

Review

Non-viral predators of marine picocyanobacteria

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The Earth's most abundant photosynthetic cells, the picocyanobacteria – *Prochlorococcus* and *Synechococcus* – play a fundamental global role in aquatic ecosystems. The success of these picocyanobacteria is interpreted through a cross-scale systems framework that integrates bottom-up controls on growth (e.g., nutrients and light), diversity, and the selective pressures and response to predation. While viral predators are well studied and experimentally tractable, the diverse non-viral predators of picocyanobacteria are disconnected from this framework and experimentally challenging, leaving a major gap in understanding the picocyanobacteria. This review presents existing research on non-viral picocyanobacterial predators and promising research frontiers that will expand knowledge of the ecology and evolution of these crucial microorganisms.

Picocyanobacterial mortality matters

The marine picocyanobacteria *Prochlorococcus* (~0.5 μm) (see [Glossary](#)) and *Synechococcus* (~1 μm) are the most abundant photosynthetic cells on Earth [1]. *Prochlorococcus* dominates the nutrient-poor open ocean and is the most globally abundant photosynthetic cell. *Synechococcus* is abundant in nutrient-rich coastal and temperate waters. Both lineages deliver organic material to microbial communities [2] and support global carbon fixation.

Much is understood about 'bottom-up' controls on picocyanobacterial growth, diversity, and evolution. These advances have been supported by the tractability of manipulating bottom-up controls experimentally and technological advances, including flow cytometry and sequencing, which quantify growth rates and decode stress responses [3]. The outcome of this work is understanding that large population sizes, cellular minimalism, high genomic diversity (i.e., ecotypes and subecotypes), and genetic flexibility in mobile genetic elements and genomic islands, support the high abundance of picocyanobacteria on Earth [4].

Much less is understood about the **mortality** of picocyanobacteria, despite the critical role of mortality in the ecology and evolution of microorganisms. How a cell dies determines the type and fate of carbon compounds released. For example, viral lysis releases different carbon compounds than mechanical lysis [5], protist predators can couple microbial carbon to higher trophic levels, and some zooplankton predators can facilitate export of microbial carbon to the deep ocean. Further, mechanisms of mortality determine selective pressures and mechanisms of predator resistance. For example, picocyanobacteria modify surface properties in response to viruses [6], and soil bacteria resist protist predators through antibiotic production [7]. The full picture of picocyanobacteria contributions to carbon cycles, food webs, and their own evolutionary history cannot be known without renewed focus on their mortality.

Apart from viruses [8] the 'top-down' dimensions of picocyanobacterial ecology (i.e., mortality interactions) are not well integrated into this framework and have limited experimental tractability.

Highlights

The mechanisms by which the super-abundant marine picocyanobacteria die are important to understanding the global carbon cycle, the structure of marine food webs, and the evolutionary pressures that have shaped microbial life in the ocean.

The cross-scale systems biology framework for understanding marine picocyanobacteria is missing a key component of ecology and evolution: the diverse and widespread non-viral predators of picocyanobacteria.

Prochlorococcus and *Synechococcus* non-viral predators are unidentified, patchy, fragile, challenging to collect, have complex life cycles, and are frequently intractable in laboratory studies.

Mortality of picocyanobacteria by viruses is more well studied than mortality by non-viral predators owing to tractability of viruses in laboratory experiments and viral isolation from the wild; however, numerous unknowns still exist about viral mortality.

Approaches that integrate across methodologies (e.g., *in situ* incubations via SCUBA combined with flow cytometry, sequencing, and predator cultivation), are promising for future work to reveal the grazing impacts of cosmopolitan non-viral predators, including protists, pelagic tunicates, and thecosome pteropods on marine picocyanobacteria ecology and evolution.

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The non-viral predators of picocyanobacteria are diverse and poorly understood. Thus, critical aspects of picocyanobacterial ecology cannot be placed in the **cross-scale systems framework** that is used to understand these cells [4]. To this end, we propose that advances can come from: (i) building a more comprehensive picture of the mechanisms of picocyanobacterial mortality, and (ii) integrating these mechanisms into picocyanobacterial genomics, evolution, and ecology. This review examines the non-viral predators of picocyanobacteria, their diverse feeding mechanisms, and suggests future work towards a holistic understanding of marine picocyanobacteria.

Trapped on a mucous mesh

Filter-feeding gelatinous zooplankton are emerging as important predators of marine picocyanobacteria. These filter feeders include **pelagic tunicates (salps, pyrosomes, doliolids, and appendicularians; Figure 1A–D)** and **thecosome pteropods (Figure 1E)**, which are zooplankton widely occurring from polar to tropical waters and all use sophisticated filtering systems made of interwoven mucous fibers (Figure 1F,G) to capture picocyanobacteria alongside other suspended prey. Once overlooked and understudied, blending conventional and novel techniques has enabled quantification of gelatinous zooplankton predation on microbial prey [9].

Salps. Salps are barrel-shaped tunicates (1 to >20 cm; Figure 1A) that use muscular pumping for propulsion and filtration of cell-laden seawater across their mucous mesh filters. Best known to capture eukaryotic phytoplankton [10], salp mesh pore sizes are small enough (~1 µm) to capture submicron sized particles owing to low Reynolds number filtration mechanisms that operate at the microscale [11,12].

Salps feed differently on *Prochlorococcus* and *Synechococcus*. Salps clear *Synechococcus* faster than *Prochlorococcus* [13,14], *Synechococcus* is enriched over *Prochlorococcus* in salp guts relative to surrounding seawater [13–15], and microscopy shows limited retention of cells less than 1 µm (i.e., *Prochlorococcus*) [10,16]. Thus, salps may be a substantial predator of *Synechococcus* but not *Prochlorococcus*, raising the question of whether this selective feeding contributes to small cell dominance in the open ocean.

Many dimensions of the salp–picocyanobacteria interaction remain unexplored. Picocyanobacterial retention could vary as salp mesh changes with life stage, size, and species [10,11,16–19]. Further, the low capture of *Prochlorococcus* by salps may be due to factors other than small size. Cell shape [20] and surface properties [21] could also dictate cell capture, as shown for SAR11 that also escapes salp grazing. It is also unknown how distinct picocyanobacterial ecotypes compare in their susceptibility to salps. And finally, uncertainty still remains in the salp–picocyanobacteria interaction. In contrast to the recent cellular and molecular based works, early studies on phytoplankton pigment found within salp fecal pellets suggested that they could capture *Prochlorococcus* [22]. Thus, additional work, with multiple methods applied simultaneously, is needed to resolve the dynamics of salp feeding on *Prochlorococcus* and *Synechococcus*.

Pyrosomes. Pyrosomes (typically ≤1 m; Figure 1B) are colonial zooplankton that retain diverse microbial prey [23,24]. Despite their high filtration rates [25], rapid blooms [26,27], and economic threat [28], pyrosomes are one of the least studied gelatinous grazers. While their predation on eukaryotic phytoplankton is well accepted [29], evidence of picocyanobacterial predation is new.

Pyrosome feeding on *Synechococcus* is supported by two studies which detected the phycoerythrin [30], intact cells [31], and sequences [31] of *Synechococcus* in pyrosome tissue. Like the other pelagic tunicates, feeding is selective, with a preference for larger phytoplankton (>10 µm)

Glossary

Appendicularian: filter-feeding zooplankton with global abundance.

Choanoflagellate: protist predator that creates a feeding current with a flagellum.

Ciliate: protist predator that moves and feeds with cilia.

Cross-scale systems biology framework: the investigation of an organism in the laboratory and in the wild, where integrating understanding from the molecular to the ecosystem level provides insight into how evolution, genes, metabolism, and ecological interactions are connected. The marine picocyanobacteria are well suited as models for this integrated approach to biology [3].

Doliolid: barrel-shaped filter-feeding zooplankton.

Flagellate: protist predator that moves and feeds with a flagellum.

Mixotrophs: microorganisms that obtain energy from photosynthesis and phagocytosis of prey.

Mortality: cell death.

Pelagic tunicate: gelatinous zooplankton that swim freely in the ocean and use mucous meshes to feed.

Picocyanobacterium: a small cyanobacterium, less than 3 µm.

Prochlorococcus: a picocyanobacterium that thrives in warm nutrient-poor areas of the ocean.

Pyrosome: colonial filter-feeding zooplankton.

Salp: barrel-shape filter-feeding zooplankton.

Synechococcus: a picocyanobacterium that thrives globally.

Thecosome pteropods: shelled planktonic gastropods that feed with an external mucous mesh.

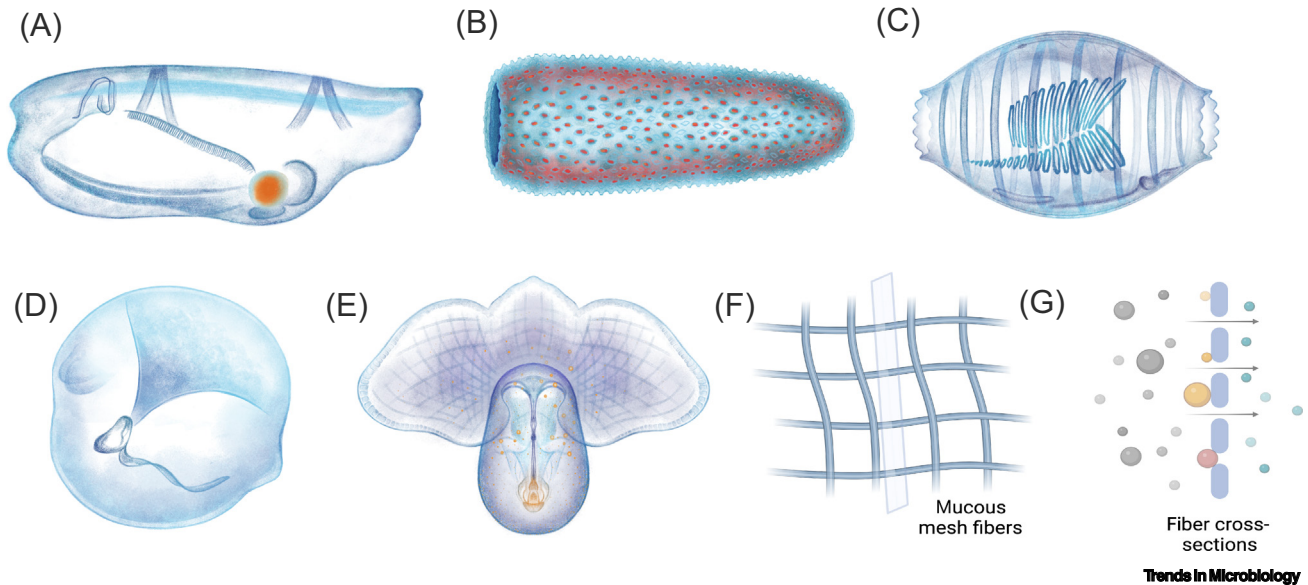


Figure 1. Mucous mesh grazer schematics. (A) Salp (e.g., *Pegea*). (B) Pyrosome (e.g., *Pyrosoma*). (C) Doliolid gonozooid (e.g., *Doliolotta*). (D) Appendicularian (e.g., *Oikopleura*). (E) Thecosome pteropod (e.g., *Corolla*). (F) Diagram of mucous mesh fiber networks based on microscopy of salp mucous mesh net from Sutherland *et al.* (2010) with cross-section indicated by the shaded rectangle [12]. (G) Cross-section [rectangle from (F)] of mucous fibers (blue) and how they interact with potential prey particles (gray spheres) by adherence to the fiber (yellow particles), trapping in fiber openings (red particle), or passing through pores (turquoise particles). Modified from Thompson *et al.* (2024) [14]. Flow direction is indicated by arrows. Illustrations (A–E) by Franz Anthony. Panels F and G created with BioRender.com.

when they are available over *Synechococcus* [25,30]. However, prey-specific clearance rates are unknown. Thus, while pyrosomes appear to be a mortality source for *Synechococcus*, the scale of predation is not known. While pyrosomes' small mesh pore sizes (0.6 μm ; [11]) and tropical habitat [24] suggest *Prochlorococcus* capture, it has not been explicitly addressed.

Doliolids. Doliolids (<4 cm; Figure 1C) have a high capacity to impact picocyanobacterial communities. Represented by 23 known species, doliolids are ubiquitous [32] and abundant during blooms (up to 2000 individuals m^{-3} [33]). However, their complex life cycle [34], arduous cultivation [35], and fragility make their impact on microorganisms difficult to study.

Doliolid ciliary action generates feeding currents, which capture particles on a mucous mesh net that fills their barrel-shaped body [36,37]. Particle capture is efficient relative to **flagellates, ciliates**, and copepods but slower than that of salps and pyrosomes [38]. Doliolid feeding on large particles is established, yet interactions with smaller microbial prey are less known. Limited observations from mesocosms [39] and wild doliolids [40–42] suggest capture of submicron prey. Indeed, two studies discovered *Synechococcus* sequences within doliolids, which may indicate active feeding [41,42]. Selection of *Synechococcus* relative to other phytoplankton is unknown, and retention of *Prochlorococcus* has not been addressed.

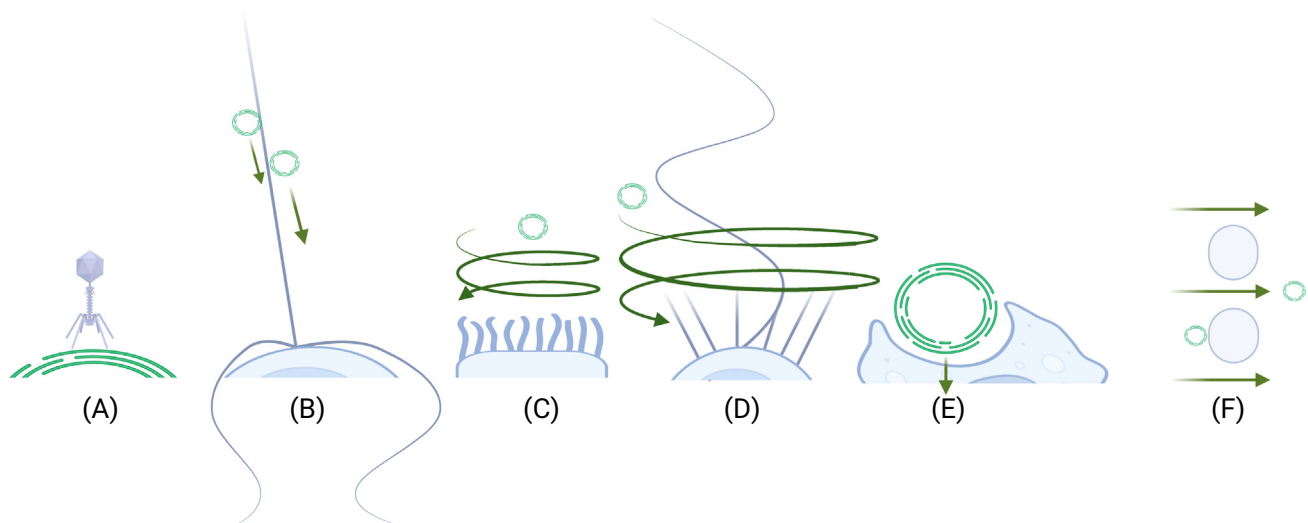
Appendicularians. Appendicularians are small tadpole-shaped pelagic tunicates (0.5–10 mm; Figure 1D) that consume diverse microbial prey [43]. Represented by ~70 species, appendicularians inhabit tropical to polar regions and can rival copepods as the most numerous zooplankton [44], suggesting high potential to influence picocyanobacteria populations.

Multiple studies show *Prochlorococcus* and *Synechococcus* predation by appendicularians. Both picocyanobacteria were cleared from tropical-subtropical waters more slowly than larger

phytoplankton and faster than heterotrophic bacteria [45,46]. Appendicularians clear *Synechococcus* more quickly than *Prochlorococcus* when both are present [46]. However, given the natural conditions in these studies, prey concentrations could not be controlled, so whether appendicularians select between *Prochlorococcus* and *Synechococcus*, or even between ecotypes within each lineage, is not known.

Appendicularians capture prey through one of the most intricate filter-feeding systems known in nature [47]. Sinusoidal tail-beating forces suspended particles onto an external food-concentrating filter. Through experiments with eukaryotic phytoplankton and beads, prey selection is known to be based on prey size [48], shape [20], surface properties [21], nutritive quality [48], and defense [49]. Predator factors such as taxonomy [45], life stage [50], and temperature [46] also alter feeding rates. Because ingestion requires release and rebinding of the prey [51], complex interactions at the mesh–cell interface govern selectivity and may be relevant to picocyanobacterial interactions (Figure 2F). These studies highlight the powerful yet dynamic potential of appendicularians in picocyanobacterial mortality and evolution. Given their successful cultivation [52], experiments discerning the details of appendicularian feeding on picocyanobacteria are more tractable than other mucous mesh feeders.

Pteropods. Thecosome pteropods (0.5–4 cm; Figure 1E) are shelled planktonic gastropods that feed with an external mucous mesh. They are globally abundant, include ~125 species [53,54], and indicate past ocean conditions as they appear in the fossil record [55]. Like the other gelatinous zooplankton, pteropods are sensitive to handling and culture [56]. While they feed on large phytoplankton [56–58], feeding on picocyanobacteria is unclear.



Trends in Microbiology

Figure 2. Examples of the diverse intimate interactions picocyanobacteria experience during predation. (A) Recognition and attachment of viruses. (B) Capture and transport by the haptonema [64,127]. (C) Entrainment in feeding current made by cilia (D) Entrainment in feeding current made by a flagellum such as for the dinoflagellate *Oxyrrhis marina* [128] or choanoflagellates, which also use a ‘collar’ made of microvilli (straight lines) to capture prey [86]. (E) Phagocytosis as a final step of ingestion by many protists after interception or collection [129] [following from capture in (B–D)]. (F) Interaction with mucous mesh fibers where prey may stick to the fiber or passage around/through the space between fibers (blue circles). Green lines or circles indicate a picocyanobacterial membrane (as in (A)) or intact cell (as in (B–F)). Blue shapes and lines are predator features, including membranes, haptonema, flagella, microvilli, and mucous mesh fibers. Dark green arrows indicate direction of movement of the picocyanobacterial cell and/or fluid flow. Figure created with [BioRender.com](https://www.biorender.com).

Bluewater SCUBA and underwater photography provided early suggestions of pteropods feeding on picocyanobacterial-sized prey [59]. Incubations with natural seawater also demonstrated that pteropods removed prey 1–2 μm in diameter faster than copepods [60]. *Synechococcus* (and fewer *Prochlorococcus*) sequences were present in pteropods from the Gulf Stream; however, enrichment beyond the seawater prey field was unclear [15]. Future work assessing pteropod predation on picocyanobacteria could mirror work with Antarctic pteropods [58], which examined many replicate pteropods for prokaryotic and eukaryotic prey using molecular techniques.

Up close and personal: predation by diverse protists

Protists are widely accepted as important non-viral predators of picocyanobacteria [61], and their predation rates are well quantified due to the development and refinement of the ‘Dilution Experiment’ [62,63], which compares growth and loss rates in complex natural samples but excludes larger grazers (such as those discussed earlier). Despite well-discussed caveats of the dilution experiment [62,63], protists are well-accepted picocyanobacterial predators. However, we know little about the specific predators and feeding mechanisms picocyanobacteria experience at this cell-to-cell scale and how this intense top-down pressure has shaped picocyanobacterial genomes, ecology, and evolution. Here, we gather the existing research on specific picocyanobacteria–protist interactions and promising future directions.

Ciliates

Ciliates are planktonic microzooplankton that capture picocyanobacteria in currents generated by coordinated cilia [64] (Figure 2A). Known marine ciliate diversity is ~1200 species [65] and total global diversity may be higher [66], with abundances up to 10 000 cells per ml across varied environments [67].

Synechococcus consumption by ciliates has been demonstrated and varies by ciliate species [68–72], oral diameter [68], and body size [73,74]. *Synechococcus* cell size [69–71], motility [75], and surface proteins [76] also influence the rate, selectivity, and vulnerability to ciliate predation. However, *Synechococcus* may be a poor food source to ciliates as it does not support growth [69,77]. Thus, much work remains to reveal the importance of this predation to the larger ecosystem and food webs.

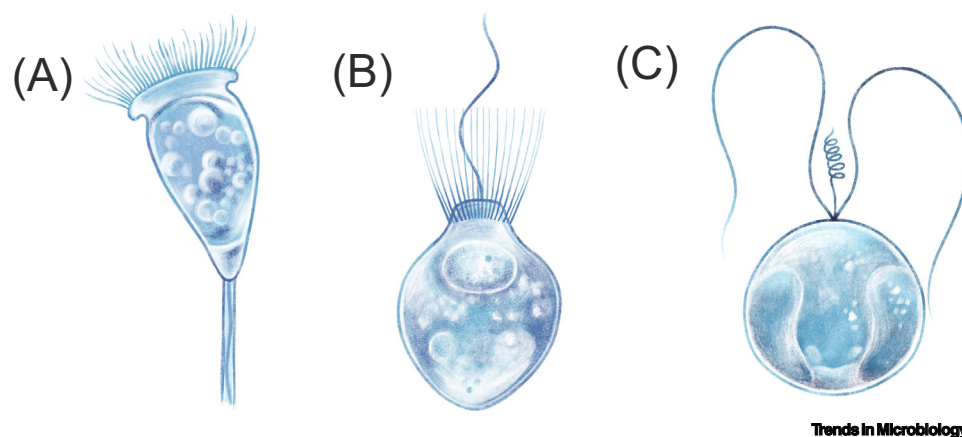


Figure 3. Schematics of select protist functional groups that predate on picocyanobacteria. (A) Ciliate, for example, *Vorticella* sp. (B) Flagellate, for example, choanoflagellate *Salpingoeca rosetta*. (C) Mixotroph and haptophyte, for example, *Chrysochromulina* sp. Illustrations by Franz Anthony.

Prochlorococcus is also susceptible to ciliate predation; however, ciliate impact on *Prochlorococcus* may be lower than that on *Synechococcus*. In experiments where the two picocyanobacteria were compared, *Prochlorococcus* were consumed less than *Synechococcus* [69]. Similarly, in natural communities, few ciliates contained stable isotopes from *Prochlorococcus* [78]. These studies suggest that *Prochlorococcus* may be escaping ciliate predation through an unknown mechanism. Experimental combinations of *Prochlorococcus* and ciliates could address these open questions.

Flagellates

Flagellate grazers are well known bacterial predators [79–81], are about one-fifth of the eukaryotes in the sunlit ocean [82] and span all major eukaryotic groups (Figure 3B). However, in marine surface waters where picocyanobacteria thrive, the flagellates are represented by only dozens of taxa from marine stramenopile clades, Picozoa, Bicosoecida, and Chrysophyceae [83].

Stable isotope probing has identified many and diverse flagellate species that consume *Prochlorococcus* and *Synechococcus* [78,84]. **Choanoflagellates** (Figure 3B) stand out as flagellate bacterivores that consume *Prochlorococcus* and *Synechococcus* [84] and an example of how much remains to be discovered, as choanoflagellates were well studied for other aspects of their biology [85] but had not been previously considered as important marine predators. Choanoflagellates use a single flagellum to create a feeding current, which brings bacterial particles onto a microvilli collar then to the choanoflagellate's surface for phagocytosis and ingestion [86] (Figure 2D). This feeding interaction presents multiple distinct points of contact between predator and prey. The reliability of choanoflagellates in culture [85] and their ecological relevance makes for a promising experimental system for future work.

A few other studies have revealed important characteristics of flagellate feeding on picocyanobacteria. Comparison of the feeding of two stramenopiles revealed dramatic differences in feeding behavior. *Symbiomonas scintillans* fed on neither **picocyanobacterium**, while *Picophagus flagellates* consumed both *Prochlorococcus* and *Synechococcus*, though *Synechococcus* was poorly assimilated and did not support *P. flagellates* growth [87]. A study on the marine heterotrophic nanoflagellate *Pseudobodo* sp. produced similar results, with both picocyanobacteria removed from seawater, and a preference for *Synechococcus*, but poor support of flagellate growth [88]. These results were mirrored with naturally occurring flagellates, where major species-specific differences were observed for selection between *Prochlorococcus* and *Synechococcus* and their support of predator growth [89]. Together, these studies emphasize critical differences between flagellate species and the importance of studying not only picocyanobacterium retention, but also assimilation, to reveal the full consequences of the feeding interaction.

Mixotrophs

Mixotrophic protists are emerging as an important group of picocyanobacterial predators [90] (Figure 3C). Mixotrophic protists contain chloroplasts and consume particles [91] and occur across many different protist groups [92], including bolidophytes, chrysophytes, haptophytes, cryptophytes, dictyophytes, dinoflagellates, chloroarachinophyte, and chlorophytes. Though work remains for assigning mixotrophy to uncultivated taxa [93], this metabolic strategy is key in the marine carbon cycle [94–96] and is of emerging interest for picocyanobacterial mortality.

For *Synechococcus*, there is ample evidence that identifies mixotrophs as influential predators. Mixotrophic predators of *Synechococcus* include the phototrophic ciliate *Mesodinium rubrum* [97], the nanoflagellate *Poterioochromonas* sp. [98], some rapidophytes [99], dictyophytes [100], and mixotrophic dinoflagellates [101,102]. Approaches that do not rely on cultivation, such as stable isotopes, suggest even more diverse mixotrophic predators of *Synechococcus*

[78]. Therefore, *Synechococcus* encounters many different protist feeding strategies in the ocean (Figure 2), such as contact with haptonema, phagocytosis, and entrainment in cilia- and flagella-generated feeding currents, which may exert complex evolutionary pressures.

For *Prochlorococcus*, evidence is also building for the importance of mixotrophic predators. Using stable isotopes, labeled *Prochlorococcus* was assimilated into diverse mixotrophs in an open-ocean microbial community [78]. These results were later supported in the same habitat, when the mixotrophs were isolated, including the nanoflagellate *Florenciella* and haptophyte *Chrysochromulina*, and consumed *Prochlorococcus* in controlled experiments [100,103]. This targeted culture-based approach of Li *et al.* (2021 and 2022) [100,103] is particularly promising as a foundation for future work as a robust experimental system to compare grazers, quantify rates of predation under a range of conditions, compare ecotypes, and characterize defenses against predation.

Existing work on picocyanobacterial mortality by protists only scratches the surface of the complexity of this interaction. Only a very few prey–predator systems have been studied from the thousands of protist species that could coexist with distinct *Prochlorococcus* and *Synechococcus* clades. Of the known protist predators, many distinct prey capture systems are at work, which differ from the mechanisms of viral predation (Figure 2A), and include attachment to haptonema (Figure 2B), entrainment in feeding currents (Figure 2C,D), and ultimately phagocytosis at the protist membrane (Figure 2E). Each of these interactions may present distinct selective pressures on picocyanobacteria, which remain to be discovered.

Further opportunities for discovery lie in comparing predation across the diverse picocyanobacterial lineages, which has been an important strategy in developing the picocyanobacterial cross-scale biological model systems [3]. Among the ecotypes studied so far, *Synechococcus* Clade III [69,104] and *Prochlorococcus* SS120 LLII/III Clade [69], are not globally abundant. The true globally dominant ecotypes (i.e., *Prochlorococcus* HLI and HLII and marine *Synechococcus* Clades I and II) remain untested. Addressing questions of the magnitude, diversity, feeding mechanisms, and picocyanobacterial acclimation and adaptation to protist grazers could fuel novel future research.

Other potential underexplored grazers

Several other animal phyla may also be picocyanobacterial consumers; however, they have been very sparsely studied. Some ctenophores capture *Synechococcus* with their branched tentacles [105]. Benthic filter feeders, including bivalve mollusks, ascidians, and sponges also capture and consume *Prochlorococcus* and *Synechococcus* [21,106–108]. Barnacle nauplii feed on *Synechococcus* [109], indicating that picocyanobacteria could be prey to other larval zooplankton. Corals are another understudied predator, as marine corals selectively capture *Synechococcus* over *Prochlorococcus* [110,111] and coral mucous traps *Synechococcus* [112].

Copepods are another well-studied group that is only recently being considered picocyanobacterial predators. Two studies suggest direct capture of *Synechococcus* [113,114], while others suggest indirect capture through detrital or aggregate feeding [115]. Resolving the copepod capture mechanism has implications for picocyanobacteria contributions to food webs and the carbon cycle. Promisingly, copepods are robust for sampling and laboratory rearing [116], and ecological models [117], offering a strong foundation for future inquiry.

Other bacteria are also an extremely underexplored mortality source for the marine picocyanobacteria. While antagonistic interactions between *Prochlorococcus* and diverse heterotrophs are known [118], much of the focus on heterotroph–picocyanobacteria interactions has been on the positive outcomes

of the relationship, such as coping with stress [119,120]. The challenges of uncovering the mechanisms and selectivity of anti-picocyanobacterial behaviors in heterotrophic bacteria face challenges similar to revealing the role and importance of other predators, including the challenges of cultivation.

Diverse predators create complex pathways through carbon cycles and food webs

The most well-recognized sources of predation (viral lysis and protistan predation) recycle picocyanobacterial carbon, fuel the microbial loop [5,96], or transfer picocyanobacterial carbon to higher trophic levels via protists [121]. However, recognizing more diverse predators (Figures 1 and 3) opens previously unrecognized pathways for picocyanobacterial carbon and biomass in carbon cycles and food webs.

Predation by zooplankton could help explain observations of picocyanobacterial contributions to carbon export [122], as the picocyanobacteria are often considered too small to sink by themselves. Salps, doliolids, and pteropods produce fast-sinking fecal pellets [123] that could transport picocyanobacteria to the deep ocean. Through entrapment in mucous, picocyanobacteria could also become part of marine snow, which is common for appendicularian houses [124] and pteropod webs [60], and an important vertical carbon transport mechanism. As *Prochlorococcus* and *Synechococcus* contain diverse and unique metabolites [2], discovering how these different predation mechanisms govern the form and fate of carbon will advance understanding of ocean carbon cycles.

Picocyanobacterial predation by diverse predators contributes to the view that marine food webs are extremely complex [96]. Protist predators are already recognized as a crucial link between the microbial and classical food chains (bacterial consumers and zooplankton prey) [125] and a contributor to dissolved organic material pools. This role will become more complex as more specific protists are recognized as picocyanobacterial predators. Picocyanobacterial predation by larger predators also makes food webs more complex. For example, gelatinous zooplankton 'short-circuit' traditional food webs by moving microbial carbon to high trophic levels in few steps. As some of these larger predators, such as the appendicularians, are exclusive prey for juvenile tuna [126], picocyanobacteria could also play a more direct role in supporting economically important fisheries than previously recognized.

Concluding remarks and future perspectives

Marine picocyanobacteria face numerous predators and feeding strategies (Figures 1–3), but the details of these interactions are understudied relative to their importance in biogeochemical cycles, biogeography, community structure, and the ecology and evolution of superabundant microorganisms. While viruses are the best-known predators of picocyanobacteria, many aspects of their interaction remain to be discovered. For example, picocyanobacteria deploy different resistance strategies against generalist compared with specialist viruses [6], which may have complex repercussions to picocyanobacteria population structure and diversity. This complexity of predator resistance is likely mirrored in picocyanobacterial responses to non-viral predators as well and remains to be discovered. Understanding of both viral and non-viral predation share many challenges, which include working across biological scales (i.e., microorganisms to macroplankton), intricate and often unknown predator ecology (i.e., life cycles, biogeography, and growth rates) that make them difficult to study, the delicacy of predators that makes them hard to retrieve from the ocean, and lack of clarity on which specific predators are the most impactful.

There are several examples where researchers have overcome these challenges. For example, Li *et al.* (2022) [103] identified *Chrysochromulina* as a predator, brought the mixotroph into culture, quantified feeding rates, and then deposited the strain into a bioresource facility to support the work of others. The approach of Apple *et al.* (2011) [75] and Strom *et al.* (2012) [104] is also

Outstanding questions

How does the abundance and distribution of non-viral predators overlap with the biogeography of *Prochlorococcus* and *Synechococcus*?

Which non-viral predators exert the heaviest predation on marine picocyanobacteria, and how does this impact vary in space and time?

What are the fates of grazed picocyanobacteria, for example, do some survive in fecal pellets and serve to seed future populations?

What evolutionary pressure do non-viral predators exert on picocyanobacteria?

Do non-viral predators distinguish between the diverse ecotypes of *Prochlorococcus* and *Synechococcus*?

Do picocyanobacteria respond to, or evade, non-viral predators?

inspiring because it used *Synechococcus*' genetic system to reveal a surface protein that protects against one predator but increases susceptibility to another predator. Finally, the combination of the classic and modern approaches (i.e., bluewater SCUBA and sequencing) [45] revealed appendicularian selection between coexisting picocyanobacteria. For scientists interested in taking on these substantial experimental challenges many exciting discoveries remain which will advance understanding of the ecology, evolution, and biogeochemistry of the most abundant photosynthetic cells on Earth (see [Outstanding questions](#)).

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Declaration of interests

The authors declare no competing interests.

References

- Flombaum, P. *et al.* (2013) Present and future global distributions of the marine Cyanobacteria *Prochlorococcus* and *Synechococcus*. *Proc. Natl. Acad. Sci. U. S. A.* 110, 9824–9829
- Kujawinski, E.B. *et al.* (2023) Metabolite diversity among representatives of divergent *Prochlorococcus* ecotypes. *mSystems* 8, e01261-22
- Coleman, M.L. and Chisholm, S.W. (2007) Code and context: *Prochlorococcus* as a model for cross-scale biology. *Trends Microbiol.* 15, 398–407
- Biller, S.J. *et al.* (2015) *Prochlorococcus*: the structure and function of collective diversity. *Nat. Rev. Microbiol.* 13, 13–27
- Ma, X. *et al.* (2018) Distinct molecular signatures in dissolved organic matter produced by viral lysis of marine cyanobacteria. *Environ. Microbiol.* 20, 3001–3011
- Zborowsky, S. and Lindell, D. (2019) Resistance in marine cyanobacteria differs against specialist and generalist cyanophages. *Proc. Natl. Acad. Sci. U. S. A.* 116, 16899–16908
- Nguyen, Thi Bao-Anh *et al.* (2023) Protistan predation selects for antibiotic resistance in soil bacterial communities. *ISME J.* 17, 2182–2189
- Lindell, D. *et al.* (2007) Genome-wide expression dynamics of a marine virus and host reveal features of co-evolution. *Nature* 449, 83–86
- Sutherland, K.R. and Thompson, A.W. (2022) Pelagic tunicate grazing on marine microbes revealed by integrative approaches. *Limnol. Oceanogr.* 67, 102–121
- Stukel, M.R. *et al.* (2021) Size-specific grazing and competitive interactions between large salps and protistan grazers. *Limnol. Oceanogr.* 66, 2521–2534
- Bone, Q. *et al.* (2003) Tunicate feeding filters. *J. Mar. Biol. Assoc. U. K.* 83, 907–919
- Sutherland, K.R. *et al.* (2010) Filtration of submicrometer particles by pelagic tunicates. *Proc. Natl. Acad. Sci. U. S. A.* 107, 15129–15134
- Dadon-Pilosof, A. *et al.* (2019) Prey taxonomy rather than size determines salp diets. *Limnol. Oceanogr.* 64, 1996–2010
- Thompson, A.W. *et al.* (2024) Ubiquitous filter feeders shape open ocean microbial community structure and function. *PNAS Nexus* 3, pgae091
- Thompson, A.W. *et al.* (2023) Selective and differential feeding on marine prokaryotes by mucous mesh feeders. *Environ. Microbiol.* 25, 880–893
- Fender, C.K. *et al.* (2023) Prey size spectra and predator to prey size ratios of southern ocean salps. *Mar. Biol.* 170, 40
- Harbison, G.R. and Gilmer, R.W. (1976) The feeding rates of the pelagic tunicate *Pegea confederata* and two other salps 1. *Limnol. Oceanogr.* 21, 517–528
- Kremer, P. and Madin, L.P. (1992) Particle retention efficiency of salps. *J. Plankton Res.* 14, 1009–1015
- Stone, J. and Steinberg, D. (2014) Long-term time-series study of salp population dynamics in the Sargasso Sea. *Mar. Ecol. Prog. Ser.* 510, 111–127
- Conley, K.R. and Sutherland, K.R. (2017) Particle shape impacts export and fate in the ocean through interactions with the globally abundant appendicularian *Oikopleura dioica*. *PLoS ONE* 12, e0183105
- Dadon-Pilosof, A. *et al.* (2017) Surface properties of SAR11 bacteria facilitate grazing avoidance. *Nat. Microbiol.* 2, 1608–1615
- Goericke, R. *et al.* (2000) Distribution and sources of cyclic Pheophorbides in the marine environment. *Limnol. Oceanogr.* 45, 200–211
- Schram, J. *et al.* (2020) Abundance, distribution, and feeding ecology of *Pyrosoma atlanticum* in the Northern California Current. *Mar. Ecol. Prog. Ser.* 651, 97–110
- Lilly, L.E. *et al.* (2023) A global review of pyrosomes: shedding light on the ocean's elusive gelatinous 'fire-bodies'. *Limnol. Oceanogr. Lett.* 8, 812–829
- Perissinotto, R. *et al.* (2007) Grazing by *Pyrosoma atlanticum* (Tunicata, Thaliacea) in the south Indian Ocean. *Mar. Ecol. Prog. Ser.* 330, 1–11
- Henschke, N. *et al.* (2019) Large vertical migrations of *Pyrosoma atlanticum* play an important role in active carbon transport. *JGR Biogeosci.* 124, 1056–1070
- O'Loughlin, J.H. *et al.* (2020) Implications of *Pyrosoma atlanticum* range expansion on phytoplankton standing stocks in the Northern California Current. *Prog. Oceanogr.* 188, 102424
- Sutherland, K.R. *et al.* (2018) Range expansion of tropical pyrosomes in the northeast Pacific Ocean. *Ecology* 99, 2397–2399
- Lyle, J.T. *et al.* (2022) Fine-scale vertical distribution and diel migrations of *Pyrosoma atlanticum* in the northern California Current. *J. Plankton Res.* 44, 288–302
- Décima, M. *et al.* (2019) The unique ecological role of pyrosomes in the Eastern Tropical Pacific. *Limnol. Oceanogr.* 64, 728–743
- Thompson, A.W. *et al.* (2021) Host-specific symbioses and the microbial prey of a pelagic tunicate (*Pyrosoma atlanticum*). *ISME Commun.* 1, 11
- Greer, A.T. *et al.* (2020) High-resolution sampling of a broad marine life size Spectrum reveals differing size- and composition-based associations with physical oceanographic structure. *Front. Mar. Sci.* 7, 542701
- Takahashi, K. *et al.* (2015) *In situ* observations of a doliolid bloom in a warm water filament using a video plankton recorder: bloom development, fate, and effect on biogeochemical cycles and planktonic food webs. *Limnol. Oceanogr.* 60, 1763–1780

34. Deibel, D. and Lowen, B. (2012) A review of the life cycles and life-history adaptations of pelagic tunicates to environmental conditions. *ICES J. Mar. Sci.* 69, 358–369
35. Walters, T.L. *et al.* (2019) Diet and trophic interactions of a circumglobally significant gelatinous marine zooplankter, *Doliolletta gegenbauri* (Uljanin, 1884). *Mol. Ecol.* 28, 176–189
36. Alldredge, A.L. and Madin, L.P. (1982) Pelagic tunicates: unique herbivores in the marine plankton. *BioScience* 32, 655–663
37. Bone, Q. *et al.* (1997) On the filter-feeding of *Doliolum* (Tunicata: Thaliacea). *J. Exp. Mar. Biol. Ecol.* 214, 179–193
38. Conley, K.R. *et al.* (2018) Mammoth grazers on the ocean's minuteness: a review of selective feeding using mucous meshes. *Proc. Biol. Sci.* 285, 20180056
39. Katechakis, A. *et al.* (2002) Changes in the phytoplankton community and microbial food web of Blanes Bay (Catalan Sea, NW Mediterranean) under prolonged grazing pressure by doliolids (Tunicata), cladocerans or copepods (Crustacea). *Mar. Ecol. Prog. Ser.* 234, 55–69
40. Frischer, M.E. *et al.* (2021) Selective feeding and linkages to the microbial food web by the doliolid *Doliolletta gegenbauri*. *Limnol. Oceanogr.* 66, 1993–2010
41. Pereira, T.J. *et al.* (2023) The microbiome of the pelagic tunicate *Doliolletta gegenbauri*: a potential link between the grazing and microbial food web. *Mol. Ecol.* 32, 6564–6579
42. Steinman, M. *et al.* (2024) The microorganisms associated with doliolids in a productive coastal upwelling system. *Limnol. Oceanogr.*, (in press)
43. Jaspers, C. *et al.* (2023) Gelatinous larvacean zooplankton can enhance trophic transfer and carbon sequestration. *Trends Ecol. Evol.* 38, 980–993
44. Lombard, F. *et al.* (2010) Prediction of ecological niches and carbon export by appendicularians using a new multispecies eco-physiological model. *Mar. Ecol. Prog. Ser.* 398, 109–125
45. Dadon-Pliouf, A. *et al.* (2023) Differential clearance rates of microbial phylotypes by four appendicularian species. *Mar. Ecol. Prog. Ser.* 706, 73–89
46. Scheinberg, R.D. *et al.* (2005) Grazing of two common appendicularians on the natural prey assemblage of a tropical coastal ecosystem. *Mar. Ecol. Prog. Ser.* 294, 201–212
47. Hiebert, T.C. *et al.* (2023) The hydrodynamics and kinematics of the appendicularian tail underpin peristaltic pumping. *J. R. Soc. Interface* 20, 20230404
48. Troedsson, C. *et al.* (2007) Molecular quantification of differential ingestion and particle trapping rates by the appendicularian *Oikopleura dioica* as a function of prey size and shape. *Limnol. Oceanogr.* 52, 416–427
49. Lombard, F. *et al.* (2011) Active prey rejection in the filter-feeding appendicularian *Oikopleura dioica*. *Limnol. Oceanogr.* 56, 1504–1512
50. López-Urrutia, Á. *et al.* (2003) *In situ* feeding physiology and grazing impact of the appendicularian community in temperate waters. *Mar. Ecol. Prog. Ser.* 252, 125–141
51. Conley, K.R. *et al.* (2018) A self-cleaning biological filter: How appendicularians mechanically control particle adhesion and removal. *Limnol. Oceanogr.* 63, 927–938
52. Bouquet, J.-M. *et al.* (2009) Culture optimization for the emergent zooplanktonic model organism *Oikopleura dioica*. *J. Plankton Res.* 31, 359–370
53. Bednaršek, N. *et al.* (2012) The global distribution of pteropods and their contribution to carbonate and carbon biomass in the modern ocean. *Earth Syst. Sci. Data* 4, 167–186
54. Thibodeau, P.S. *et al.* (2019) Environmental controls on pteropod biogeography along the Western Antarctic Peninsula. *Limnol. Oceanogr.* 64, S240–S256
55. Keul, N. *et al.* (2017) Pteropods are excellent recorders of surface temperature and carbonate ion concentration. *Sci. Rep.* 7, 12645
56. Howes, E.L. *et al.* (2014) Sink and swim: a status review of thecosome pteropod culture techniques. *J. Plankton Res.* 36, 299–315
57. Silver, M.W. and Bruland, K.W. (1981) Differential feeding and fecal pellet composition of salps and pteropods, and the possible origin of the deep-water flora and olive-green cells. *Mar. Biol.* 62, 263–273
58. Thibodeau, P. *et al.* (2022) Feeding ecology and microbiome of the pteropod *Limacina helicina antarctica*. *Aquat. Microb. Ecol.* 88, 19–24
59. Gilmer, R.W. (1974) Some aspects of feeding in thecosomatous pteropod molluscs. *J. Exp. Mar. Biol. Ecol.* 15, 127–144
60. Noji, T.T. *et al.* (1997) Clearance of picoplankton-sized particles and formation of rapidly sinking aggregates by the pteropod, *Limacina reiroversa*. *J. Plankton Res.* 19, 863–875
61. Cai, L. *et al.* (2023) Biological interactions with *Prochlorococcus*: implications for the marine carbon cycle. *Trends Microbiol.* 32, 280–291
62. Cram, J.A. *et al.* (2016) Dilution reveals how viral lysis and grazing shape microbial communities. *Limnol. Oceanogr.* 61, 889–905
63. Landry, R. *et al.* (1995) A refined dilution technique for measuring the community grazing impact of microzooplankton, with experimental tests in the central equatorial Pacific. *Mar. Ecol. Prog. Ser.* 120, 53–63
64. Bloodgood, R.A. (2020) Prey capture in protists utilizing microtubule filled processes and surface motility. *Cytoskeleton* 77, 500–514
65. Grattepanche, J. *et al.* (2016) Unexpected biodiversity of ciliates in marine samples from below the photic zone. *Mol. Ecol.* 25, 3987–4000
66. Canals, O. *et al.* (2020) Ciliate diversity and distribution across horizontal and vertical scales in the open ocean. *Mol. Ecol.* 29, 2824–2839
67. De Vargas, C. *et al.* (2015) Eukaryotic plankton diversity in the sunlit ocean. *Science* 348, 1261605
68. Bernard, C. and Rassoulzadegan, F. (1993) The role of picoplankton (cyanobacteria and plastidic picoflagellates) in the diet of tintinnids. *J. Plankton Res.* 15, 361–373
69. Christaki, U. *et al.* (1999) Growth and grazing on *Prochlorococcus* and *Synechococcus* by two marine ciliates. *Limnol. Oceanogr.* 44, 52–61
70. Christaki, U. *et al.* (1998) Consumption of picoplankton-size particles by marine ciliates: Effects of physiological state of the ciliate and particle quality. *Limnol. Oceanogr.* 43, 458–464
71. Kivi, Setälä (1995) Simultaneous measurement of food particle selection and clearance rates of planktonic oligotrich ciliates (Ciliophora: Oligotrichina). *Mar. Ecol. Prog. Ser.* 119, 125–137
72. Barua, R. *et al.* (2024) *In situ* imaging of a kleptoplastic ciliate thin layer indicates traditional sampling underestimates oceanic mixotroph biomass. *Commun. Earth Environ.* 5, 534
73. Bernard, C. and Rassoulzadegan, F. (1990) Bacteria or microflagellates as a major food source for marine ciliates: possible implications for the microzooplankton. *Mar. Ecol. Prog. Ser.* 64, 147–155
74. Claessens, M. *et al.* (2008) Ciliate community in the oligotrophic Gulf of Aqaba, Red Sea. *Aquat. Microb. Ecol.* 53, 181–190
75. Apple, J.K. *et al.* (2011) Variability in protist grazing and growth on different marine *Synechococcus* isolates. *Appl. Environ. Microbiol.* 77, 3074–3084
76. Strom, S. *et al.* (2017) The *Synechococcus* cell surface protein SwmA increases vulnerability to predation by flagellates and ciliates. *Limnol. Oceanogr.* 62, 784–794
77. An-Yi, T. *et al.* (2009) Diel patterns of grazing by pigmented nanoflagellates on *Synechococcus* spp. in the coastal ecosystem of subtropical western Pacific. *Hydrobiologia* 636, 249–256
78. Frias-Lopez, J. *et al.* (2009) Use of stable isotope-labelled cells to identify active grazers of picocyanobacteria in ocean surface waters. *Environ. Microbiol.* 11, 512–525
79. Azam, F. *et al.* (1983) The ecological role of water column microbes in the sea. *Mar. Ecol. Prog. Ser.* 10, 257–263
80. Fenchel, T. (1984) Suspended marine bacteria as a food source. In *Flows of Energy and Materials in Marine Ecosystems: Theory and Practice*. NATO Conference Series (Fasham, M.J.R., ed.), pp. 301–315, Springer
81. Gonzalez, J.M. *et al.* (1990) Size-selective grazing on bacteria by natural assemblages of estuarine flagellates and ciliates. *Appl. Environ. Microbiol.* 56, 583–589
82. Jürgens, K. and Massana, R. (2008) Protistan grazing on marine bacterioplankton. In *Microbial Ecology of the Oceans* (Kirchman, D.L., ed.), pp. 383–441, Wiley
83. Obiol, A. *et al.* (2021) Oceanic heterotrophic flagellates are dominated by a few widespread taxa. *Limnol. Oceanogr.* 66, 4240–4253

84. Wilken, S. *et al.* (2023) Choanoflagellates alongside diverse uncultured predatory protists consume the abundant open-ocean cyanobacterium *Prochlorococcus*. *Proc. Natl. Acad. Sci.* 120, e2302388120
85. King, N. (2005) Choanoflagellates. *Curr. Biol.* 15, R113–R114
86. Pettitt, M.E. *et al.* (2002) The hydrodynamics of filter feeding in choanoflagellates. *Eur. J. Protistol.* 38, 313–332
87. Guillou, L. *et al.* (2001) Grazing impact of two small heterotrophic flagellates on *Prochlorococcus* and *Synechococcus*. *Aquat. Microb. Ecol.* 26, 201–207
88. Christaki, U. *et al.* (2002) Dynamic characteristics of *Prochlorococcus* and *Synechococcus* consumption by bacterivorous nanoflagellates. *Microb. Ecol.* 43, 341–352
89. Christaki, U. *et al.* (2005) Grazing impact of different heterotrophic nanoflagellates on eukaryotic (*Ostreococcus tauri*) and prokaryotic picocautotrophs (*Prochlorococcus* and *Synechococcus*). *Environ. Microbiol.* 7, 1200–1210
90. Edwards, K.F. *et al.* (2023) Ingestion kinetics of mixotrophic and heterotrophic flagellates. *Limnol. Oceanogr.* 68, 917–927
91. Mitra, A. *et al.* (2014) The role of mixotrophic protists in the biological carbon pump. *Biogeosciences* 11, 995–1005
92. Stoecker, D. *et al.* (2009) Acquired phototrophy in aquatic protists. *Aquat. Microb. Ecol.* 57, 279–310
93. Wilken, S. *et al.* (2019) The need to account for cell biology in characterizing predatory mixotrophs in aquatic environments. *Philos. Trans. R. Soc. B Biol. Sci.* 374, 20190090
94. Caron, D.A. (2016) Mixotrophy stirs up our understanding of marine food webs. *Proc. Natl. Acad. Sci. U. S. A.* 113, 2806–2808
95. Stoecker, D.K. *et al.* (2017) Mixotrophy in the marine plankton. *Annu. Rev. Mar. Sci.* 9, 311–335
96. Worden, A.Z. *et al.* (2015) Rethinking the marine carbon cycle: factoring in the multifarious lifestyles of microbes. *Science* 347, 1257–1264
97. Yoo, Y.D. *et al.* (2015) Ingestion of the unicellular cyanobacterium *Synechococcus* by the mixotrophic red tide ciliate *Mesodinium rubrum*. *Algae* 30, 281–290
98. Callieri, C. *et al.* (2016) Grazing-induced *Synechococcus* microcolony formation: experimental insights from two freshwater phylogenies. *FEMS Microbiol. Ecol.* 92, fiv154
99. Jeong, H.J. *et al.* (2010) Feeding by raphidophytes on the cyanobacterium *Synechococcus* sp. *Aquat. Microb. Ecol.* 58, 181–195
100. Li, Q. *et al.* (2021) Plasticity in the grazing ecophysiology of *Florentiella* (Dichtyochophyceae), a mixotrophic nanoflagellate that consumes *Prochlorococcus* and other bacteria. *Limnol. Oceanogr.* 66, 47–60
101. Gilbert, P.M. *et al.* (2009) Grazing by *Karenia brevis* on *Synechococcus* enhances its growth rate and may help to sustain blooms. *Aquat. Microb. Ecol.* 55, 17–30
102. Jeong, H.J. *et al.* (2005) Feeding by red-tide dinoflagellates on the cyanobacterium *Synechococcus*. *Aquat. Microb. Ecol.* 41, 131–143
103. Li, Q. *et al.* (2022) Broad phylogenetic and functional diversity among mixotrophic consumers of *Prochlorococcus*. *ISME J.* 16, 1557–1569
104. Strom, S.L. *et al.* (2012) A giant cell surface protein in *Synechococcus* WH8102 inhibits feeding by a dinoflagellate predator. *Environ. Microbiol.* 14, 807–816
105. Majaneva, S. *et al.* (2014) Feeding of the Arctic ctenophore *Mertensia ovum* in the Baltic Sea: evidence of the use of microbial prey. *J. Plankton Res.* 36, 91–103
106. Amit, T. *et al.* (2023) Feeding on the smallest cells: an in situ study of picoplankton capture by bivalve molluscs from oligotrophic waters. *Front. Mar. Sci.* 10, 1184773
107. Garrison, J.A. *et al.* (2022) Molecular diet analysis enables detection of diatom and cyanobacteria DNA in the gut of *Macoma balthica*. *PLoS ONE* 17, e0278070
108. Yahel, G. *et al.* (2005) InEx – a direct *in situ* method to measure filtration rates, nutrition, and metabolism of active suspension feeders: pumping and fluxes in suspension feeders. *Limnol. Oceanogr. Methods* 3, 46–58
109. Bernal, S. and Anil, A.C. (2019) Picophytoplankton *Synechococcus* as food for nauplii of *Amphibalanus amphitrite* and *Artemia salina*. *Hydrobiologia* 835, 21–36
110. Houlbrèque, F. *et al.* (2006) Picoplankton removal by the coral reef community of La PrÉvoyante, Mayotte Island. *Aquat. Microb. Ecol.* 44, 59–70
111. Patten, N.L. *et al.* (2011) Uptake of picophytoplankton, bacterioplankton and viroplankton by a fringing coral reef community (Ningaloo Reef, Australia). *Coral Reefs* 30, 555–567
112. Naumann, M. *et al.* (2009) Coral mucus as an efficient trap for picoplanktonic cyanobacteria: implications for pelagic–benthic coupling in the reef ecosystem. *Mar. Ecol. Prog. Ser.* 385, 65–76
113. Motwani, N.H. and Gorokhova, E. (2013) Mesozooplankton grazing on picocyanobacteria in the Baltic Sea as Inferred from molecular diet analysis. *PLoS ONE* 8, e79230
114. Shoemaker, K.M. and Moisaner, P.H. (2017) Seasonal variation in the copepod gut microbiome in the subtropical North Atlantic Ocean. *Environ. Microbiol.* 19, 3087–3097
115. Wilson, S. and Steinberg, D. (2010) Autotrophic picoplankton in mesozooplankton guts: evidence of aggregate feeding in the mesopelagic zone and export of small phytoplankton. *Mar. Ecol. Prog. Ser.* 412, 11–27
116. Vijverberg, J. (1989) Culture techniques for studies on the growth, development and reproduction of copepods and cladocerans under laboratory and *in situ* conditions: a review. *Freshw. Biol.* 21, 317–373
117. Bi inicu, E. *et al.* (2024) Qualitative model of the causal interactions between phytoplankton, zooplankton, and environmental factors in the Romanian Black Sea. *Phycology* 4, 168–189
118. Sher, D. *et al.* (2011) Response of *Prochlorococcus* ecotypes to co-culture with diverse marine bacteria. *ISME J.* 5, 1125–1132
119. Coe, A. *et al.* (2016) Survival of *Prochlorococcus* in extended darkness. *Limnol. Oceanogr.* 61, 1375–1388
120. Morris, J.J. *et al.* (2011) Dependence of the cyanobacterium *Prochlorococcus* on hydrogen peroxide scavenging microbes for growth at the ocean's surface. *PLoS ONE* 6, e16805
121. Barnes, C. *et al.* (2010) Global patterns in predator–prey size relationships reveal size dependency of trophic transfer efficiency. *Ecology* 91, 222–232
122. De Martini, F. *et al.* (2018) Clade and strain specific contributions of *Synechococcus* and *Prochlorococcus* to carbon export in the Sargasso Sea. *Limnol. Oceanogr.* 63, S448–S457
123. Turner, J.T. (2002) Zooplankton fecal pellets, marine snow and sinking phytoplankton blooms. *Aquat. Microb. Ecol.* 27, 57–102
124. Lombard, F. and Kiorboe, T. (2010) Marine snow originating from appendicularian houses: age-dependent settling characteristics. *Deep-Sea Res. I Oceanogr. Res. Pap.* 57, 1304–1313
125. Calbet, A. and Saiz, E. (2005) The ciliate–copepod link in marine ecosystems. *Aquat. Microb. Ecol.* 38, 157–167
126. Llopiz, J.K. *et al.* (2010) Distinctions in the diets and distributions of larval tunas and the important role of appendicularians. *Limnol. Oceanogr.* 55, 983–996
127. Kawachi, M. *et al.* (1991) The haptoneura as a food-capturing device: observations on *Chrysochromulina hirta* (Prymnesiophyceae). *Phycologia* 30, 563–573
128. Roberts, E.C. *et al.* (2011) Feeding in the dinoflagellate *Oxyrrhis marina*: linking behaviour with mechanisms. *J. Plankton Res.* 33, 603–614
129. Montagnes, D.J.S. *et al.* (2008) Selective feeding behaviour of key free-living protists: avenues for continued study. *Aquat. Microb. Ecol.* 53, 83–98