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Planktonic predator selectivity: Eating local with global implications

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Marine plankton play crucial roles in nearly all global biogeochemical cycles, generating approximately half of Earth's organic matter (1). Consumption by microscopic predators, often termed grazing, constitutes the single largest loss factor for primary production in the ocean (2), which is the foundation for virtually all marine food webs (3). Grazing has shaped the evolution of both form and function of marine phytoplankton (4) and impacts the small but critical fraction of primary production that is exported from the surface ocean. Export of surface production through a biologically mediated gradient in carbon and other elements from the atmosphere to the deep sea (5) is estimated to have removed approximately half of human fossil fuel emissions from the atmosphere (6). Predation also controls the abundance of heterotrophic bacteria (7) that play a key role in remineralizing marine organic matter (8). Thus, predation is a major determinant of the types and magnitudes of ocean ecosystem production and elemental cycling processes.

There is a vital need to mechanistically determine how microbial communities are structured both to understand how ocean ecosystems function and make accurate predictions about how organisms and the processes they regulate respond to change. By examining growth and grazing mortality rates, Landry et al. (9) shed light on predation processes, preferences, and tradeoffs that shape the diversity and function of marine microbial communities. Their research revealed predator selectivity in choosing between heterotrophs and photoautotrophs, a fundamental trait which is nevertheless often ignored in ocean ecosystem analyses. Focused predation pressure on particular functional groups in turn has ramifications for ecosystem production, fisheries yields (10), and carbon export (5).

Despite the importance of predation on microbial communities, the factors that determine the magnitude and selectivity of predation are not well understood. This paucity of information can be attributed to the wide variety of phylogenies and behaviors represented by planktonic consumers. Predation in the plankton can involve an intricate series of steps including prey encounter, selection, processing, and ingestion (11), many of which could have cinematic appeal. Prey characteristics also affect predation pressure. Predators of picoplankton have been documented to select prey based on such properties as prey size, stoichiometry, cell surface properties, and motility (refs. 7 and 12 and references therein). This biological diversity is embedded within a tremendous matrix of environmental drivers that can also influence grazing pressure and make grazing difficult to parameterize and predict.

Several mechanisms have been put forth to describe planktonic grazing. One is the idea of shared predation (13) in which predators consuming the most abundant prey coincidentally impose elevated predation pressure on co-occurring organisms.

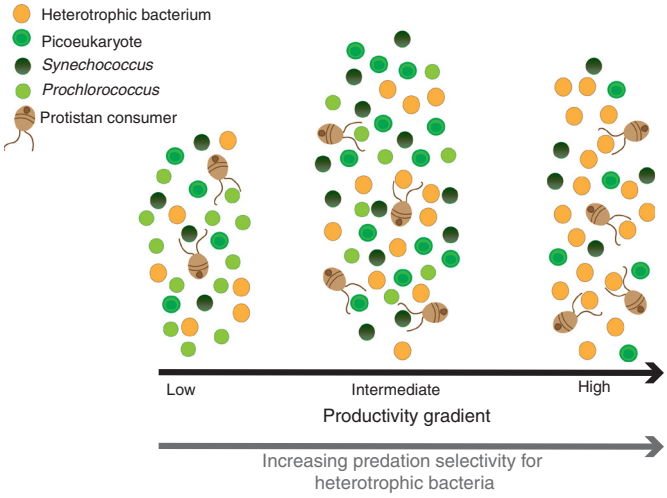

Fig. 1. Schematic of picophytoplankton and heterotrophic bacteria relative abundances as they vary over a productivity gradient in the California Current Ecosystem. Also shown are relative grazing preferences of protistan consumers from low to high productivity rates.

Another is the Enhance Microbial Loop (EML) hypothesis (14), based on previous work that includes the California Current Ecosystem (CCE), the study region of Landry et al. (9). According to the EML hypothesis, high primary production by large photoautotrophs generates dissolved organic matter that stimulates increased heterotrophic bacterial growth and ultimately increased shared predation pressure on co-occurring organisms. Examining these hypotheses, Landry et al. (9) leveraged a rich dataset that included over one hundred process studies of planktonic growth and grazing mortality rates over a wide productivity gradient. Based on these data, Landry et al. (9) found that heterotrophic bacterial abundances and growth rates, supported by increased organic matter availability and unmatched by predation rates, increased appreciably as primary production increased. Picophytoplankton had relatively constant growth rates across the productivity gradient. Picophytoplankton abundances were generally highest at

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intermediate productivity rates and decreased at higher productivity rates, with the photosynthetic cyanobacterial *Prochlorococcus* decreasing first, *Synechoccocus* next, and finally picoeukaryotes. Many of these patterns match the EML hypothesis and shared predation of *Prochlorococcus* (15). However, when primary productivity was high, grazing on picophytoplankton did not increase despite increased grazing on heterotrophic bacteria (Fig. 1). Instead, grazing mortality decreased across the productivity gradient for picophytoplankton, most prominently for *Synechococcus*. This result is in contrast with the shared predation hypothesis. Grazing mortality of *Synechococcus* relative to heterotrophic bacteria was particularly depressed at high temperatures, which has implications for picoplankton community composition, function, and biogeochemical cycling as global ocean temperatures increase (16).

By examining growth and grazing mortality rates, Landry et al. shed light on predation processes, preferences, and tradeoffs that shape the diversity and function of marine microbial communities.

Landry et al. (9) examined the potential drivers for these mortality rates. They refuted size-dependent selective pressures, which is notable given that size is often an important explanatory variable for predation pressure. The data instead suggested that the mortality patterns were due either to taxonomic or behavioral differences in predators or due to tradeoffs between optimized growth and grazing vulnerabilities of heterotrophic bacteria. Predator selectivity for fast-growing heterotrophic bacteria at high productivity rates was evident. Such selection based on the fundamental difference between heterotrophic and autotrophic organisms has large-scale ramifications because predators altered the abundance of consumers rather than producers of organic matter at high productivity rates. The capacity to select based on this very basic difference in trophic mode is likely the tip of the iceberg, with many more and nuanced layers of predator selection lurking beneath.

The results of Landry et al. (9) also challenge the view that picoplankton community diversity is determined in a highly taxon-specific manner through viral lysis, as suggested by the "kill the winner" hypothesis (17). Landry et al. (9) showed that grazers can play a similar role by removing the fastest-growing heterotrophic bacteria at high productivity rates, preferring heterotrophs over photosynthetic picoplankton. Thus, bacterivory can alter microbial diversity, with implications for microbial community structure and abundance. This distinction between predation and viral lysis is also important because viral lysis produces dissolved organic matter that stays in the microbial loop, whereas protistan grazing of picoplankton has the potential to transfer energy and matter to higher trophic levels (3).

Whether predators select picophytoplankton or bacterial prey has important effects on the structure and function of microbial communities and ultimately global scale processes. The vast open ocean is dominated by the microbial food web that yields relatively inefficient secondary production. These regions are predicted to expand in a warming ocean, with coincident decreases in primary production (18). However, observational time series indicate that carbon export can be maintained in a warmer ocean as cells adapt through changes in stoichiometry and efficiency of nutrient use (19). Selectivity by microbial grazers is important not only because of its effect on natural communities but also because of the degree to which human-engineered materials such as microplastics are consumed and thus enter planktonic food webs (20), with the potential to ultimately enter the human food supply. These examples highlight how urgently we need basic insights into the structure and function of planktonic communities in which predation is a major but often unruly and intractable process. The work by Landry et al. (9) provides such foundational knowledge for how grazing might alter the structure and function of microbial communities. This important progress supports critical research needs, including incorporation of predation into mathematical models that reflect diverse environmental and biological conditions in ocean ecosystems. Better understanding of the mechanisms driving the abundance and diversity of microbial communities will ultimately lead to more accurate predictions of how ocean ecosystems function, including under changing environmental conditions.

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