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LETTER

Changes in phytoplankton size–structure alter trophic transfer in a temperate, coastal planktonic food web

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Scientific Significance Statement

Phytoplankton size–structure emerged as a key determinant of trophic transfer from primary producers to microzooplankton grazers in a coastal, planktonic food web. Deviations from typical seasonal patterns in a time series revealed that shifts in grazing pressure by microzooplankton, the main consumers of microscopic algae, were associated with reversals in the dominant phytoplankton size class, despite frequent and significant changes in environmental conditions. This suggests that phytoplankton size–structure, rather than environmental conditions, plays a key role in determining the structure and function of the planktonic food web. Identifying drivers of microzooplankton grazing is key to predicting effects of both short-term disturbances and long-term climate change on food webs that support coastal ecosystems globally.

Abstract

Microzooplankton grazing is an essential parameter to predict the fate of organic matter production in planktonic food webs. To identify predictors of grazing, we leveraged a 6-yr time series of coastal plankton growth and grazing rates across contrasting environmental conditions. Phytoplankton size–structure and trophic transfer were seasonally consistent with small phytoplankton cell dominance and low trophic transfer in summer, and large cell dominance and higher trophic transfer in winter. Departures from this pattern during two disruptive events revealed a critical link between phytoplankton size–structure and trophic transfer. An unusual summer bloom of large phytoplankton cells yielded high trophic transfer, and an atypical winter dominance of small phytoplankton resulted in seasonally atypical low trophic transfer. Environmental conditions during these events were neither seasonally atypical nor unique. Thus,

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Data Availability Statement: Metadata, the analyzed data, used in this manuscript and the MATLAB scripts used to produce the figures are available in the Zenodo repository at https://doi.org/10.5281/zenodo.10914602 (accessed 03 April 2024) and in Marrec (2024). In addition, the data generated for this study are available at the EDI Data Portal (https://portal.edirepository.org) and are regularly updated. The growth and grazing rate data package are publicly available under CC-BY license and in Menden-Deuer and Marrec (2023). The dissolved inorganic nutrient data package is publicly available under CC-BY license in Sosik et al. (2021). The CTD and the underway data are publicly available through the NES-LTER REST-API (https://github.com/WHOIGit/nes-lter-ims/wiki/Using-REST-API-to-access-NES-LTER-data) and these raw data are available in the University National Oceanographic Laboratory System (UNOLS) Rolling Deck to Repository (R2R, https://www.rvdata.us/).

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

phytoplankton size–structure rather than environmental conditions held a key-role driving trophic transfer. Phytoplankton size–structure is easily measurable and could impart predictive power of food-web structure and the fate of primary production in coastal ecosystems.

Most of the ocean's contribution to human well-being is rooted in vast quantities of matter produced by phytoplankton in the sunlit surface ocean (Falkowski et al. 1998). The majority of this oceanic primary production is consumed by the dominant grazers of phytoplankton, microzooplankton ($< 200\,\mu$m, Steinberg and Landry 2017). Grazing is foundational to the transfer of organic matter to higher trophic levels and its fate in marine biogeochemical cycling (Worden et al. 2015). Trophic transfer in planktonic food webs is commonly expressed as the ratio between microzooplankton grazing and phytoplankton growth rates, with microzooplankton consuming on average 60–70% of phytoplankton primary production globally (Calbet and Landry 2004). While phytoplankton growth rates can be reasonably understood as a function of temperature (Anderson et al. 2021), light, nutrient availability, and phytoplankton species composition (Edwards et al. 2016), microzooplankton grazing is notoriously difficult to constrain and cannot be predicted based on environmental conditions or prey concentration (Schmoker et al. 2013). Although temperature is foundational to physiological rates, temperature effects on heterotrophic protist growth and grazing rates are highly variable, uncertain, and often indirect (Rose and Caron 2007; Franzè and Menden-Deuer 2020; Chen et al. 2023). Although prey type and concentration can be strong predictors of grazing and grazer types (Lawerence and Menden-Deuer 2012; Anderson and Harvey 2019), these insights have not led to a mechanistic understanding or reliable drivers of grazing pressure. The challenge of identifying predictors of grazing rates suggests interactive or indirect effects are at play (Menden-Deuer et al. 2023). This challenge is compounded by the immense effort involved in obtaining empirical measurements of grazing, resulting in sparse records across the matrix of ocean habitats, seasons, and biological communities (Schmoker et al. 2013). Consequently, grazing effects on the fate, flow, and reservoirs of organic matter remain one of the main unknowns and key knowledge gaps in global climate and ecosystem models (Rohr et al. 2023).

In regions with strong environmental gradients, sustained observations provide the opportunity to quantify grazing as a function of biotic and abiotic conditions and to identify correlations across ecologically relevant parameter ranges (Cloern and Jassby 2010). The Northeast US Continental Shelf (NES) is a temperate ecosystem characterized by intense seasonality and coastal to open ocean gradients (Townsend et al. 2006). This dynamic hydrography is foundational to a highly productive ecosystem. Here, cold and relatively fresh water with sub-Arctic origin flows southward along the shelf (Chapman and Beardsley 1989), while the Gulf Stream carries warm and salty tropical water northeastward. In winter, the phytoplankton community is dominated by large, slow-growing phytoplankton cells (Peacock et al. 2014) and most of the primary production is consumed by microzooplankton (Marrec et al. 2021). In contrast, during summer, fast-growing small phytoplankton cells dominate (Fowler et al. 2020; Stevens et al. 2023) and microzooplankton consume only a small fraction of primary production (Marrec et al. 2021). The strong seasonal and spatial contrasts in environmental conditions and planktonic food-web structure make the NES ecosystem an ideal study site to investigate the drivers of trophic transfer from phytoplankton to microzooplankton. These efforts are essential as the NES is undergoing fast climate-change induced alterations in physical (warming, Thomas et al. 2017) and ecological (biodiversity, Blowes et al. 2019) characteristics. Surface waters of the NES are warming 3-fold faster than the global average (Saba et al. 2016). This warming trend results in northerly distributional shifts in many marine species (Friedland et al. 2023) and alterations in the abundances, distributions, and phenologies of organisms from phytoplankton (Hunter-Cevera et al. 2020) to top predators (Lucey and Nye 2010).

Here, we leverage measurements of phytoplankton growth and microzooplankton grazing within the NES Long-Term Ecological Research (NES-LTER) site to identify environmental or biological drivers of trophic transfer at the base of the planktonic food web. Using data from 12 summer and winter NES-LTER cruises, we identify 2 deviations from otherwise consistent seasonal patterns in abiotic and biotic conditions (Marrec et al. 2021). The two events were characterized by unusual shifts in phytoplankton size–structure and reversal of seasonally typical predation pressure and trophic transfer, while environmental conditions were indistinguishable from those typical for the season and region.

Materials and methods

Phytoplankton growth and microzooplankton grazing rates were measured from 2018 to 2023 on 12 transect-cruises, 6 in summer and winter each, from the coastal island of Martha's Vineyard to the shelf break due south (Fig. 1; Supporting Information Table S1). Measurements were made at four to seven stations along the NES-LTER transect. The transect was divided into three regions based on bathymetry: Inner-Shelf (< 50 m), Mid-Shelf (50–100 m), and Outer-Shelf (> 100 m).

Underway sea surface temperature (SST) and salinity (SSS) were measured continuously with SBE38 and SBE45 sensors (Seabird Electronics). Vertical profiles of depth, temperature, and salinity were collected with a SBE911. Surface whole

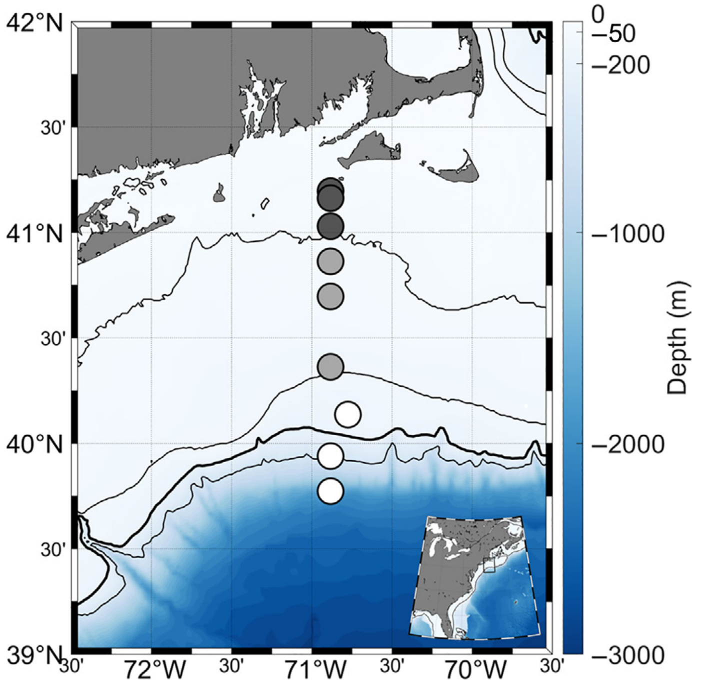

Fig. 1. Map and bathymetry of the NES-LTER with Inner-Shelf (< 50 m, dark gray), Mid-Shelf (50–100 m, light gray) and Outer-Shelf stations (> 100 m, white). Solid lines show the 50 m, 100 m, 200 m (bold) and 500 m isobaths. The bottom right inset indicates where the study area is located (black rectangle) along the North American East Coast from Florida (USA) to Nova Scotia (Canada).

seawater (WSW) was transferred from Niskin bottles mounted on a CTD-rosette (SBE32) into 10-liter polycarbonate carboys through a 200-μm mesh to remove mesozooplankton. Diluent was prepared by gravity filtration through a 0.2-μm membrane filter (PALL®) and mixed with WSW to obtain a target 20% WSW dilution. Total and size-fractionated chlorophyll *a* (Chl *a*) concentrations were obtained from triplicate 150 mL subsamples filtered onto GF/F (> 0.7 μm) and > 10-μm polycarbonate membrane filters, without freezing the filters (Graff and Rynearson 2011), and measured using a calibrated Turner 10AU fluorometer after a 12 h dark extraction in a temperature-controlled room (20–25°C) using 95% ethanol (Wasmund et al. 2006). Chl *a* concentration in the < 10 μm fraction was calculated from the difference between the GF/F and the > 10 μm concentrations. Chl *a* data were quality controlled as in Menden-Deuer and Marrec (2023). We recognize that the carbon to Chl *a* ratio is variable (Jakobsen and Markager 2016) and base our comparisons of trophic transfer on the ratio of growth and grazing rates for each experiment avoiding contrast across seasons or stations. No correction was made for photoacclimation of the Chl *a* concentration (e.g., Gutiérrez-Rodríguez et al. 2010; Morison et al. 2020) because experimental manipulations of light intensity had no effect on phytoplankton growth rates (Marrec et al. 2021).

Phytoplankton growth and protistan grazing rates were measured using a two-point modification of the dilution method (Landry et al. 2008; Chen 2015; Morison and Menden-Deuer 2017). This approach has been validated in the NES region across different plankton communities at different times of the year (Lawerence and Menden-Deuer 2012). To ensure the instantaneous growth rate of the phytoplankton was independent of dilution (Landry and Hassett 1982), incubation bottles were amended with macronutrients (10 mmol m^{-3} silicate and nitrate, 1 mmol m^{-3} phosphate). A total of six 1.2-liter bottles per experiment were prepared for incubations: two bottles each with nutrient-amended 20% WSW and WSW and two bottles with unamended WSW to assess nutrient limitation. From summer 2022 onward triplicate nutrient-amended bottles yielded a total of eight bottles.

Bottles were incubated for 24 h in clear 1 m^3 deck-board incubators with water temperature maintained at ambient SST, and monitored with Onset HOBO® data loggers. Incubation temperature varied as the ship moved through different water masses. The mean 24 h difference between in situ and incubator temperature was +1°C in winter and +1.7°C in summer. Bottles were placed in mesh-bags to control light intensity between 15% and 65% of sea surface irradiance from winter 2018 to summer 2020. Because rate measurements did not differ significantly between light-levels over 3 years (Marrec et al. 2021), starting in winter 2021, incubations of surface waters were only performed at 65% sea surface irradiance. Rate data from both light treatments are reported in this study.

Rates of phytoplankton instantaneous growth (μ_0, d^{-1}) and grazing mortality (g, d^{-1}) were estimated from changes in Chl *a* concentrations over a 24-h incubation period (Morison and Menden-Deuer 2017). Nutrient limitation was assessed from apparent phytoplankton growth rates (k, d^{-1}) in nutrient amended (k_N) and non-amended (k_{NoN}) 100% WSW replicates using a paired *t*-test. If nutrient limitation was evident through a significantly greater k_N than k_{NoN}, grazing rates were calculated using k_N values only. In the absence of nutrient limitation, all k-values were included in estimates of g and μ_0. When grazing rates were not significantly different from 0, g was set to zero. In those instances, μ_0 was set equal to the average of apparent growth rates k_{dil} and k_{NoN} (or k_{dil}, k_{NoN}, and k_N without nutrient limitation). A significant positive slope (i.e., higher growth in the WSW treatment than in the diluted) represents a violation of the method's assumption and has been attributed to different causes, such as trophic cascades (Calbet and Saiz 2013), or toxicity effects inhibiting phytoplankton growth (Stoecker et al. 2015). In these cases, g is reported as "undetermined," and k in the undiluted bottles represent μ_0.

Statistical analyses for rate calculations are detailed above. Statistical significance was assigned when $p \leq 0.05$. ANOVAs and multiple post hoc comparisons (*anovan*, *multcompare*, Matlab) tested for significant differences among regions defined from bathymetry and seasons and to determine differences among typical (no-event) and atypical (event) conditions. Principal component analyses (*f_pca*, Matlab, Jones 2017) were performed on abiotic environmental data, including macronutrients and light (photosynthetically available radiation) data following Marrec et al. (2021).

Results

Environmental conditions in the NES region exhibited strong seasonal and spatial patterns. SST and SSS along the transect were similar among years (Supporting Information Fig. S1). Irrespective of season, SST and SSS increased from the Inner-Shelf to the Outer-Shelf and differed significantly among regions (max $p = 0.04$). Seasonality in the NES was intense, with up to 15°C difference in SST between summer and winter. Inner-Shelf and Mid-Shelf waters exhibited SSS < 33, while SSS in Outer-Shelf waters were > 33 (Supporting Information Table S2).

Chl *a* concentrations were significantly ($p < 0.001$) higher in winter (> 1 mg m^{-3}) than in summer (< 1 mg m^{-3}), and, irrespective of season, decreased progressively from Inner-Shelf to Outer-Shelf (Supporting Information Fig. S2a). Phytoplankton size–structure was dominated by large cells (> 10 μm) in winter and by small cells (< 10 μm) in summer (Supporting Information Fig. S2b). The contribution from small phytoplankton was up to 3- to 4-fold lower in winter than in summer ($p < 0.001$).

Phytoplankton growth was characterized by clear seasonal and spatial patterns, while microzooplankton grazing rates remained relatively constant across time and space (Supporting Information Fig. S3). Summer growth rates were 2- to 3-fold greater than winter growth rates ($p < 0.001$, Supporting Information Table S2). Irrespective of season, median phytoplankton growth rates increased from Inner-Shelf to Outer-Shelf, but differences between adjacent regions were not significant (min. $p = 0.85$). Mean seasonal and regional grazing rates ranged from 0.17 to 0.24 d^{-1} (Supporting Information Table S3) and did not differ significantly among regions (min. $p = 0.95$) and seasons ($p = 0.53$).

The ratio of protistan grazing to phytoplankton growth provides an estimate of trophic transfer, that is the percent of primary production consumed by microzooplankton (% PP, Supporting Information Fig. S4). Trophic transfer was strongly contrasted seasonally ($p = 0.009$). In winter, $> 50\%$ of PP was consumed by microzooplankton grazers, while in summer, $< 50\%$ of PP was consumed (Supporting Information Table S2). Median consumption decreased from Inner-Shelf to Outer-Shelf, but differences among adjacent regions were not significant (min. $p = 0.62$).

We observed two events that exhibited dominance of seasonally atypical phytoplankton size classes associated with seasonally atypical trophic transfer (Fig. 2). Across the 6-yr observational record in the NES region, the small size fraction of Chl *a* in winter was consistently $< 50\%$ (Supporting Information Table S2). Similarly, and equally consistently, the small size fraction of Chl *a* in summer was $> 50\%$. There were

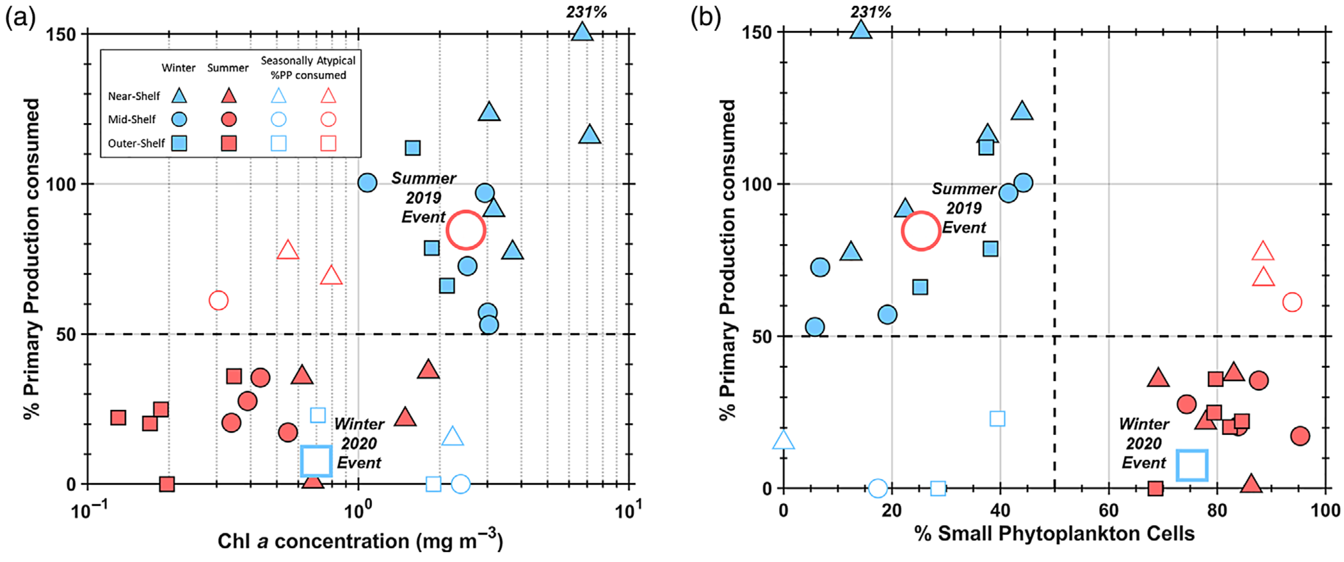

Fig. 2. (**a**) Average Chl *a* concentration (mg m^{-3}) and (**b**) phytoplankton small size fraction (< 10 μm, %) vs. primary production consumed by microzooplankton (%PP consumed) in Inner-Shelf (triangles), Mid-Shelf (circles), and Outer-Shelf (squares) during winter (blue) and summer (red) cruises. Seasonally atypical %PP consumed is represented by open symbols. The reversal in seasonally typical size–structure is readily apparent for the "Summer 2019" (large red circle) and the "Winter 2020" (large blue square) events. Dashed lines indicate summer and winter contrasts in typical phytoplankton small size fraction (< 10 μm) and primary production consumed of $\sim 50\%$.

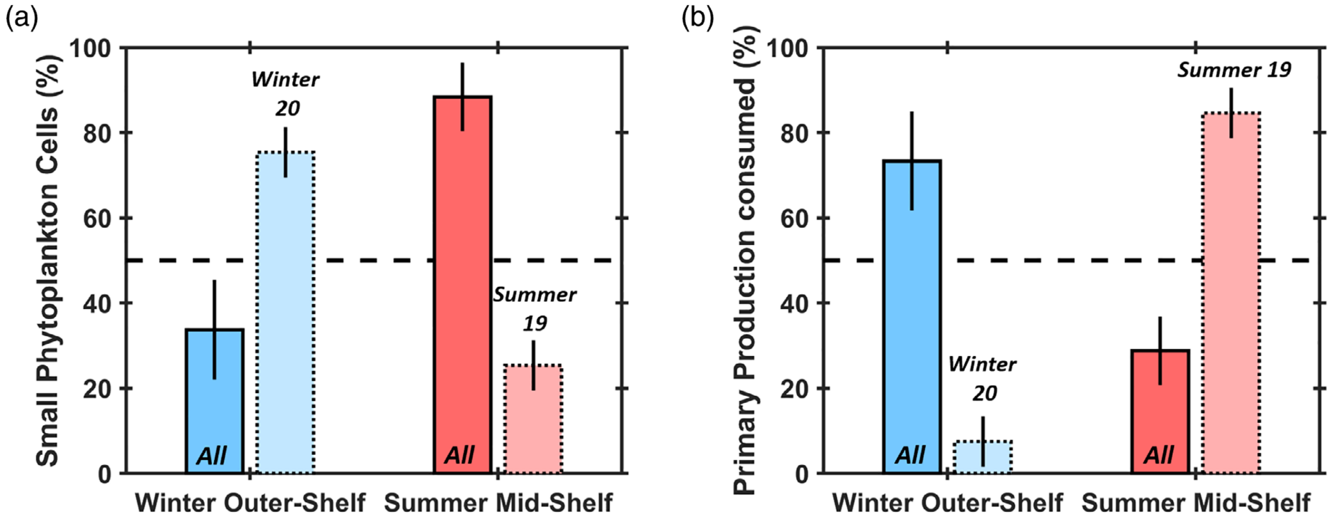

Fig. 3. (**a**) Small phytoplankton (Chl $a < 10\ \mu$m, %) and (**b**) primary production consumed by microzooplankton (primary production consumed, %) for the winter 2020 and summer 2019 events compared to all data, excluding the events, from that region and season contrasting winter in blue and summer in red. Dashed lines as in Fig. 2.

only two occasions when the phytoplankton size–structure differed from this seasonally typical pattern: in winter 2020 in the Outer-Shelf and in summer 2019 in the Mid-Shelf (Fig. 3a).

The first reversal event occurred in Mid-Shelf waters during the summer of 2019 (Fig. 2) when large phytoplankton cells dominated and Chl *a* concentrations were atypically high (up to 3.58 mg m^{-3}). Though small cells typically dominate Chl *a* in summer by ~80%, they contributed < 30% of total Chl *a* during the summer 2019 event (Fig. 3a). Simultaneously, phytoplankton growth was lower-than-summer-average (0.20 d^{-1}), with grazing remaining typical for the season and region (0.17 d^{-1}, Supporting Information Table S3). In combination, this resulted in a > 3-fold increase in the trophic transfer typically observed in summer, with 85% of PP consumed by microzooplankton grazing (Fig. 3b).

The second reversal event in phytoplankton biomass (Chl *a* < 1 mg m^{-3}), size–structure, and trophic transfer was observed in winter 2020 in Outer-Shelf waters (Fig. 2). Here, we measured an atypical dominance of small phytoplankton cells (75% instead of 45%, Fig. 3a) and an atypically low %PP consumed by microzooplankton (8%) compared to the seasonally typical average of 64% of PP consumed (Fig. 3b).

The reversal of phytoplankton size–structure could not be attributed to unique environmental conditions (Fig. 4). Both SST and SSS varied substantially over time due to interannual variability (Supporting Information Fig. S5). However, the combination of SST and SSS observed during both events were not unique and also observed during other years. SST and SSS during winter 2020 reflected average values that were not significantly different from winters 2018, 2021, and 2022 in that region (min. $p = 0.491$). Similarly, warmer and fresher SST and SSS during the summer 2019 event were nearly identical to summer 2020 (min. $p = 0.859$). The similarity in abiotic conditions is also reflected when considering additional environmental parameters, such as macronutrients and light (Supporting Information Fig. S6). While phytoplankton size–structure is ultimately rooted in environmental conditions, no unique linkage or causation between specific and unique abiotic factors and the reversal in phytoplankton size–structure and trophic transfer rates is observable for either event.

There were other deviations from seasonally typical trophic transfer rates. Low %PP (< 50%) were observed in winter, and inversely (> 50%) in summer, over a wide range of SST and SSS (Fig. 4), but they occurred when phytoplankton size–structure was typical (Fig. 2). Seasonally atypical %PP occurred in wide-ranging environmental conditions that do not reveal a common link between environment and trophic transfer magnitude (Fig. 4). Notably, some winter instances of atypical low trophic transfer were linked to high SST and SSS (Fig. 4a), while others (Outer-Shelf 2022; Supporting Information Table S3) were not. These fluctuations in trophic transfer reflect inherent variability of predation pressure and were not associated with a reversal in any of the underlying abiotic and biotic factors. However, reversal in phytoplankton size–structure did result in the reversal of seasonally typical predation pressure that altered planktonic food-web structure.

Discussion

From a 6-yr time series, we quantified planktonic food-web structure and function in temperate waters of the Northeast US Shelf (NES) ecosystem within their seasonally constrained

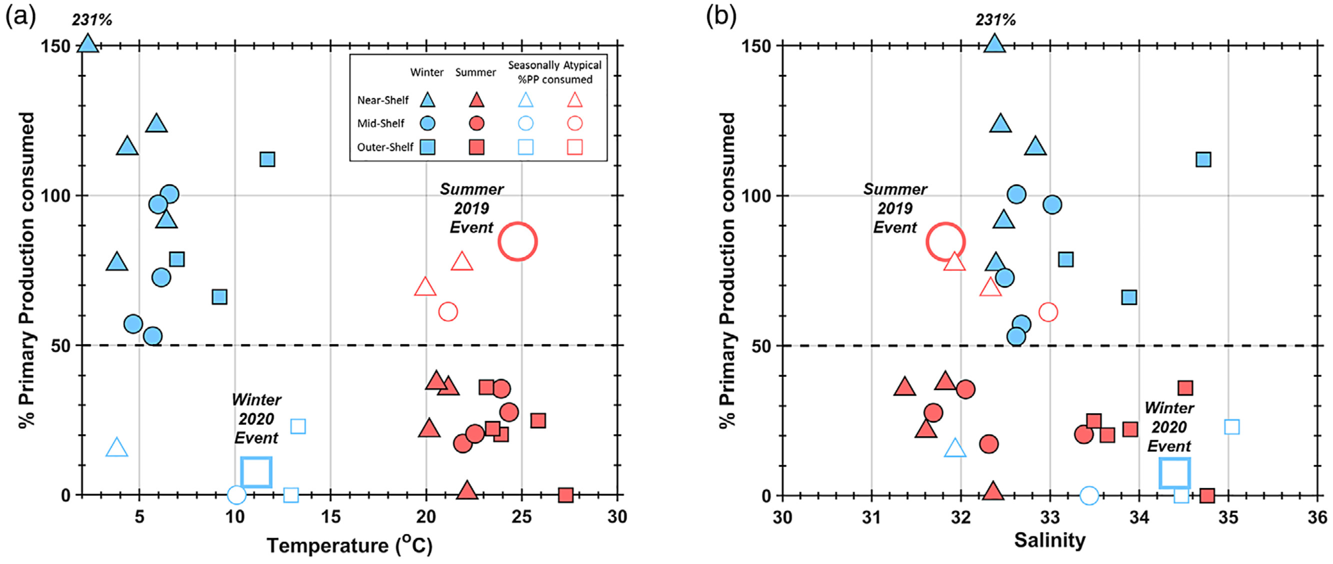

Fig. 4. (**a**) Average SST (°C) and (**b**) SSS vs. primary production consumed by microzooplankton (%PP consumed) in Near-Shelf (triangles), Mid-Shelf (circles), and Outer-Shelf (squares) waters during winter (blue) and summer (red). Seasonally atypical trophic transfer is represented by open symbols. The summer 2019 event is represented by a large red circle and the winter 2020 event by a large blue square. The horizontal dashed line represents the 50% of primary production consumed delineation between typical winter (> 50%) and typical summer (< 50%) conditions.

and contrasting environmental characteristics (Marrec et al. 2021). Seasonally atypical shifts in the dominant size class of phytoplankton reversed the predation impact by microzooplankton grazers on primary production. A time series that resolved seasonal and spatial patterns was necessary to identify deviations that highlight the unique role phytoplankton size–structure played in driving shifts in trophic transfer. Phytoplankton size is a characteristic that is measurable by a wide range of instruments (Menden-Deuer et al. 2020) and thus our results could help unravel complex ecological processes that are still vastly under-sampled. Moreover, phytoplankton size–structure is a useful indicator for evaluating the state of marine ecosystems and their ability to adapt to environmental change (Morán et al. 2010). Deconstructing the relative impacts of environmental conditions and biotic factors on planktonic food-web structure and function is fundamental to predicting the effects of local disturbances or long-term climate impacts on planktonic food webs that are foundational to coastal ecosystems globally.

In summer 2019, the phytoplankton community was dominated by large phytoplankton cells, composed of *Hemiaulus* spp., a chain-forming diatom with a symbiotic nitrogen fixer (Castillo Cieza et al. 2024). In the NES, the highest trophic transfer was observed when the phytoplankton community structure was dominated by large cells. While it is well known that microzooplankton are important grazers of small phytoplankton (Caron et al. 2012), some microzooplankton readily feed on large diatom cells (Sherr and Sherr 2009). Prior field observations in Pacific continental shelf ecosystems documented enhanced grazing (Liu et al. 2023) and tightened trophic transfer (Strom et al. 2001) in the presence of large phytoplankton cells, and thus support the importance of phytoplankton size composition as a driver of grazing pressure. Microzooplankton grazing pressure is modulated by grazer selectivity of prey type (Taniguchi et al. 2023). Grazer selectivity is likely foundational to the link between phytoplankton size–structure and its role in food-web coupling.

The atypical dominance of small cells in winter 2020 emerged as the primary factor disrupting the trophic transfer of organic carbon from phytoplankton to microzooplankton. This result contradicts many observations in oligotrophic systems, with low Chl *a* concentrations (< 0.20 mg m^{-3}) and dominance of small phytoplankton, where microzooplankton grazing pressure is high and coupling is tight (Landry et al. 1995, 2022). Although oligotrophy is observed in the NES in summer, Chl *a* values are typically > 0.20 mg m^{-3}. Moreover, while mesozooplankton biomass and thus top-down control on microzooplankton grazing pressure or phytoplankton abundance is low in oligotrophic ecosystems (Hernández-León and Ikeda, 2005), the NES harbors abundant crustacean (Kane 2014) and gelatinous (Madin et al. 2006) mesozooplankton populations in summer that can limit microzooplankton biomass and thus grazing impact.

Although trophic transfer within season was variable, seasonally atypical shifts in trophic transfer always, and only, occurred when the dominant size fraction of the phytoplankton community inverted. In the 6-yr record, other deviations from seasonally typical trophic transfer were observed, both in winter and summer, but could not be linked to a particular environmental or biological factor, including phytoplankton size–structure. One exception was the prevalence of atypical low trophic transfer in winter associated with high SST and SSS in Outer-Shelf waters that could be attributed to onshore intrusion of Gulf Stream warm-core rings that often impinge on the shelf-edge (Chen et al. 2020). However, the phytoplankton size–structure was seasonally typical and similar environmental conditions were observed in Outer-Shelf waters in winter 2022 without being associated with low trophic transfer. The absence of a consistent association between these environmental factors and trophic transfer indicates that environmental conditions cannot explain the magnitude of trophic transfer.

Fluctuations in trophic transfer are to be expected and reflect inherent variability of predation pressure that could be due to shifts in predator or prey abundance or species (Lawerence and Menden-Deuer 2012; Anderson and Harvey 2019; Taniguchi et al. 2023), which were not examined in this study. Microzooplankton and phytoplankton biomass or species composition could reveal the influence of species and abundance on the functioning of the planktonic food web. However, estimates of biomass and diversity of plankton community composition that represent the two events are unlikely to provide reliable insights in the absence of a multiyear record that estimates variability of these metrics across seasons and regions. A long-term record of microzooplankton and phytoplankton community structure and biomass will help identify associations among environmental and biological processes in the NES. Moreover, top-down control by mesozooplankton could affect trophic transfer through direct predation on phytoplankton or trophic cascades (Saiz and Calbet 2011; Stukel et al. 2021). Multiple biological factors likely cause variability of trophic transfer, but only phytoplankton size–structure could uniquely be linked to reversal in trophic transfer.

Climate-mediated changes in the NES, in particular temperature (Chen et al. 2020), are expected to induce changes in phytoplankton community structure and have already been linked to shifts in emergent biological properties (Friedland et al. 2023). NES waters are expected to become warmer, and more stratified (Li et al. 2015), with limited nutrient availability to primary producers. Such conditions may lead to low production and a dominance of small phytoplankton cells (Beaugrand et al. 2010) resulting in a decrease in the magnitude of energy transfer from the lowest trophic levels (Dickman et al. 2008) to fisheries production (Friedland et al. 2020). Changes to phytoplankton size–structure have direct impacts on microzooplankton communities (Calbet 2008), which are essential prey for mesozooplankton that contribute to marine production and carbon export (Turner 2015). While ocean ecosystem models predict that warming and enhanced stratification will reduce phytoplankton biomass (Boyce et al. 2010) and biological-mediated export of particulate carbon to the deep ocean (Kwiatkowski et al. 2018), long-term observations suggest that phytoplankton could adapt to environmental change, without a reduction in carbon export (Lomas et al. 2022). The rare, seasonally atypical events highlighted here suggest that changes to phytoplankton size–structure in the NES can lead to alterations in the energy transfer pathways and efficiency from primary producers to higher trophic levels. Characterization of trophic linkages at the base of the food web is thus crucial for a predictive understanding of organic matter production and flow in a changing coastal ocean.

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