing by protozooplankton becomes increasingly important in nutrient-rich environments (Chen et al. 2012; Wilken et al. 2013; Cabrerizo et al. 2024). Additionally, prey growth rates generally exceed grazing rates with

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depth until light becomes limiting (Landry and Yang 2011). Meanwhile, mixotrophic strategies, especially in dinoflagellates and ciliates, suggest competition with phytoplankton for shared resources such as nutrients (Stoecker et al. 2017). Mixotrophs tend to perform more phototrophic activity with rising temperatures when chlorophyll a concentration is low (Chen et al. 2024). Consistent with this, model simulations showed that phagotrophy is favored under nitrogen or light limitation (Moeller et al. 2024).

Ocean warming also directly influences phytoplankton bloom dynamics by altering timing of initiation, duration, and termination (Gittings et al. 2018). Warming induces positive primary production when nutrients are sufficient, but nutrient limitation suppresses phytoplankton growth despite rising temperature (Lee et al. 2019). Stratification driven by rising temperature reduces nutrient availability for diatoms, whereas warming favors less sensitive dinoflagellates (Xiao et al. 2018). However, some studies suggest that diatoms may adapt to warmer conditions by reducing cell size and increasing cellular biogenic silica contents or by adjusting their vertical positioning in the water column (Fan et al. 2023). In stratified systems, more competition for limiting nutrients among phytoplankton is predicted because stratification decreases nutrient availability to phytoplankton in the sunlit layer (Marinov et al. 2010). Thus, species with efficient nutrient uptake and thermal tolerance may outcompete others under warm and nutrient-limited environments (Bestion et al. 2018; Fernández-González et al. 2022).

The northern East China Sea is ideal for studying these dynamics due to complex hydrography influenced by coastal waters, the Tsushima Warm Current (TWC), Changjiang Discharge Water, and Yellow Sea Bottom Cold Waters (Lie and Cho 2002; Lee et al. 2015). TWC intrusion forms thermal fronts in the South Sea of Korea, driving stratification and contributing to distinct water masses including warm, saline offshore waters and cooler, low salinity coastal waters (Cho and Kim 1998; Hur et al. 1999; Kang et al. 2024). Moreover, recent studies have highlighted the impact of accelerating Kuroshio intrusion and surface warming on shelf water temperatures in the East China Sea (Sasaki and Umeda 2021). In addition, phytoplankton peak their biomass at the subsurface chlorophyll maximum (SCM) due to the balance of light and nutrients (Cullen 2015). SCM layers are important for primary production and grazing activity, playing a critical role in carbon cycling and export (Moeller et al. 2019; Miao et al. 2023). The SCM layer is developed around the front region in the northern East China Sea (Kang et al. 2024), however, the role of protozooplankton has not been linked to the bloom dynamics in the SCM layer.

In this context, we hypothesized that rising temperatures driven by TWC intrusion will alter protozooplankton grazing, linking to bloom dynamics and intensifying nutrient competition among plankton. Spatial variations in grazing impact on major bloom-forming species are also expected in response to temperature changes in the northern East Cina Sea. To test this hypothesis, we examined bloom dynamics across spring, summer, and fall, during which TWC intrusion is typically accelerated. A total of 30 in situ dilution experiments were conducted using waters collected from surface and SCM layers to estimate grazing impacts on diatom and dinoflagellate blooms, where growth and grazing were assessed under naturally encountered in situ temperature gradients (Brussaard et al. 1996; Montagnes and Franklin 2001; Ignatiades 2012).

Materials and methods

Field surveys

Three cruises were conducted at 15 stations in the northern East China Sea on the board of R/V Sae-chungkyung or Sae-dongbaek of Chonnam National University from April 15 to 17 August 15 to 17, 2023, and October 16 to 18, 2023 (Fig. 1). Temperature, salinity, and fluorescence were measured using a conductivity-temperature-depth recorder (CTD; SBE 32, Sea-bird Electronics, USA). Seawater samples were collected using Niskin bottles mounted on the sampling platform at the surface, subsurface chlorophyll maximum (SCM), and bottom layers. The bottom layer was defined as the depth 5 m above the seafloor at each station, considering the height of the CTD frame. To measure dissolved inorganic nutrients including NO_3^-, NO_2^-, NH_4^+, PO_4^{3-}, and $Si(OH)_4$, 20 mL of seawater was filtered through pre-combusted GF/F filters (2 h at 450°C). Then, the filtered samples were stored at −20°C until analysis. To measure chlorophyll a (chl a) concentrations of size-fractionated phytoplankton (micro-, nano-, and picoplankton), 1 L of seawater was filtered to create three replicates. The collected seawater was sequentially filtered through 20 μm (Nylon membrane filter; Merk, Germany), 2 μm (Polycarbonate track etched membrane; GVS, Italy), and GF/F filters (Whatman glass microfiber filters; Cytiva, USA) with a 47 mm diameter. The filters were then stored at −20°C until analysis. To examine the abundance of phytoplankton communities and protozooplankton, seawater was collected in a 1 L polyethylene bottle, and the sample was fixed with Lugol's solution to a final concentration of 1%. The bottle was then wrapped in aluminum foil to block light and stored in a cool place until processing in the laboratory.

Measurement of chl a of major phytoplankton groups and Fv/Fm using Phyto-PAM II

Although various groups of phytoplankton are present in the ocean, this study measured chl a and photosynthetic efficiency (Fv/Fm) for the phytoplankton group (cryptophytes, cyanobacteria, diatoms/dinoflagellates, green algae) detectable by the Phyto-PAM II (Heinz Walz GmbH, Germany). The method of analyzing phytoplankton groups using Phyto-PAM II can distinguish different groups in real time using measurement wavelengths of 440, 480, 540, 590, and 625 nm, allowing for the measurement of green algae, cyanobacteria, diatoms/dinoflagellates, and cryptophytes (Heinz Walz 2019).

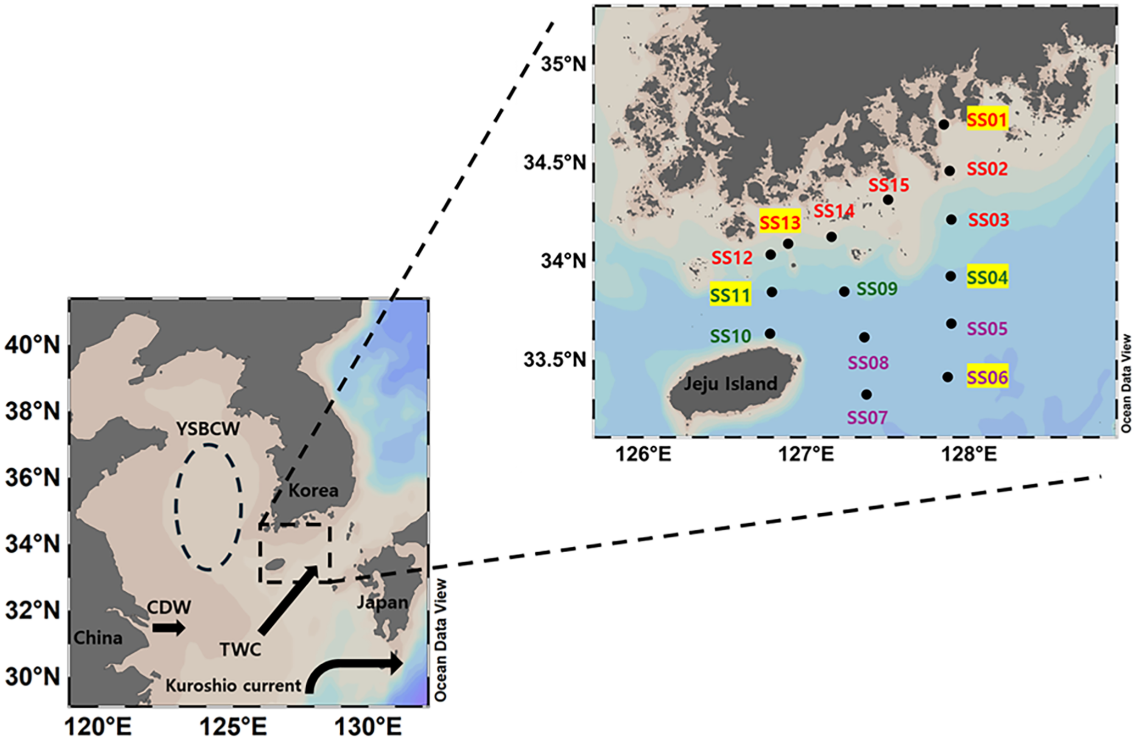

Fig. 1. Map showing the study region in the northern East China Sea. Fifteen stations are shown on the map and stations highlighted in yellow indicate the locations where dilution experiments were performed. Stations highlighted in red represent the coastal region, those in green represent the frontal region, and those in purple represent the offshore region. Abbreviations are as follows: CDW = Changjiang Discharge Waters, TWC = Tsushima Warm Current, and YSBCW = Yellow Sea Bottom Cold Water.

Although diatoms/dinoflagellates are different classes, they are considered a single group because similar antenna pigments show similar responses at wavelengths and have similar excitation (Heinz Walz 2019). Fv/Fm, the maximum photochemical quantum yield, indicates photochemical efficiency and is used as an indicator of stress in phytoplankton in response to environmental conditions (Behrenfeld and Milligan 2013). Although filtering blanks would have been ideal, it was not feasible to filter all samples given the 5 mL sample volume. Instead, we used a zero offset with distilled water as recommended in the Walz manual, which is sufficient for relative comparisons among stations. Prior to sample analysis, the Phyto-PAM II was calibrated to improve measurement accuracy, and a zero setting (blank) was performed to establish the baseline fluorescence. Chl a values represent the pigment specific fluorescence detected by the measurement, and each algae group was quantified based on pre-defined reference excitation settings. Phyto-PAM II chl a values exhibited a strong correlation (Supporting Information Fig. S1; $R^2 = 0.62$, $p < 0.001$). Although the values obtained may differ from those measured using the acetone-extraction methods, the use of the Phyto-PAM II is appropriate for comparing relative differences in phytoplankton biomass across stations in the study region and calculating growth rates. Triplicate seawater samples (5 mL) collected from each depth were transferred into a container that had been light-blocked using black tape, was dark-adapted for 15 min. The dark adaptation time was set to 15 min following the Walz manual. Trimborn et al. (2019) have shown that measurements obtained under different light intensities yield similar results when the same adaptation period was applied. Chl a and Fv/Fm for each phytoplankton group were then measured using the PhytoWin software. After measurement, Fv/Fm was calculated using the following equation (Parkhill et al. 2001).

$$\mathrm{Fv/Fm} = (\mathrm{Fm} - \mathrm{Fo})/\mathrm{Fm}$$

Fo represents the minimum fluorescence after dark adaptation, and Fm represents the maximum fluorescence. Fv/Fm of 0.6 indicates that phytoplankton is not affected by nutritional stress, while values below 0.3 suggest nutrient limitation or high light exposure.

Sample analysis

Size-fractionated chl a were measured by extracting chlorophylls from the filters while being stored at −20°C in 5 mL of 90% acetone for 24 h. The extract was then measured using a fluorometer (Trilogy; San Jose, USA). The samples fixed with Lugol's solution were transported to the laboratory, where they were allowed to settle in the dark for at least 48 h. The supernatant was discarded, and 10 mL of the sample was prepared. The prepared sample (1 mL) was placed in a Sedgewick Rafter chamber, and then phytoplankton and protozooplankton were observed using an optical microscope (Primo Star, ZEISS, Göttingen, Germany). Ciliates and heterotrophic dinoflagellates were quantified, whereas copepod nauplii were excluded from the group because they were rarely observed or not observed (Lynn 2008; Dolan et al. 2012; Mitra et al. 2023). The latest species names were updated by checking AlgaeBase (www.algaebase.org) and the World Register of Marine Species (www.marinespecies.org). Dissolved inorganic nutrients were measured using the SEAL QuAAtro Auto Analyzer (Seal Analytical Ltd., Southampton, UK) following the seawater processing test methods at the Seoul National University (Parsons 2013).

Performance of dilution experiments

A total of 30 in situ dilution experiments were performed on board following the method of Landry et al. (1995). Polycarbonate bottles (1 L) were filled with seawater collected from the surface and SCM layers at concentrations of 100%, 70%, 40%, and 15%, and then filled with seawater filtered through a 0.2 μm Versapore® membrane Pall pleated filter capsule. Two replicates were created for each treatment group. In the treatment bottles, 10 μM NO_3^- and 1 μM PO_4^{3-} were added to ensure that nutrients were not limited during incubation, while the control bottles contained only 100% seawater with no nutrient addition. Experimental bottles were placed in a tank for 24 h with a circulation system that allowed continuous inflow of natural seawater to maintain in situ temperature. Experimental bottles with surface seawater were placed directly into the tank. As the SCM layer often occurs at the depth receiving approximately 1% of surface irradiance (Cullen 2015), we used a black mesh that blocked 99% of incoming light to approximate this light condition during sampling. The bottles placed in the tank were incubated under natural sunlight during the day, and after sunset, a tarp was used to block light as much as possible to maintain dark conditions. After 24 h of incubation, duplicate 1 L bottles were combined to minimize potential variation in incubation conditions. Form the mixed samples, three 5 mL samples were taken for Phyto-PAM II measurements. Before the measurement, the samples were dark adapted for 15 min in darkness. Subsequently, samples (1 L) were preserved with Lugol's solution to quantify phytoplankton and protozooplankton using an optical microscopy.

Data analysis

Physical parameters

To assess the TWC intrusion in the study region, sea surface temperature was examined (Supporting Information Fig. S2). The study region was categorized as a coastal region, front, and offshore based on the TWC intrusion (Supporting Information Fig. S3). In spring (14 ± 1°C in the coastal to 17 ± 1°C in the offshore), summer (25 ± 1°C to 28 ± 1°C), and fall (20 ± 1°C to 24 ± 1°C), a distinct thermal front was observed. Stations with relatively low temperatures, which were less influenced by TWC (St. 1, 2, 3, 12, 13, 14, 15), were categorized as a coastal region, while stations with high temperatures (St. 5, 6, 7, 8) were categorized as offshore. Meanwhile, stations (St. 4, 9, 10, 11), where a horizontal temperature gradient was rapid between the coastal region and offshore, were defined as front. The mixed layer depth and euphotic zone depth were defined following de Boyer Montégut et al. (2004) and Mojica et al. (2015). Details are described in Supporting Information Text S1.

Dominant species and carbon contents

The most abundant three species were identified as dominant species while the top three species with highest carbon biomass were chosen as carbon-based dominant species. Relative abundance of major phytoplankton groups and dominant species was estimated based on chl a concentrations of major phytoplankton groups measured using Phyto-PAM II, and cell density and carbon biomass of phytoplankton communities quantified using microscopy, respectively. Carbon content of microplankton and protozooplankton was estimated based on cell volume following Menden-Deuer and Lessard (2000), Putt and Stoecker (1989) and Verity and Lagdon (1984). Details are described in Supporting Information Text S1.

Growth rates and grazing rates from dilution experiments

The calculation of growth and mortality rates followed Landry and Hassett (1982) and modified according to Landry et al. (1995). The net growth rate (k) of the diatoms/dinoflagellates group was calculated using the equation $k = \ln(Bt/B0)/t$, where Bt represents the chl a concentration of the group after 24 h of incubation, $B0$ is the chl a concentration at the beginning of the experiment (0 h), and t is the experimental duration (i.e., 1 d). The intrinsic growth rate (μn) was determined from the y-intercept, and the mortality rate (m) was derived from the slope. The ratio m : μn was used to assess the grazing impact on phytoplankton by comparing it to 1. The same procedure was conducted to measure the grazing rates and growth rates of major microplankton species using species composition data quantified using microscopy. Details are described in Supporting Information Text S1.

Results

Characteristics of spatiotemporal distribution of environmental variables

Physical variables including salinity and temperature were presented in Supporting Information Fig. S3. Sea surface temperature was higher in coastal regions while surface temperature was lower offshore. Sea surface temperature ranged from 11.6°C to 18.1°C in spring, 15.0°C to 29.7°C in summer, and 15.0°C to 24.8°C in fall. Sea surface salinity exhibited the opposite pattern of surface temperature, with lower surface salinity in coastal regions and higher surface salinity offshore. Surface salinity varied within ranges of 33.1–34.6 in spring, 23.8–35.0 in summer, and 28.3–34.6 in fall. The sea temperature of the SCM layer ranges from 12.0°C to 18.1°C in spring, 20.8°C to 27.6°C in summer, and 18.7°C to 23.4°C in fall. The salinity of the SCM layer ranges from 33.2 to 34.6 in spring, 30.7 to 35.0 in summer, and 32.3 to 34.5 in fall. Salinity sharply decreased below 25 in summer from coasts to the front region, and the lowest salinity of 10.74 was observed in summer.

Dissolved inorganic nutrient levels were higher in the bottom layers, particularly NO_3^-, PO_4^{3-}, and $Si(OH)_4$. Dissolved inorganic nutrient levels did not significantly differ between the surface and SCM layers (Supporting Information Fig. S4; $p < 0.05$; Two-Way ANOVA with Tukey's Post-Hoc test), whereas the levels were significantly different in the bottom layers (Supporting Information Fig. S4; $p > 0.05$; Two-Way ANOVA with Tukey's Post-Hoc test). The light limitation index (Zm/Zeu) was lower than 1 throughout the sampling period (Supporting Information Fig. S4).

Spatiotemporal variation of phytoplankton community and biomass

High concentrations of microplankton chl a were observed in coastal regions, whereas picoplankton chl a concentration was high offshore (Supporting Information Fig. S5A). Microplankton accounted for up to 75% of the total chl a in coastal regions, while picoplankton dominated offshore, comprising up to 75% in spring and more than 50% of the total chl a beyond the front region in summer. The proportion of nanoplankton did not vary spatially as much as that of microplankton or picoplankton (Supporting Information Fig. S5B). Diatoms/Dinoflagellates group was dominant in coastal regions, comprising more than 80% of major phytoplankton groups in these areas. However, the dominance significantly decreased to below 40% at most stations, except in SCM layers, where it remained around 60%. As depth increased, the proportion of cyanobacteria increased, exceeding 50% in the bottom layers throughout the sampling period (Supporting Information Fig. S6).

In a coastal region, the cell density (cells L^{-1}) of total microplankton and nanoplankton exceeded 100,000 cells L^{-1}, whereas offshore, it was generally below 2500 cells mL^{-1} (Supporting Information Fig. S7A). The total microplankton cell density remained stable from spring to summer; however, the cell density sharply increased in fall, particularly at St. 2 in the surface and SCM layers (Supporting Information Fig. S7A). Diatoms dominated throughout the sampling period, and dinoflagellates were predominant at coastal stations, especially in SCM and bottom layers in summer. Consequently, carbon biomass (μg C L^{-1}) varied among seasons (Supporting Information Fig. S7B). In spring and fall, carbon biomass did not exceed 80 μg C L^{-1}, except at St. 1 in spring, where it reached 340 μg C L^{-1}. However, the biomass sharply increased in the summer, peaking at 760 μg C L^{-1} (Supporting Information Fig. S7B) because a marked increase in the abundance of *Tripos furca* during this season drove to the rise in dinoflagellates biomass. Interestingly, dinoflagellates dominated in the western coastal waters of the study region during summer, particularly in SCM layers, while diatoms were dominant in surface layers across the study region, especially in the eastern region and from the front to offshore region (Supporting Information Fig. S7).

While diatoms dominated in the relative abundance during the study period, a high relative abundance of dinoflagellates was observed in spring, but lower values were in summer and fall. In contrast, the relative carbon biomass was high throughout the entire water column in summer (Fig. 2). In spring, *Thalassisosira* sp. succeeded in *Heterocapsa circularisquama* from coastal regions to front regions. *Pseudo-nitzschia* spp. was dominant across all depths and regions in summer and offshore in fall, while *Tripos furca* and *Skeletonema costatum* were the bloom-forming species in coastal regions in summer and fall, respectively. Inconsistent with cell density, carbon biomass was mainly dominated by either bloom species such as *Thalassisosira* sp. and *Tripos furca* or large-sized species such as *Coscinodiscus* sp., *Guinardia flaccida*, and *Rhizosolenia* sp. (Fig. 2).

Carbon biomass of ciliates including both oligotrichs and tintinnids as well as mixotrophic dinoflagellates was higher in the SCM layer than the surface layer ($p < 0.05$; Wilcoxon Rank Sum test; Fig. 3a,b; Supporting Information Fig. S8A). In contrast, the carbon biomass of heterotrophic dinoflagellates did not differ significantly between the two layers ($p > 0.05$; Wilcoxon Rank Sum test; Supporting Information Fig. S8B). With elevated temperature, carbon biomass of oligotrichs and mixotrophic dinoflagellates increased from 3.58 to 6.45 log ng C L^{-1} and from 1.13 to 4.67 log ng C L^{-1} respectively (Fig. 3c,d), while tintinnid and heterotrophic dinoflagellate carbon biomass remained relatively stable at the mean of 5.18 and 2.20 log ng C L^{-1}, respectively (Fig. 3c,d).

Characteristics of growth and grazing rates and nutrient impacts

At the surface layer, mortality rate (m) was 1.5 d^{-1} at temperatures below 15°C, the mortality rate remained 1 d^{-1} between 20°C and 25°C, and then sharply increased up to 25°C and 30°C. Unlike the surface layer, m continuously increased from 1.1 to 1.9 d^{-1} in the SCM layer (Fig. 4). The pattern of growth rate (μn) was opposite to m in the surface, increasing from 1.27 to 1.75 d^{-1} at 20°C, and decreasing to 1 d^{-1} at 30°C, while in the SCM layer, μn increased continuously with temperature, with an increase in mortality (Fig. 4). The grazing impact ($m : \mu n$) was the lowest at the temperate range between 20°C and 25°C, and higher grazing impacts were observed at lower temperatures and higher temperatures (Fig. 4). Similar to m and μn, $m : \mu n$ gradually increased in the SCM layer (Fig. 4).

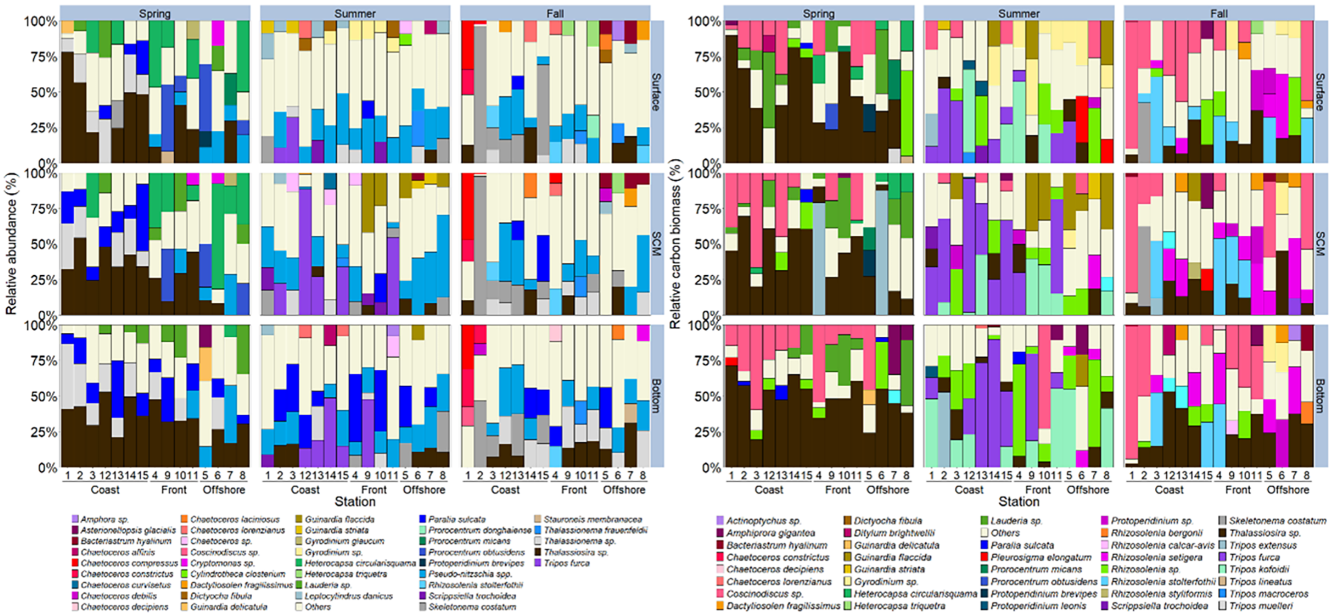

Fig. 2. Spatiotemporal variations in dominant species throughout the sampling period. (**a**) Relative abundance (%) of dominant species, (**b**) relative carbon biomass (%) of dominant species.

The mean grazing impacts on dominant species were significantly lower compared to that on non-dominant species ($p < 0.05$; Mann–Whitney *U* test; Fig. 5a). Across regions, grazing impact increased toward offshore (Fig. 5b). Grazing impact on dominant species varied seasonally, with higher mortality in spring and increasing growth toward fall (Fig. 5c). Interestingly, grazing impacts on the major bloom species gradually increased toward offshore and were significantly lower in coastal waters than those offshore ($p < 0.05$; Mann–Whitney *U* test; Fig. 5d). Particularly, the grazing impact on major diatom bloom-forming species including *Pseudo-nitzschia* spp. and *Thalassisosira* sp. exhibited significantly different results between coastal and offshore regions in the surface and SCM layers ($p < 0.05$; Mann–Whitney *U* test), whereas the difference was not significant in major dinoflagellate bloom-forming species including *H. circularisquama* and *Tripos furca* ($p > 0.05$; Mann–Whitney *U* test; Fig. 5b).

The difference in photosynthetic efficiency between 100% and 15% exhibited a sharp decrease in both layers (Fig. 6). While the difference remained relatively stable, a large variation in the difference was observed in the SCM layer, with a range below −0.05 to above 0.05. The median values were positioned at 0.025. Nutrient limitation was estimated using a ratio of $\mu n : \mu o$ and the difference in growth rates between 100% and control (Fig. 7). During experiments, most values of $\mu n : \mu o$ were below 1 and the values were not significantly different between the surface and SCM layers ($p > 0.05$; Wilcoxon Rank-Sum test; Fig. 7a,b). The difference in growth rates between 100% and control was not significantly different between autotrophs and mixotrophs ($p > 0.05$; Wilcoxon Rank-Sum test; Fig. 7c).

Discussion

Characteristics of top-down and bottom-up processes on bloom dynamics

In the northern East China Sea, diatoms and dinoflagellates dominated coastal waters, while offshore regions were characterized by increased chl *a* concentrations of picoplankton, particularly cyanobacteria, which was also illustrated by Kang et al. (2024) with TWC intrusion during the study period. Although light and nutrients are key factors for phytoplankton growth (Cloern 1999), the light limitation index (Zm/Zeu < 1) indicates that light was generally not limiting, even at offshore where the SCM occurred at greater depths. Diatoms and dinoflagellates were present both in surface and SCM layers under favorable light conditions (Bracher et al. 2009; Jiang et al. 2015). Nutrients were not initially limited (Supporting Information Fig. S4). Therefore, even before nutrient enrichment, ambient nutrient levels were sufficient to support phytoplankton growth, which likely explains why no substantial increase in growth occurred in response to the added nutrients. This characteristic makes the study region a suitable natural setting for directly quantifying temperature-driven grazing effects and phytoplankton growth rates under in situ conditions. Despite potential coastal nutrient influence, no significant differences between intrinsic growth rates (μn) and in situ growth rates without nutrient addition (μo) indicate nutrient limitation in prey growth was also negligible

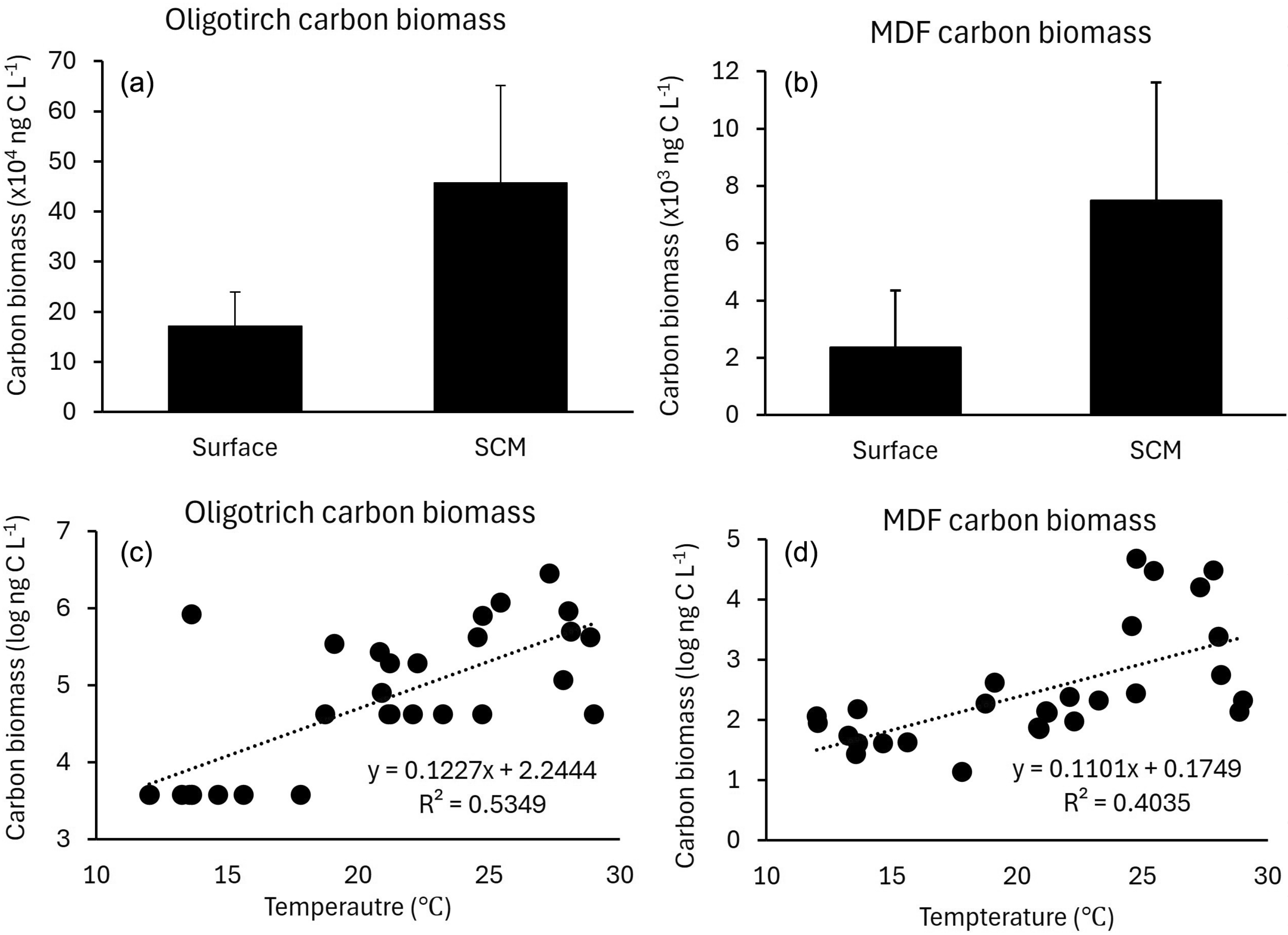

Fig. 3. Responses of carbon biomass of oligotrich and mixotrophic dinoflagellates to temperature in surface and SCM layers. (**a**) Carbon biomass of oligotrichs in surface and SCM layers, (**b**) carbon biomass of mixotrophic dinoflagellates (MDF) in surface and SCM layers, (**c**) variation in oligotrich carbon biomass with rising temperature, and (**d**) variation in MDF carbon biomass with rising temperature.

during the study period. Additionally, most values exhibited the ratio of $\mu n : \mu o$ greater than 1, further indicating that nutrients were not limited during experiments.

Dominant species experienced lower grazing impacts compared to non-dominant species, and the region where blooms occurred had lower grazing impacts, regardless of the bloom location across the region. While relatively large species such as *Pseudo-nitzshia* spp., *Thlassiosira* sp., and *Tripos furca* can be grazed by large protozooplankton (e.g., > 50 μm), grazing pressure on these dominant bloom-forming species remained low under bloom condition. Such reduced grazing can increase phytoplankton biomass in the region, and even when measured chlorophyll a concentrations appear relatively low, high biomass levels can still indicate the presence of a bloom (Ribalet et al. 2010). Overall, the mean grazing impact on bloom-forming species was lower in coastal waters than offshore and did not exceed 1, indicating that reduced grazing pressure was a key mechanism driving bloom proliferation in coastal waters. In particular, in the SCM layer, favorable light conditions and elevated temperatures enhanced microzooplankton grazing activity, thus top-down control by grazers became particularly important at this depth, even though net phytoplankton dynamics are ultimately determined by the balance between growth and grazing. This suggests that a close coupling between grazing and growth promoted the phytoplankton production (Irigoien et al. 2005; Gutiérrez-Rodríguez et al. 2023). Grazing failure often initiates bloom developments, while increased grazing rates contribute to bloom decline (Ladds and Gobler 2025). Thus, this tight coupling exerted a strong top-down control on phytoplankton

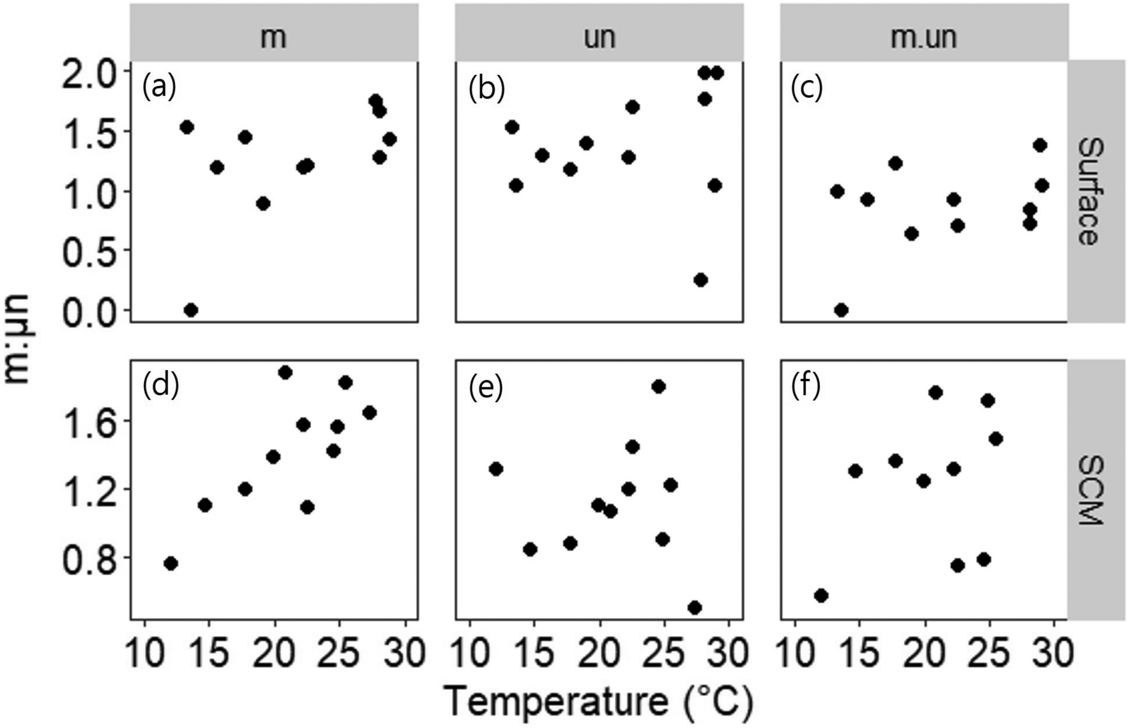

Fig. 4. Variations in grazing rate (m), growth rate (μn), and grazing impact (m : μn) with rising temperature. (**a**–**c**) are m, μn, and m : μn with rising temperature in the surface layer. (**d**–**f**) are the same in the SCM layer.

populations, potentially limiting bloom magnitude and duration in the study region.

Temperature-dependent grazing and the importance of the SCM layer

Considering the response to rising temperature, diatoms and dinoflagellates experienced low grazing pressure and high growth at ~20°C in surface waters, suggesting that growth benefits within their thermal optimum can outweigh protozooplankton grazing (Boyd et al. 2013; Edwards et al. 2016; Barton and Yvon-Durocher 2019). However, the overall grazing impact increased with increased temperature, indicating intensified trophic interactions under thermal elevation. This was consistent with the evidence that *Pseudo-nitzschia* spp., *Thalassiosira* sp., and *Tripos furca* exhibited higher grazing impacts in offshore waters, where TWC induces high temperature and high salinity (Cho and Kim 1998; Hur et al. 1999; Kang et al. 2024). According to Calbet and Saiz (2022), moderate warming can enhance grazing activity, but high temperatures exceeding 22°C limit grazer adaptation. Surprisingly, our results showed that grazing impact increased with rising temperatures up to 29°C in the surface layer and 27°C in the SCM layer, suggesting that strong top-down control can still regulate phytoplankton blooms even during extreme weather events such as heatwaves. The principal component analysis confirmed that temperature is the dominant variable compared to other environmental variables (Supporting Information Fig. S9).

In the SCM layer, both growth and grazing rates increased with temperature, but grazing rose more rapidly, resulting in a gradual rise in grazing impact. Unlike the surface layer, protozooplankton exerted greater grazing pressure in the relatively cooler SCM, where nutrient-replete and light-sufficient conditions allowed grazing rates to match or exceed those at the surface (Strom 2001; Chen et al. 2012). Proximity to the nitracline also supported high phytoplankton growth and primary productivity (Cullen 2015; Chen and Zhao 2021). Greater variation in Fv/Fm between full and diluted seawater in the SCM suggests complex interactions among nutrients, dilution, and predator presence (Stoecker et al. 2014). The variable responses imply indirect physiological effects through nutrient competition or dilution. The coexistence of negative and positive Fv/Fm values indicates variable photophysiological responses under predation. Overall, rapid growth and intensified grazing maintain high SCM biomass, and increasing grazing impact with temperature suggests accelerated ecosystem turnover under warming.

Under global warming in the Baltic Sea, the time-lag between phytoplankton blooms and the peak of microzooplankton biomass narrows, because a higher growth rate of microzooplankton strengthens the predator–prey coupling and increases grazing pressure (Horn et al. 2016). Metabolic evolution model also demonstrates that as temperature

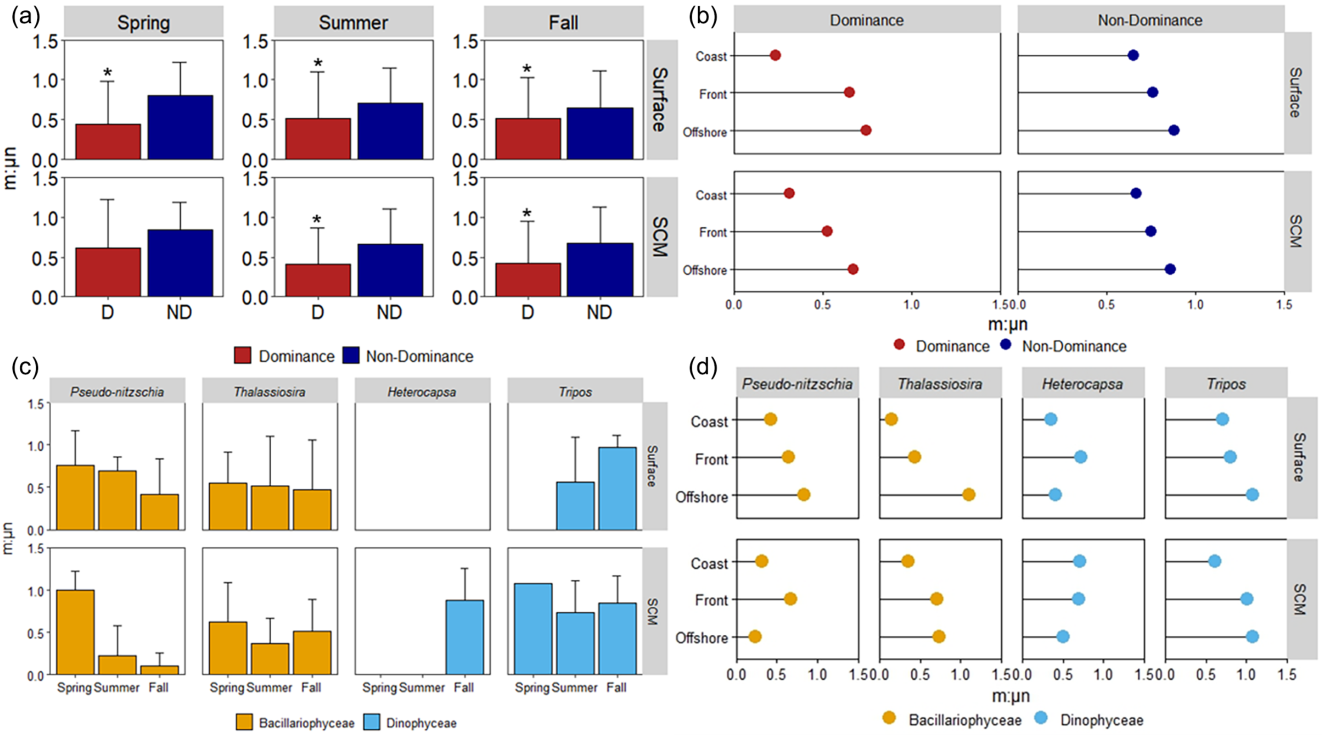

Fig. 5. Grazing impacts (m : μn) in surface and SCM layers. (**a**, **b**) Seasonal and regional variability in grazing impacts on dominant and non-dominant phytoplankton. (**c**, **d**) Seasonal and regional variability in grazing impacts on dominant diatoms and dinoflagellates, and (d) regional variability in grazing impacts. *T*-test was performed to estimate the significant difference in grazing impacts between dominant species and non-dominant species. Asterisks (*) indicate the significant difference with $p < 0.05$.

gradually increases, the abundance of heterotrophic feeding types initially rises (Gonzalez et al. 2022). Once temperatures exceed a certain threshold, however, intense predation leads to a depletion of prey resources. This reduction in food availability decreases grazing efficiency and allows autotrophic types to become more dominant. Over longer timescales, mixotrophic types that can perform both photosynthesis and grazing emerge as the most advantageous strategy. These findings suggest that in regions experiencing warming, similar shifts in trophic strategies and predator–prey dynamics may occur across both geographic and temporal scales.

In addition to temperature-dependent changes in trophic interactions, seasonal shifts in phytoplankton community composition likely contributed to the observed variability in grazing rates. Because prey size and quality strongly influence protozooplankton feeding (Verity 1986), seasonal dominance of different taxa affected grazing outcomes. In spring, *Thalassiosira* sp. with long setae dominated, and reduced ciliate growth during blooms suggests that their morphology lowered grazing pressure (Lürling 2021), allowing high biomass to persist. In summer, heat-tolerant pennate diatoms such as *Pseudo-nitzshia* spp. increased, and as protozooplankton efficiently grazer pennate forms at high temperatures (Landry et al. 2000; Verity et al. 2002), grazing was likely intensified. In

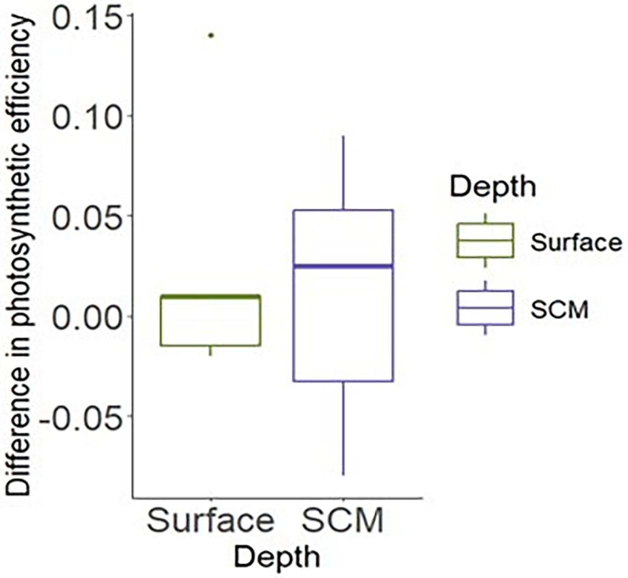

Fig. 6. Difference in photosynthetic efficiency between 100% and 15% in the surface and SCM layers, showing physiological response of phytoplankton to the presence of predator. 100% is full seawater, while 15% is a combination of 15% of seawater and 85% of filtered seawater. The difference varied more in the SCM layer, indicating higher variations in the physiology of autotrophs in the SCM layer in response to the presence of predator.

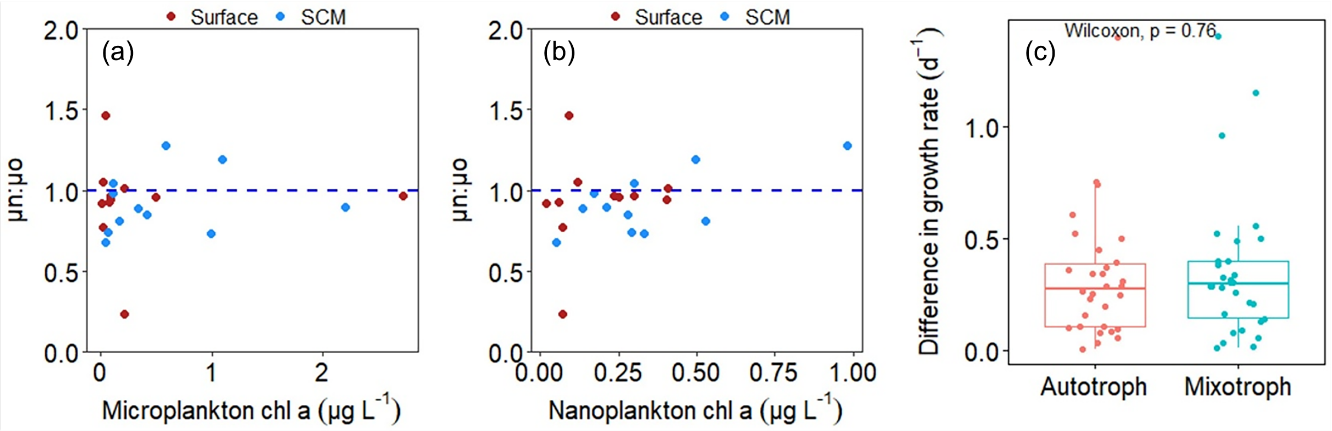

Fig. 7. Nutrient limitation and potential nutrient competition. (**a**, **b**) $\mu n : \mu o$ in response to microplankton and nanoplankton chl a. $\mu n : \mu o > 1$ indicates values experienced nutrient limitation. Most values were below 1. No significant difference in values between the surface layer and the SCM layer. (**c**) Difference in growth rates between 100% and control of autotrophs and mixotrophs. 100% was with nutrient addition, while control was without nutrient addition. No significant difference between autotrophs and mixotrophs indicates potential resource competition for nutrients between autotrophs and mixotrophs.

fall, chain-forming diatoms dominated, and their morphology likely hindered feeding, resulting in lower mortality. Thus, seasonal variation in prey traits may modulate grazing impacts independently of temperature and should be considered alongside thermal effects when interpreting phytoplankton-protozooplankton dynamics (Lürling 2021).

Potential competition for sharing nutrients between phytoplankton and protozooplankton

Carbon biomass of ciliates and mixotrophic dinoflagellates was significantly higher in the SCM layer than in the surface layer, suggesting the potentially higher grazing pressure in this layer. Mixotrophs sustained growth via heterotrophy under nutrient poor conditions but competed effectively with autotrophs for nutrients in enriched environments (Glibert and Mitra 2022; Moeller et al. 2024). The degree to which nutrient availability limits the growth of autotrophic and mixotrophic plankton was not significantly different during this study. This further suggests that nutrient competition concomitantly occurred between autotrophs and mixotrophs during experiments (Stoecker et al. 2017). The competitive role in nutrient acquisition was likely to be more pronounced in the SCM layer, where the carbon biomass of mixotrophic dinoflagellates were higher and the strong stratification occurred below the subsurface layer (Kang et al. 2024). For *Tripos furca* photoautotrophic activity dominated bloom formation under nutrient-replete conditions with access to deep water (Smalley et al. 1999; Eom et al. 2021), while feeding on ciliates occurred primarily under nutrient limitation (Smalley et al. 2003; Ok et al. 2023).

Mixoplankton tend to decrease grazing but increase photosynthesis at higher temperatures, while protozooplankton generally increase grazing rates with warming (Ferreira et al. 2022). During experiments, carbon biomass of ciliates and mixotrophic dinoflagellates increased with elevated temperatures, further suggesting that warming may advantage mixotrophs in nutrient competition with prey while ciliates may be responsible for top-down control of phytoplankton blooms. Given that the synergistic warming from Kuroshio intrusion (Sasaki and Umeda 2021) and intensified stratification over the past half-century (Li et al. 2020), these dynamics imply simultaneous enhancement of protozooplankton grazing and nutrient competition between mixotrophs and phytoplankton can be enhanced simultaneously. Thus, our findings highlight important implications of top-down controls in microbial food web functioning and carbon cycling under future climate scenarios.

Author Contributions

Eunbi Lee: Data curation, formal analysis, visualization, writing-original draft preparation. Chan-Woo Kwon: Investigation. Hyeong Kyu Kwon: Investigation. Yoonja Kang: Conceptualization, review and editing, funding acquisition.

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Conflicts of Interest

None declared.

Data Availability Statement

Data that support the findings of this study are publicly available in the Zenodo repository at https://doi.org/10.5281/zenodo.20388679.

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Supporting Information

Additional Supporting Information may be found in the online version of this article.

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