An Integrated View of Diatom Interactions

Flora Vincent and Chris Bowler

Abstract

Marine microbial communities, composed of bacteria, archaea, and protists, as well as viruses, play essential roles in the functioning and regulation of Earth's biogeochemical cycles and in providing resources at the base of marine food webs. Their roles within planktonic ecosystems have typically been studied under the prism of bottom-up research, namely, understanding how resources and abiotic factors affect their abundance, diversity, and functions. However, how species interact with each other is critical to form the ecosystems that sustain life on Earth. Top-down direct interactions (such as symbiosis, viral infection, or epibiosis) drive coevolution, influence species distribution, contribute to ecosystem stability, and affect global biogeochemical cycles. Diatoms are an extremely good case study for exploring biotic interactions. They are pivotal in marine microbial communities and are known to interact with numerous other organisms in the ocean. These interactions can provide insights about why diatoms can thrive in oligotrophic waters, how they can outcompete other organisms in eutrophic conditions, and ultimately how these interactions impact plankton communities and evolution.

Keywords

Diatoms · Biogeochemistry · Microbial communities · Biotic interactions

---

F. Vincent (✉)
Department of Plant and Environmental Sciences, Weizmann Institute of Science, Rehovot, Israel
e-mail: flora.vincent@cri-paris.org

C. Bowler
Institut de Biologie de l'Ecole Normale Supérieure (IBENS), PSL Research Université, Paris, France

A. Falciatore, T. Mock (eds.), *The Molecular Life of Diatoms*,
https://doi.org/10.1007/978-3-030-92499-7_3

Abbreviation

3D	three dimensions
CO_2	carbon dioxide
DDA	diatom–diazotroph associations
DiOC6	3,3′-dihexyloxacarbocyanine iodide
DNA	deoxyribonucleic acid
e-HCFM	environmental high content fluorescence microscopy
HNLC	high-nutrient, low-chlorophyll
MAST	marine stramenopile
NO_3^-	nitrate
O_2	dioxygen
PUA	polyunsaturated aldehydes
rRNA	ribosomal ribonucleic acid
T°C	temperature

1 Introduction

1.1 Biotic Interactions in Phytoplankton

Diatoms are prolific phototrophic organisms that inhabit the open ocean, polar waters, tropical waters, all fresh water areas, soil, snow, and even glacial ice. They dominate phytoplankton communities in well-mixed coastal and upwelling regions, as long as sufficient light, inorganic nitrogen, phosphorus, silicon, and trace elements are available to sustain their growth (Morel and Price 2003; Pierella Karlusich et al. 2020). In particular, diatoms can be at the source of massive algal proliferations called “blooms” that last weeks or longer, and are often triggered by bottom-up factors such as incident irradiance, nutrient availability, and surface mixed layer shallowing (Platt et al. 2009). Diatom blooms typically occur in the early spring and last until late spring or early summer. This seasonal event is characteristic of the temperate North Atlantic Ocean, subpolar, and coastal waters. Yet, diatom blooms cannot be explained just by the fact that they have a superior environmental tolerance or more efficient nutrient uptake systems relative to other photosynthetic blooming organisms. Several additional explanations involve biotic interactions between diatoms and other members of the plankton.

A decade ago, Smetacek introduced a top-down view of diatom biology, arguing that the evolution of plankton was likely ruled by protection against grazing, and not by competition for resources, and therefore that the interpretation of blooms as being the outcome of superior environmental tolerance and resource competition among photosynthetic protists was incomplete. For him, the many different morphologies and life histories of diatoms reflected responses to specific top-down pressures such as predation. Our understanding of the evolution of form and function in terrestrial

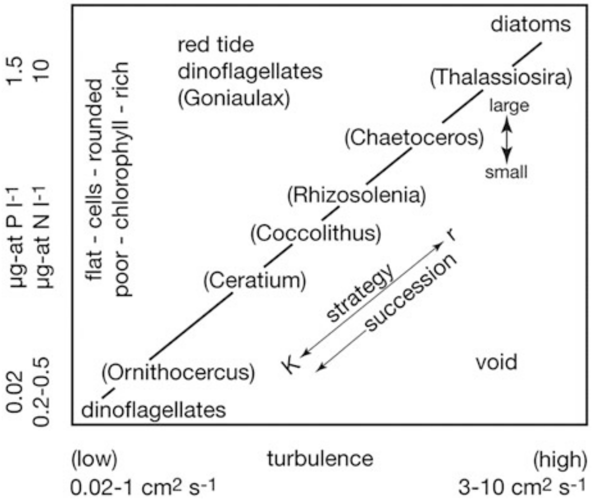

Fig. 1 The original mandala of Margalef, R. (1978) "Life-forms of phytoplankton as survival alternatives in an unstable environment." Oceanologica Acta, 1493–509

vegetation—driven by competition for resources and resource space (bottom-up)—could thus not be applied to phytoplankton. In particular, predators, pathogens, and parasites represent the 3 "Ps" of Smetacek: top-down drivers of phytoplankton evolution, composing the "mortality environment" (Smetacek 2012). Is this reflected in the fact that diatom species dominating blooms experience less grazing mortality than do co-occurring diatom species (Assmy et al. 2007; Strom et al. 2007)?

Despite the strong biotic and abiotic selective pressures that seem to weigh on diatom biogeography and evolution, they are considered as successful r-selected species (Armbrust 2009). r-selection is an evolutionary strategy in which species can quickly produce many offspring in unstable environments, at the expense of individual "parental investment" and low probability of surviving to adulthood, such as rats. This is opposed to K-selection, in which species produce fewer descendants with increased parental investment such as elephants or whales (Pianka 1970). The r-K gradient of microalgae evolutionary strategies can be situated in Margalef's mandala, an insightful road map providing the variations of phytoplankton composition in time and space, and the causes of these variations (Fig. 1). Margalef's mandala maps phytoplankton species into a phase-like diagram defined by turbulence and nutrient concentrations that divide the space into four domains (Margalef 1997; Wyatt 2014). Diatoms thrive in high-nutrient and high-turbulence environments, in the top right corner of the mandala, such as upwelling regions, at the expense of the other major phytoplankton groups, for instance, dinoflagellates and haptophytes. However, Margalef's mandala only incorporates bottom-up governing rules related to nutrient acquisition and mixing regimes, largely overlooking top-down factors.

How diatom species interact is critical for life in the ocean. They support the microbial community by releasing copious amounts of photosynthesis-derived polysaccharides as well as small molecules and can extend their own ecological niches thanks to symbiosis with nitrogen-fixing bacteria (Foster and Zehr 2006). They are then grazed upon by eukaryotic microzooplankton, transferring carbon to higher trophic levels, which makes them the foundation of the marine food web. The discovery of viruses has challenged this view, suggesting that upon viral lysis, a large proportion of algal biomass can be redirected to heterotrophic prokaryotes and the deep sea, thereby shunting carbon away from zooplankton, and potentially remodeling our understanding of the fate of carbon in the ocean (Yamada et al. 2018).

Diatoms are an extremely good case study for biotic interactions. They are pivotal in marine microbial communities and are known to interact with numerous other organisms in the plankton. These interactions can have a big impact and provide insights about why diatoms can thrive in oligotrophic waters, how they can outcompete other organisms in eutrophic conditions, and ultimately how these interactions shape planktonic communities. The goal of this chapter is to provide the reader with an integrated view of known diatom biotic interactions, across all domains of life. Excitingly, recent advances suggest that the reservoir of diatom interactions to be discovered is immense, as is their potential to transform our understanding of ecosystem functioning and eukaryotic cell evolution.

1.2 Studying Biotic Interactions

There are many ways to describe biotic interactions—by their type (antagonistic or mutualistic), their strength (weak or strong), their specialization (specialists or generalists)—though it is, in practice, difficult to make microbial interactions fit in one box as many of them are still not mechanistically understood and change depending on circumstances. The words interaction and association are used interchangeably in the chapter and can be primarily classified in two distinct groups: mutualism and antagonism (Fig. 2).

Mutualism involves the exchange of goods and services among two species, which become mutualistic partners. Each partner receives a benefit from the interaction, but this generally has a cost. The benefit is not always equal, and, in any case, species do not behave altruistically. Instead, the benefit is considered as an unintended consequence of the interaction, by which species pursue their own selfish interest (Bronstein 1994). Mutualism can break apart due to changes in circumstances, or develop into mandatory ones (detailed below). Emblematic examples in the terrestrial realm are represented by flowering plants and animal pollinators, or acacia trees and the ants that live in them and protect them in return, or between plants and fungal species that form mycorrhizae.

Antagonism, on the other hand, is an association in which one organism gains benefit at the expense of the other. In predation, one bigger organism often captures biomass from a smaller one and kills it. In parasitism, the smaller parasite will acquire food and shelter from a bigger host but will not kill it, contrary to parasitoids that kill their host. For instance, the *Lithognathus* fish is parasitized by the *Cymothoa exigua* crustacean, which replaces the fish's tongue to feed on its blood and mucus,

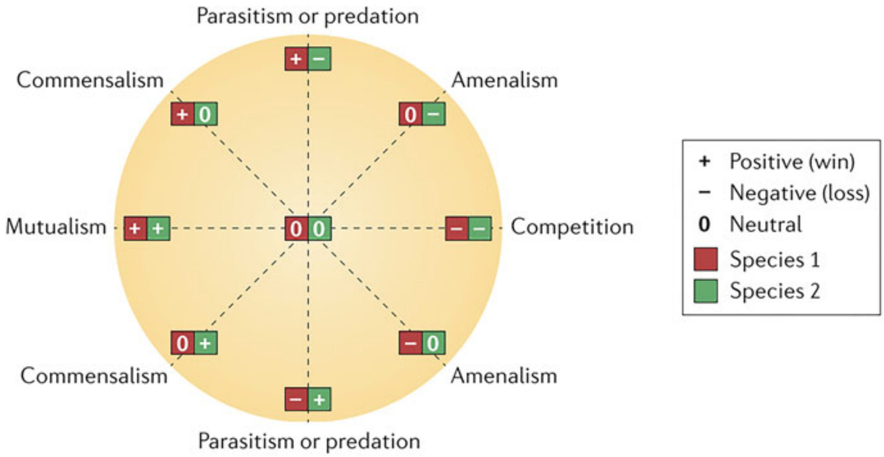

Fig. 2 Summary of ecological interactions between different species. The wheel display by Lidicker has been adapted to summarize all possible pairwise interactions. For each interaction partner, there are three possible outcomes: positive (+), negative (−), and neutral (0). For instance, in parasitism, the parasite benefits from the relationship (+), whereas the host is harmed (−); this relationship is thus represented by the symbol pair +−. In some cases, one of the species has neutral feedback, while the other one benefits (commensalism) or is harmed (amensalism) by this association (figure from Faust et al. 2012)

without apparent damage to the host (Brusca et al. 1983). Hosts and parasites coevolve, shaping the evolutionary arms race, in which the short generation time of the parasite generally provides quicker adaptation relative to the host (Dunne et al. 2013).

Interspecies interactions can be hard to observe *in situ*, especially in communities of microorganisms, and much of our understanding today comes from terrestrial environments, primarily through studies of plant–parasites, plant–pollinator, or macroorganism predation (Bascompte and Stouffer 2009). Each of these forms can be further (nonexhaustively) characterized by:

- The degree of dependence: Is the interaction obligate or facultative? If obligate, species totally rely on one another for goods and services, such as obligate parasites that depend on their host to complete their life cycle. If facultative, one of the partners can be replaced by another species without affecting the benefit for the other partner(s) (Wootton and Emmerson 2005) or the interaction can completely breakdown with both partners able to survive.
- The degree of specificity: Is the interaction between pairs of species (specialists), or pairs of groups (generalists)? Specific mutualism between two species is rare (e.g., fig plants and fig wasps), whereas generalist interactions are more common, e.g., whereby honey bees are known to visit the flowers of multiple plant species. Such phenomena lead to highly interconnected networks of plant–pollinator interactions (Vázquez and Aizen 2004).

- The degree of physical associations: Are the partners physically close when they interact? They are defined as exhabitational when species such as pollinators live separately from the plants they interact with or ectoparasites that live on the skin of their host. But they are defined as being inhabitational if the partners live with one another (Dick 1999).

Diatom interactions are cumbersome to study. They are difficult to observe in the natural environment and hard to establish in the laboratory. When detected in the environment, their study *in situ* is often limited to descriptive assays and bulk analysis of extremely complex communities. When model systems are established such as cocultures, they significantly advance molecular and mechanistic understanding, but adopt a reductionist approach, creating artificial conditions that are hardly seen in the natural context. Single-cell technologies and more advanced cell biology high-throughput techniques, that are increasingly being used both in the laboratory and in the field, have the potential to connect mechanistic and holistic approaches by providing the means to link individual microbes with population dynamics. Despite the aforementioned difficulties, the body of known diatom biotic interactions is dense, revealing the complex network of marine microbial associations, but also the current limits of our knowledge.

1.3 Diversity of Known Interactions

To date (September 2020), the most comprehensive inventory of confirmed diatom biotic interactions reports a total of 1533 associations from over 500 papers involving 83 genera of diatoms and 588 genera of other partners, illustrating a diversity of association types, such as predation, symbiosis, allelopathy, parasitism, and epibiosis, as well as a diversity of partners involved in the associations, including both prokaryotes and eukaryotes, micro- and macroorganisms (Vincent and Bowler 2020). It revealed that most validated interactions are predatory (58%), involving freshwater diatoms, and that overall our knowledge produces a highly centralized network containing a few diatoms mainly subject to grazing or epiphytic on macroorganisms, overlooking bacterial and viral interactions (Fig. 3). Yet, zooming on emblematic examples within each interaction type enables us to better appreciate the central role of biotic interactions in shaping diatom biogeography and evolution.

1.4 Antagonistic Interactions

1.4.1 Predation

Diatoms are often referred to as the "pastures of the sea" (Smetacek 2001). Indeed, out of the myriad of mechanisms that can induce phytoplankton mortality or remove phytoplankton biomass, such as viral lysis or sinking, predation is considered quantitatively dominant (Calbet and Landry 2004), maintaining ratios of primary

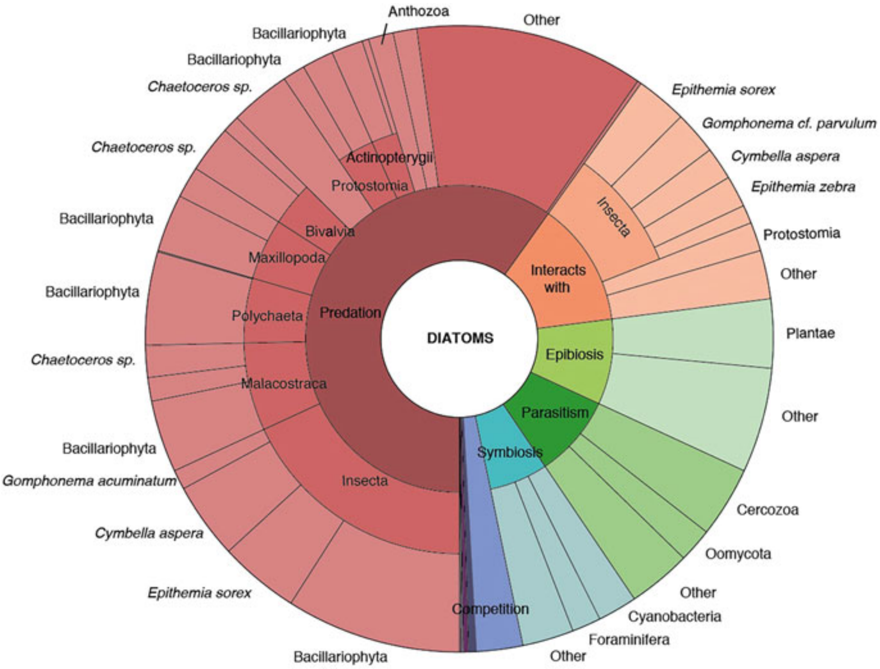

Fig. 3 Current knowledge of diatom biotic interactions based on literature surveys. KRONA plot based on available literature concerning diatom associations mined and manually curated from Web of Science, PubMed, and Globi and made available online (https://doi.org/10.5281/zenodo.2619533). The outer circle represents the diatom genera (when known), the middle circle represents the interacting partner, and the inner circle represents the type of interaction (predation, parasitism, symbiosis, etc.). Adapted from (Vincent and Bowler 2020)

producers to herbivores very low, and is therefore a structuring factor in the plankton (Sherr and Sherr 2009). Unlike parasites that also feed on diatoms, it is generally assumed that predators feed on several species (not one), tend to be bigger than their prey, and tend to kill them (Lafferty and Kuris 2002).

Metazoan predators such as copepods (crustaceans) presumably exercise strong pressure on diatoms by feeding on them (Lebour 1922; Campbell 2009). The classic pelagic food web involves a trophic linkage between diatom blooms, copepod production, and fish (Runge 1988). Numerous feeding experiments have investigated the coevolution between copepods and diatoms. Some evolutionary adaptations are mechanical: copepods modify their feeding tools (Itoh 1970; Michels et al. 2012), in response to which diatoms adjust their protecting frustules, leading to an arms race that fuels evolutionary processes (Hamm and Smetacek 2007). Some diatoms that dominate blooms experience less grazing mortality than do co-occurring species (Assmy et al. 2007; Strom et al. 2007). It was shown that in the presence of preconditioned media that contained herbivores, diatoms develop grazing resistant morphologies such as increased cell wall silicification (Hamm et al.

2003; Pondaven et al. 2007). Hence, the cell wall provides not only a "constitutive mechanical protection" for the cell but also a plastic trait that responds to grazing pressure.

Allelopathy has also been observed in response to copepod grazing. Allelopathy at large is a biochemically mediated interaction in which one organism can influence growth, survival, and reproduction of another organism. The effects can be either beneficial (positive allelopathy) or detrimental (negative allelopathy). These chemical signals can influence species interactions in the plankton, which is well illustrated in phytoplankton (Legrand et al. 2003), and particularly in diatoms. Copepods graze on diatoms, and there has been much debate about whether or not diatoms are a good food source for copepods, in what is known as the "Diatom-Copepod Paradox" (Harvey 1935). In the early 1990s, it was discovered that diatom-derived compounds (simple aldehydes) could decrease copepod egg hatching success from the usual 90% to 12% (Miralto et al. 1999), challenging the classical view of marine food webs wherein energy flows from diatoms to fish by means of copepods (along with the discovery of high grazing rates by dinoflagellates). Further studies discovered a myriad of polyunsaturated aldehydes named "PUAs" in the diatoms *Thalassiosira rotula* and *Skeletonema costatum*, which are released within seconds after mechanical crushing of the diatoms, up to 5 fmol of PUA per cell within 2 min (Pohnert 2000). The production of defensive chemicals and allelopathic molecules targeted toward predators is thought to contribute to diatom success, although still debated. Other adaptations are physiological: the existence of a mismatch between temperature optima for growth of diatoms relative to growth of potential predators is a strategy to escape predation pressure (Rose and Caron 2007). For instance, the maximal growth rates of herbivorous protists decline more rapidly with decreasing temperature than that of phototrophic protists, especially at the very low temperatures that are characteristic to high-latitude ecosystems where diatoms bloom.

The classic food web view was challenged in the early 1990s (Kleppel et al. 1991). It was suggested that copepods rather feed preferentially on microplankton such as ciliates and dinoflagellates, supported by evidence that diatoms were nutritionally insufficient for copepod growth. Additional arguments favor low copepod grazing pressure during blooms: the inability of copepods to track diatoms over winter and the existence of grazing from heterotrophic dinoflagellates. The latter led to the concept of "loophole" (Irigoien 2005), suggesting that blooming species are those able to escape microzooplankton thanks to predation avoidance mechanisms (larger size, spines, toxic compounds) at the onset of the bloom. Followed by top-down grazing of mesozooplankton on microzooplankton, blooming conditions basically disrupt the predator–prey control, opening a "loophole" in which diatom species can thrive.

Heterotrophic dinoflagellates are unicellular phagotrophic microplankton measuring between 20 and 100 microns, and are probably the highest consumers of bloom-forming diatoms, more than copepods and other mesozooplankton (Jacobson and Anderson 1986; Calbet and Landry 2004; Sherr and Sherr 2007). They can comprise more than 50% of microzooplankton biomass in diatom blooms, represented by thecate (armored, like *Protoperidinium spp.*) and athecate (*Gymnodinium spp.*) dinoflagellates. They exert a constant predation pressure on diatoms, by rapidly increasing their abundance through asexual reproduction when prey abundance increases—but also by their capacity to grow on diverse prey, therefore surviving in nonbloom conditions to better proliferate when diatoms bloom (Strom 2008). Attempts to compare the dinoflagellate and copepod pressures on diatom communities have been done in South Korean coastal waters. Dinoflagellates (*Protoperidinium bipes*) consumed 0.1% to 3.4% of diatom biomass per hour, whereas copepods (*Acartia spp.*) removed less than 0.2% of diatom biomass per hour, rather focusing on herbivore ingestion and relieving diatoms from grazing pressure (Jeong et al. 2004). Experimental simulation of trophic interactions among omnivorous copepods, heterotrophic dinoflagellates, and diatoms also suggests that dinoflagellates play a central role in the lower trophic levels of marine food webs by consuming diatoms and then serving as a quality food source for copepods (Chen and Liu 2011).

1.4.2 Parasitism

Parasitism is described as a common consumer strategy, whereby parasites generally feed on only one prey, are smaller than their host, and do not usually kill the host, unlike parasitoids (Lafferty and Kuris 2002). Parasitic epidemics frequently follow diatom blooms in lakes worldwide, sometimes affecting over 90% of the population.

Zoosporic parasites. In the marine ecosystem, the ecological role of parasites infecting diatoms is poorly understood. Knowledge about marine diatom zoosporic pathogens is summarized in Scholz et al. (2016), suggesting that marine diatom diseases may have significant impacts on the ecology of individual diatom hosts, but also at the level of the community. Zoosporic parasites are facultative or obligate and produce spores as they infect the host. Known diatom parasites involve chytrids, aphelids (*Pseudaphelidium drebesii* parasite of *Thalassiosira punctigera*), stramenopiles—including oomycetes, labyrinthuloids, and hyphochytrids—(*Ectrogella perforans* parasite of *Licmophora hyalina*), parasitic dinoflagellates (*Paulsenella vonstoschii* parasite of *Streptotheca tamesis* diatom), cercozoans (*Cryothecomonas aestivalis* parasite of *Guinardia delicatula*), and phytomyxids (*Phagomyxa bellerocheae* parasite of *Bellerochea malleus*). Scholz et al. conclude that diatom zoosporic parasites are much more abundant in the marine ecosystem than what the available literature reports.

Gsell reported an interesting case of diatom–parasitic interaction in 2013 (Gsell et al. 2013). The study investigated the susceptibility to infection of seven different genotypes of the spring bloom freshwater diatom *Asterionella formosa* by a single genotype of the chytrid parasite *Zyghorhizidium planktonicum* across five environmentally relevant temperatures. The results suggested that the thermal tolerance range of the parasite genotype was narrower than that of its host, providing the diatom with a “cold” and “hot” thermal refuge in which it was not infected by the parasite. The reaction to parasitism was host-genotype specific and varied with temperature so much so that no host genotype would outcompete the others across all temperature ranges. The authors inferred that thermal variation plays a role in the maintenance of diatom diversity in disease-related traits. This also highlights the importance of environmental factors in the establishment—or not—of an interaction. Host parasite specificity and environmental factors such as temperature can impact diatom diversity, survival, and, consequently, their role in community structure. Other environmental parameters such as nutrient availability can trigger diatom interactions whereby organisms compete for similar resources.

1.4.3 Competition for Resource

The diversity of planktonic organisms in a given environment has puzzled scientists for a long time, raising the question of how so many different plankton species could stably coexist in a given environment, especially when they are occupying the same niche and in need of the same resource, a mystery also known as the "paradox of the plankton" (Hutchinson 1959). Some—like Hardin—state that species do not cohabit but rather adhere to the "Competitive exclusion principle" according to which two species competing for the same resource cannot stably live together, as long as other ecological factors remain constant (Hardin 1960).

Intra-Taxa Competition Diatoms could compete with other diatoms for nutrient resources; however, examples suggest that they avoid so by utilizing different types of resources. A metatranscriptomic study performed on the East Coast of the USA revealed that similar marine diatom species, *Skeletonema spp.* and *Thalassiosira rotula*, utilize resources differently, thereby enabling their coexistence in the same parcel of water, despite similar requirements in nitrogen and phosphorus. The former favored uptake of inorganic nitrogen sources (nitrate and nitrite), while the latter favored the utilization of nitrogen from organic sources, such as amino acids (Alexander et al. 2015a, b). Competition among diatoms can also result from the coupling of nutrient limitation, such as silica-limited environments, and physical factors such as temperature. Different diatom species grow unequally with respect to these covarying factors, suggesting a specific niche adaptation, as was also shown in freshwater diatoms (Shatwell et al. 2013).

Inter-Taxa Competition Biogeochemically and ecologically, diatoms are believed to be the most important silicifiers in modern marine ecosystems, with radiolarians (polycystine and phaeodarian rhizarians), silicoflagellates (dictyochophyte and chrysophyte stramenopiles), and sponges with prominent roles as well. The diatom expansion 65 million years ago has been attributed to their superior competitive ability for silicic acid uptake relative to radiolarians, with the latter experiencing a reduction in weight of their minute skeletons, called tests (Harper and Knoll 1975). However, as the size reduction of radiolarian tests was insufficient to explain diatom expansion, strong long-term erosion of continental silicates has been proposed as a significant cofactor of diatom growth (Cermeño et al. 2015). Analysis of the distribution of silicifiers in the contemporary ocean at large spatial scale using the *Tara* Oceans expedition dataset can bring additional insights about the evolution of competition between different groups (Fig. 4). Functional annotation of the silicifying organisms followed by mapping of their distribution across the global

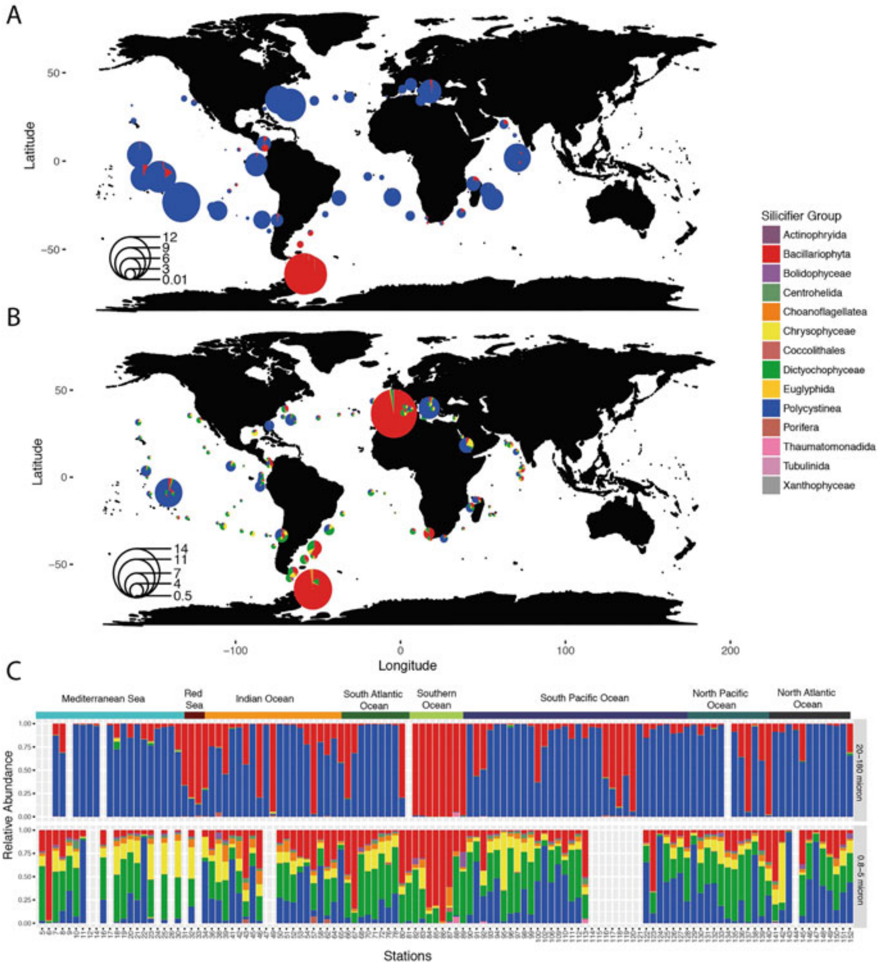

Fig. 4 Distribution of silicifiers in the sunlit ocean based on metabarcoding abundance data from the *Tara* Oceans expedition. A. Silicifiers in surface waters of the 20–180 micron size fraction—divide radius by 20 for log-transformed relative abundance. B. Silicifiers in surface waters of the 0.8–5 micron size fraction—divide radius by 30 for log-transformed relative abundance. The size of the bubble corresponds to the importance of silicifiers with respect to the whole planktonic community. C. Composition of the silicifiers' community in surface waters at each sampling station. From (Hendry et al. 2018)

ocean reveals major patterns. In larger size fractions of microplankton (20–180 microns), diversity within the silicifiers is composed essentially of *Bacillariophyta* and *Polycystinea*, so much so that both taxonomic groups represent over 99% of the microplanktonic silicifier community across the vast majority of the global ocean. Diatoms and polycystines occur in highly variable proportions, where diatoms dominate the cold high-latitude regions. Coexistence between both groups is rare, whereby the presence of one of the organisms appears to exclude the other, which may also reflect special adaptations to nutritional environments such as eutrophic, oligotrophic, or high-nutrient, low-chlorophyll areas (HNLC). Diatom-induced reduction of silicic acid availability coupled with grazing pressure may have further affected trends in silicoflagellate morphology in two ways: either to maintain a certain degree of silicification but to become smaller, or to lower silicon requirements and develop spines as a mean to maintain a defensive shield (Hendry et al. 2018).

Inter-Taxa Competition Mediated by Allelopathy: The Case of Dinoflagellates The study of nearshore blooms of the dinoflagellate *Karenia brevis* proposed that allelopathic compounds were produced to inhibit growth of phytoplankton competitors, among which are diatoms (Prince 2008; Poulson 2010). However, natural offshore diatom-dominated assemblages in the Gulf of Mexico seemed resistant (*Asterionellopsis glacialis*, *Skeletonema spp*.), even displaying slight stimulation of growth, results that are more variable when brought back to the lab. The accumulation of allelopathic compounds in the water column may create an inhospitable environment for growth among competitors, although diatom responses are clearly species specific. In the lab, *Karenia brevis* caused suppression of growth of *Thalassiosira pseudonana* and *Asterionellopsis glacialis,* and the impact of the dinoflagellate on the competitors' physiology was reflected in the metabolomes and proteomes of both diatoms. Cellular protection responses such as altered cell membrane components, inhibited osmoregulation, and increased oxidative stress were also triggered (Poulson-Ellestad et al. 2014).

1.4.4 Bacterial and Viral Pathogens

Although predation, parasitism, and competition seem to be the prevalent types of antagonistic interactions, bacterial and viral pathogens of diatoms have also been observed. Largely overlooked, they are likely to be important players in the diversity of mortality agents affecting diatom survival. For details about bacterial and viral pathogens, please refer to dedicated Chapters "The Diatom Microbiome: New Perspectives for Diatom-Bacteria Symbioses" and "Diatom Viruses", respectively.

1.5 Mutualistic Interactions

Thankfully, not all diatom interactions result in death. Evolutionarily speaking, diatoms are the product of successive symbiotic events revealing intricate relationships with bacteria. Intriguing ubiquitous epiphytic and photosymbiotic associations also suggest that diatom evolution is not only constrained by mortality agents. The Red and Black Queen hypotheses, denoting opposing microbial evolution driven by competition or cooperation, respectively, collide and complexify the picture (Fig. 5).

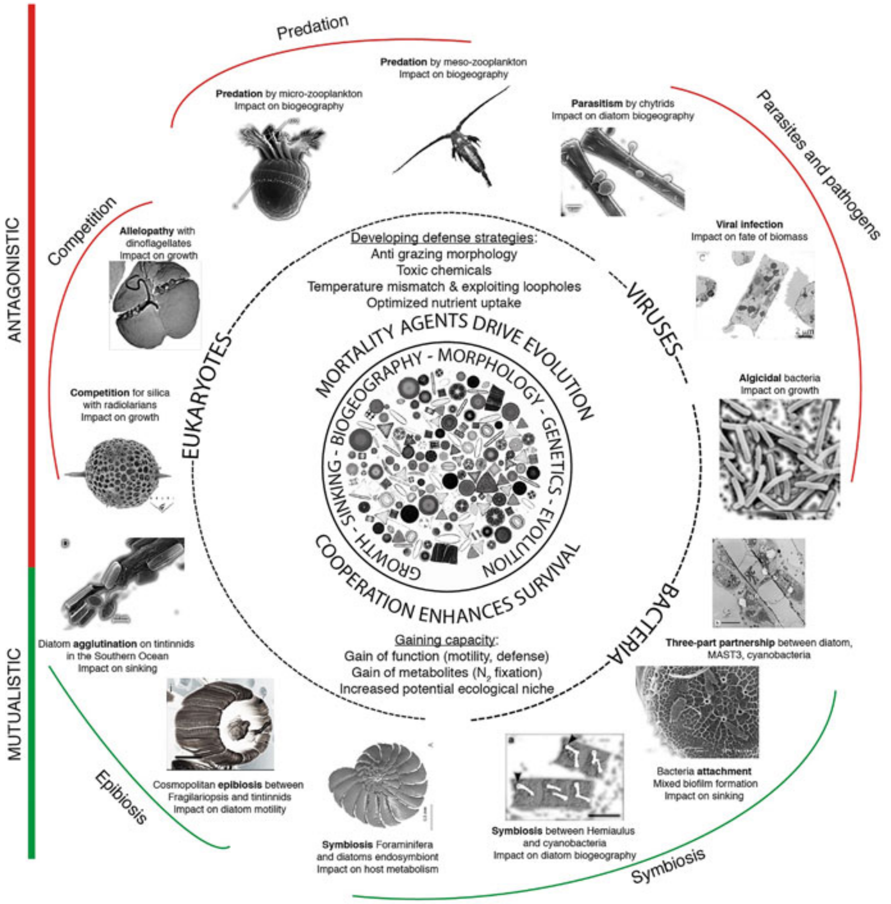

Fig. 5 Diversity of diatom interactions. Diatoms are involved in numerous interactions, both beneficial (mutualistic) and detrimental (antagonistic). Partners of interactions can be classified according to their "domain" (Eukaryotes, Bacteria, or Viruses), and interactions can be classified by their more specific definition (Symbiosis, Predation, Competition, etc.). For clarity, this is a partial view of diatom interactions, illustrating how all those biotic top-down factors can affect diatom growth, evolution, morphology, biogeography, and sinking. Credit: Diatoms By Wipeter in the center; Predation by micro-zooplankton (Modeo et al. 2003); Parasitism by chytrids (Kagami et al. 2007); Viral infection (Kimura and Tomaru 2013); Algicidal bacteria (Sohn et al. 2004); Three-part partnership (Buck and Bentham 1998); Bacteria attachment (Gärdes et al. 2011); *Hemiaulus*-cyanobacteria (Hilton et al. 2013a, b); Symbiosis with foraminifera (Briguglio et al. 2013); *Fragilariopsis doliolus* and tintinnids (Vincent et al. 2018); Diatom agglutination on tintinnids (Armbrecht et al. 2017); Competition for silica (MBARI); Allelopathy with dinoflagellates (Haywood et al. 2004)

1.5.1 Symbiosis

We restrict the meaning of symbiosis to close mutualistic relationships, whereby two species benefit from the association (Paracer and Ahmadjian 2000).

Diazotrophs A highly mutually beneficial interaction involving diatoms is known to occur with diazotrophic prokaryotes, referred to as "DDAs" (Diatom–Diazotroph Associations), such as the heterocystous cyanobacteria *Richelia intracellularis* and *Calothrix rhizosoleniae*, observed in low-nutrient oligotrophic oceans. *Richelia*, along with *Trichodesmium*, is believed to be a major prokaryotic fixer of dinitrogen gas (N_2) in the world's tropical and subtropical oceans (Carpenter and Foster 2002) recently confirmed using *Tara* Oceans data (Pierella Karlusich et al. 2021). *Richelia intracellularis* converts dinitrogen gas to ammonium and then supplies the diatom with fixed bioavailable nitrogen compounds essential for metabolism (Foster et al. 2011). In these cases, the diatom serves as a protective host as the cyanobacteria lives inside the diatom. *Richelia* lives as an endosymbiont between the cell wall and the frustule of diatoms such as *Hemiaulus*, *Rhizosolenia*, and *Bacteriastrum*, while *Calothrix* lives externally attached to *Chaetoceros* spp. (Villareal 1991), and successive efforts to molecularly identify the partners, using *nifH*, 16S rRNA, and *hetR* sequences, have revealed the phylogenetic relationships between different diazotrophs (Foster and Zehr 2006). Comparative genomics studies of two obligate and facultative symbiont strains show that the location of the symbiont (intracellular or extracellular) and its dependency on the host are linked to the evolution of the symbiont genome, especially in nitrogen metabolism, assimilation genes, and genome reduction (Hilton et al. 2013a, b). The genome of the intracellular symbiont was reduced and lacked ammonium transporters and essential nitrate/nitrate reductases, illustrating metabolic streamlining. The genome of the extracellular symbiont was similar to its free-living cyanobacteria. Other less studied symbiosis involves the chain-forming pennate diatom *Climacodium frauenfeldianum* and a unicellular cyanobacterium similar in morphology to the free-living diazotroph *Crocosphaera watsonii* (Foster et al. 2011).

Diatoms from the Rhopalodiacean family also contain an endosymbiont of cyanobacterial origin, named the "Spheroid body" that is obligate. Diatoms such as *Rhopalodia* and *Epithemia* can grow in nitrogen-poor habitats, suggesting that the endosymbiont fixes atmospheric nitrogen. The sequencing of the spheroid body genome found that it was considerably reduced compared to the genome of its close free living relatives, depleting the organism of key metabolic capacities such as photosynthesis, thus making it completely dependent on its host (Nakayama et al. 2014).

Dinotoms Monophyletic dinoflagellates known as "dinotoms" harbor intracellular diatoms, thus establishing what is known as a stable endosymbiotic association (Tomas and Cox 1973; Kite and Dodge 2004; Yamada et al. 2019). The diatom retains its nucleus, mitochondria, and endoplasmic reticulum and is separated from the dinoflagellate's cytosol by a single membrane; the diatom is present in all stages of the host cell cycle, and both host and endosymbiont divide simultaneously (Tippit and Pickett-Heaps 1976). Some studies suggest that the diatoms of dinotoms are an evolutionary intermediate stage of plastids, between kleptoplastids and genuine plastids, thus representing an attractive model to study steps of endosymbiosis.

Transcriptome analysis of two dinotoms, *Durinskia* and *Kryptoperidinium foliaceum* (Hehenberger et al. 2016), shows almost no functional reduction in the diatom nuclei and that exchange of metabolites such as photosynthates seems to structure this endosymbiosis. At least 14 different diatom species, belonging to six genera, are thought to serve as endosymbionts for 19 dinoflagellate host species.

Benthic Foraminifera Beyond dinoflagellates, four foraminifera families are known to host endosymbiotic diatoms (Leel et al. 2005). Foraminifera are important sediment builders in shallow-water coral-reef waters and thus contribute significantly to the carbon cycle (Scoffin and Tudhope 1985). As endosymbionts, diatoms do not form any frustules, making their identification cumbersome; thankfully, frustules appear once endosymbionts are cultured (Lee 1989). Surprisingly, in 2005, only six common diatom species were involved in over 75% of all the more than 3000 foraminifera hosts examined: *Nitzschia frustulum var. symbiotica, N. laevis, N. panduriformis, Fragillaria shiloi, Amphora roettgerii*, and *A. erezi* (Lee 2011). However, the list continues to grow, as *Minutocellus* has been shown to be a symbiotic species of the foraminifera *Pararotalia calcariformata* in the Mediterranean Sea (Schmidt et al. 2015). This photosymbiosis brings advantages to the host organisms that benefit from diatom photosynthates, enabling high population density as well as increased calcification rates (Lee et al. 2010).

Three-Part Partnership A rather unusual association reported in the open ocean and eastern Arabian Sea is that established between the chain-forming centric diatom *Leptocylindrus mediterraneus*, the aplastidic protist *Solenicola setigera* (from the MAST3 stramenopile lineage), and the single-celled cyanobacterium *Synechococcus sp*. Even though this is an interesting case study, the fact that the diatom is devoid of cellular content questions its mutualistic nature. The benefits for each partner remain unresolved (Buck and Bentham 1998).

2 Diatom: Ciliate Interactions, from Commensalism to Epibiosis

Tintinnids (Choreotrichida) are heterotrophic planktonic ciliates enveloped in a species-specific test composed of organic material, the lorica (Agatha et al. 2013). They represent one of the morphologically most diverse groups of planktonic protists (Bachy et al. 2013), are abundant, and are ubiquitous throughout the water column. Several extracellular associations between tintinnids and diatoms have been reported, either described as “phoretic commensalism”— wherein transport is believed to be the main benefit for diatoms—or suggested as a form of obligate epibiosis enabling predation avoidance for tintinnids, and access to nutrients for diatoms such as the association involving the radial centric diatoms *Chaetoceros* spp. and *Eutintinnus* spp. (Gómez 2007). Epibiosis (from the Greek *epi* “on top” and *bios* “life”) designates “spatially close associations between two or more living organisms belonging to the same or different species” (Harder 2008).

For example, the chain-forming pennate diatom *Fragilariopsis doliolus* was recorded with *Eutintinnus tenuis* in material collected in 10 equatorial stations between the Galapagos archipelago and the Marquesas Islands (Pavillard 1935). Small chains of *F. doliolus* were previously found associated with *Salpingella subconica* near the Prince Edward Islands in the Southern Ocean, with rates of association involving 3% to 30% of all *F. doliolus* and 35% to 83% of *S. subconica* cells encountered, as well as in the Benguela Current (Froneman et al. 1998). These authors speculate that buoyancy and protection against mesozooplankton predation are the main advantages gained by the attachment of both partners. Some of these interactions have been characterized both at large spatial scale as well as high morphogenetic resolution (Vincent et al. 2018), and behavior has been investigated using high-speed measurements (Gómez 2020). They reveal that diatoms specifically adapt their morphology to establish stable associations with tintinnids, eventually extending the ecological niche of the free-living diatom. Live flow measurements suggest that tintinnids benefit from increase in hydrodynamic drag or filtering rates, and that diatoms experience a decrease in diffusive boundary layer and enhanced antigrazing strategies.

Of another nature, *Laackmaniella* and other tintinnids were observed in the Southern Ocean with apparently empty frustules of *Fragilariopsis* and other diatoms covering their lorica, for which it has been hypothesized that the ciliates retain diatom frustules following ingestion of the cellular contents, perhaps as a means of protection through camouflage (Gowing and Garrison 1992; Wasik et al. 2000; Armbrecht et al. 2017). In this case, the association seems closer to commensalism.

3 Toward an Integrated View of Biotic Interactions

The complexity of an integrated view of diatom biotic interactions does not stop with the diversity of partners involved, or the different mechanisms developed. Additionally, these interactions cannot be considered as snapshots, but rather as dynamic processes, both spatially and temporally across multiple biological scales (Fig. 8).

3.1 Temporal Scales of Diatom Interactions

Diatoms produce a class of oxylipins known as PUAs (polyunsaturated fatty acids) in the *seconds* following the crushing of the diatom frustule induced by predation by larger grazers. In the following *hours*, the copepods will continue eating in this environment garnished with teratogenic compounds. The interaction, on the long term, will have an impact on the offspring so much so that over a few *years*, grazers should evolve to avoid eating PUA-producing diatoms. Teeling et al. (Teeling et al. 2012) investigated the bacterioplankton response to a diatom bloom in the North Sea and managed to uncover the dynamic succession of bacterial populations at the genus level. Over a few *days*, bacteria known to decompose algal-derived organic matter, such as Bacteroidetes, Gammaproteobacteria, and Alphaproteobacteria, formed distinct, successive populations controlled by algal substrate availability. Over *decades*, biotic interactions leave their imprint in the seasonal succession of plankton, an *annually* repeated process of community assembly that is the result of community interactions such as competition, predation, and parasitism in conjunction with abiotic control mechanisms that set the start and end of the growing season. The study of these dynamics, by sampling regularly at a given location, or by following a prevailing current, also known as a time series or longitudinal study, enables scientists to examine how different organisms change in relation to one another and in relation to environmental conditions (Fuhrman et al. 2015). Over *millennia*, past endosymbiontic events and other gene transfers remain traceable in the genetic information within diatom and host genomes.

3.2 Spatial Scales of Diatom Interactions

The physical contact between a copiotroph bacteria and the mucus of the diatom, the bacterial diazotroph encapsulated in its host, or what happens at the cell surface in general through defense and protection against agents of mortality happens over a few *micrometers*. Diatom interactions enter scales of *millimeters* within ephemeral microlayers, *centimeters* when copepods feed on them, and in the vertical direction, there can be significant microbial changes over hundreds of *meters*. Symbiosis with cyanobacteria can form blooms measured in *kilometers*, as was reported in the subtropical North Atlantic (Carpenter 1999), estimating that the N supply by N_2 fixation by the symbioses exceeded that of nitrate flux from below the euphotic zone, thus playing a significant role in the biogeochemistry of the surface ocean. Similarly, it was shown that DDAs drive a significant biological CO_2 pump in tropical oceans off the Amazon River plume (Yeung et al. 2012), illustrating how biotic interactions can scale up to influence biogeochemical cycling of nutrients and ecosystem-wide phenomena.

Patches of homogeneous diatom blooms, and thereby the interactions that happen among them, can be observed from scales of *kilometers* to *thousands of kilometers* at a given depth and over horizontal directions (Fig. 6).

3.3 New Approaches to Study Microbial Interactions

We therefore see that diatom interactions are diverse, spanning across multiple temporal and spatial scales, involving both macro- and microorganisms, prokaryotes and eukaryotes, and even viruses (see Chapters “The Diatom Microbiome: New Perspectives for Diatom-Bacteria Symbioses” and “Diatom Viruses”). Many of these studies rely on manipulative experiments, such as coculturing (two organisms in the same medium) and cross-culturing (cell-free filtrate from the culture of one organism added to the medium of the target) of potential competitors, feeding experiments to test specificity of prey and predators. Such studies have more recently incorporated omics approaches, single cell biology and secondary ion mass-

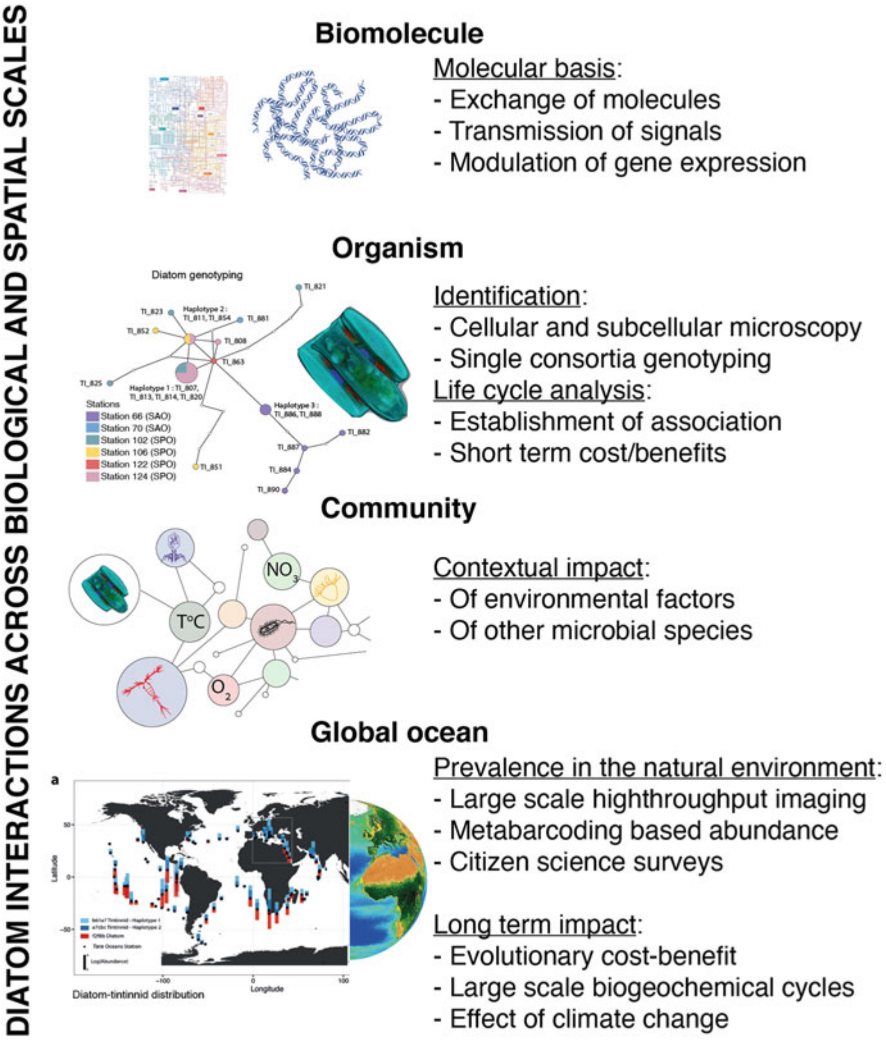

Fig. 6 Integrated study of diatom biotic interactions across biological organization and spatiotemporal scales. Adapted from (Sunagawa et al. 2020)

spectrometry. Transcriptomic data have been used to evaluate copepod responses to harmful diatoms (Carotenuto et al. 2014), DNA barcoding has been used to analyze predator gut content (Kress et al. 2015), metabolomics has helped understand allelopathy (Scognamiglio et al. 2015), and genomics has helped interpret the evolution of host-symbiont gene transfers and evolution (Vancaester et al. 2020). But microbial communities are complex, and most studies provide a reductionist view, studying one, two, or in the best of cases three organisms in isolation. The need to develop holistic approaches emerged a few years ago in marine microbiology

(Karsenti et al. 2011), and the possibility to study organisms in their natural habitats has opened the door to novel ways of looking at community structure in the microbial aquatic world.

3.3.1 *In Silico* Prediction of Microbial Interactions

Co-occurrence networks using meta-omics data have increasingly been used to study microbial communities and interactions (Faust et al. 2012; Li et al. 2016), e.g., in human and soil microbiomes (Barberán et al. 2012; Faust et al. 2012) as well as in marine and lake bacterioplankton (Fuhrman and Steele 2008; Eiler et al. 2011; Milici et al. 2016). Such networks provide an opportunity to extend community analysis toward an understanding of the relational roles played by different organisms, many of which are uncultured and uncharacterized (Proulx et al. 2005; Chaffron et al. 2010). Over large spatial scales, nonrandom patterns according to which organisms frequently or never occur in the same samples are the result of several processes such as biotic interactions, habitat filtering, historical effects as well as neutral processes (Fuhrman 2009). Quantifying the relative importance of each component is still in its infancy. However, these networks can be used to reveal niche spaces, to identify potential biotic interactions, and to guide more focused studies.

At large spatial scales using the *Tara* Oceans dataset, diatom biogeography was shown to be more constrained by biotic rather than abiotic factors (Lima-Mendez et al. 2015). Diatoms were also shown to occupy niches that were less populated with potential parasites, pathogens, and predators (Vincent and Bowler 2020), reflecting their unique ability to exclude other organisms and thrive, thus supporting Smetacek's 3 "P's" hypothesis (Fig. 7). However, only 6.5% edges of the largest diatom co-occurrence network have been confirmed independently in the literature. In many ways, this high proportion of unmatched interactions should be regarded as the "unknown" proportion of microbial diversity emerging from metabarcoding

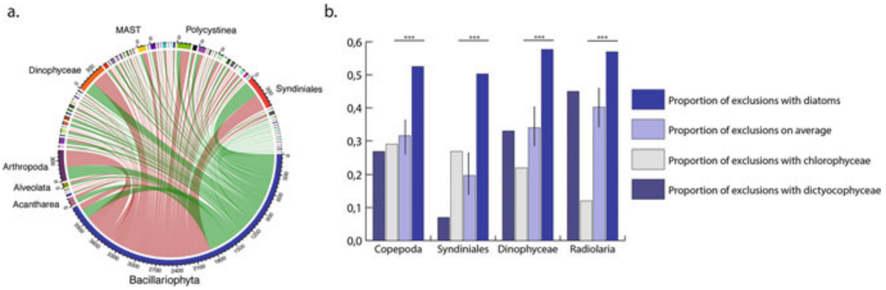

Fig. 7 Major patterns of spatial co-occurrence involving diatoms. (a) Circular representation of copresences (green bands) and exclusions (red bands) within the diatom subnetworks extracted from the *Tara* Oceans interactome (Lima-Mendez et al. 2015). The thickness of the band corresponds to the number of interactions, and major partners are labeled around the circles if they represent more than 100 associations. Data from all size fraction networks are represented here. (b) Comparison of proportions of exclusions showing that diatoms significantly exclude potential predators, parasites, and competitors such as copepods, Syndiniales, Dinophyceae, and Radiolarians, compared to control groups. From (Vincent and Bowler 2020)

surveys. Part of it is truly unknown, new, and very exciting, part of it is due to biases in data gathering and processing, and part of it is due to the lack of an extensive reference database.

Despite the difficult and sometimes misleading interpretation of co-occurrence networks, a vast body of literature already exists in the field of ecological networks, traditionally focusing on observational, noninferred data and the modeling of food webs, host–parasite, plant–pollinator networks (Ings et al. 2009; Rohr et al. 2014). Various properties linked to the architecture of these antagonistic and mutualistic networks have been formalized, such as nestedness, modularity, or the impact of combining several types of interactions in a single framework (Fontaine et al. 2011). These works could inspire the field of biotic interactions; enhanced cross-fertilization between the disciplines of ecological networks and co-occurrence networks would highly benefit both communities, ultimately helping to understand the laws governing Darwin's "tangled bank" (Darwin 1859).

3.3.2 Seeing Is Believing

After decades of omics data flooding, high-resolution environmental microscopy has caught up, to offer the same amount of information in terms of form and intracellular ultrastructure. e-HCFM—short for "environmental high content fluorescence microscopy—is a 3D-fluorescence imaging and classification tool for high-throughput analysis of microbial eukaryotes in environmental samples (Colin et al. 2017). Through high-content feature extraction, it enables accurate automated taxonomic classification and quantitative data about organism ultrastructures and interactions. Applied to environmental samples, e-HCFM has demonstrated its ability to directly detect and quantify diatom associations, involving an unknown nanoflagellate attached to the diatom *Chaeoteros simplex* (Fig. 8). However, this approach is based on dead cells, highlighting how live imaging is even more important but still remains a challenge. High-resolution time-lapse microscopy of diatom interactions has provided important insights into bacterial chemotaxis (Smriga et al. 2016) but remains restricted to the lab. Very few case studies investigate live imaging of diatom interactions in the natural environment, for this represents many technological barriers. However, these can provide undisputable evidence for the existence of ecologically relevant interactions, otherwise limited to genomic predictions, fixed dead samples subject to manipulation artifacts, or laboratory settings (Vincent et al. 2018).

3.3.3 Bringing the Lab to the Field

Beyond previous studies, the recent expansion of our knowledge about diatom diversity and biogeography (Malviya et al. 2016) offers a huge potential to discover new types of interactions in the aquatic world. On the other hand, the broader applicability of single cell or imaging technologies and genetic manipulation is a windfall for marine microbiology, to dissect biotic interactions at the cellular scale and unravel new molecular mechanisms. If laboratory studies remain mandatory to crack down molecular mechanisms involved in microbial interactions, the field of microbial interactions is dampened by limits of cultivation and genetic transformation despite major advances (Faktorová et al. 2020). One way to circumvent these

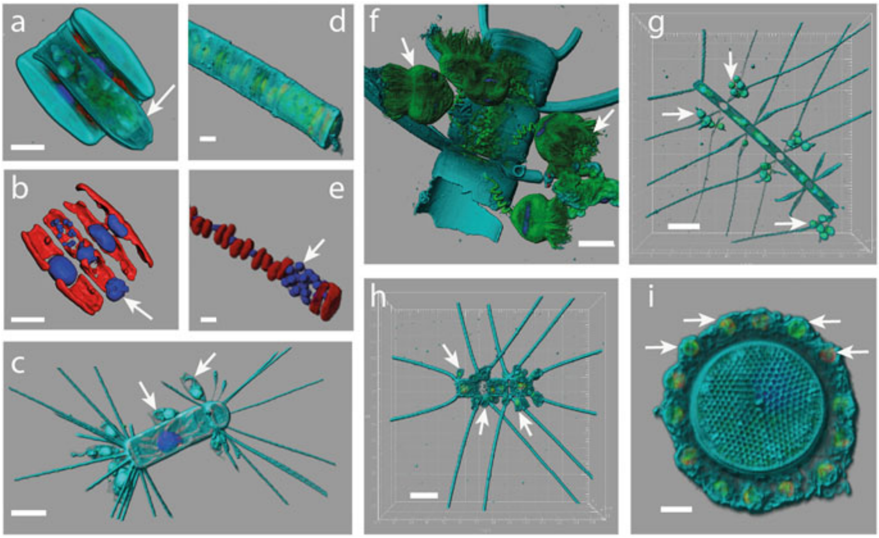

Fig. 8 Ultrastructure of diatom biotic interactions using high content fluorescent microscopy. From (Colin et al. 2017; Vincent et al. 2018). Pictures represent DNA (Hoechst, blue), chloroplasts (chlorophyll autofluorescence, red), membranes (DiOC$_6$, green), and cell surface (AlexaFluor546, cyan). Arrows point to the partner of interaction with diatoms. (a,b) *Fragilariopsis doliolus* and the tintinnid *Salpingella* sp. (c) *Corethron* sp. with nanoflagellates. (d,e) Diatom with potential parasites. (f) *Chaetoceros* sp. with *Vorticella* sp. (g) *Chaetoceros* sp. with nanoflagellates. (h) *Chaetoceros* sp. with nanoflagellates. (i) *Coscinodiscus* sp. surrounded by small cells. Scale bar a, b, f, g, h = 20 micron; c = 10 micron; d, e, i = 5 micron

current obstacles is to adapt high-end laboratory tools to real-life natural samples. This includes high-resolution live and subcellular microscopy, single-cell omics techniques, or micromanipulation of interactions *in situ*.

4 Conclusions

Diatoms have undoubtedly succeeded in adapting to the ocean's fluctuating environment, shown by recurrent, predictable, and highly diverse bloom episodes (Guillard and Kilham 1977). They are considered r-selected species with high growth rates under favorable conditions that range from nutrient-rich highly turbulent environments to stratified oligotrophic waters (Margalef 1978; Alexander et al. 2015a, b; Kemp and Villareal 2018). Their success has long been attributed to this physiological trait; yet evidence suggests that abiotic factors alone are not sufficient to explain their ecological success. The present chapter shows that diatoms are involved in diverse and abundant biotic interactions, involving all domains of life across vast scales of time and space, shedding light on the top-down forces such as mortality agents that could drive diatom evolution and adaptation in the modern ocean (Fig. 9).

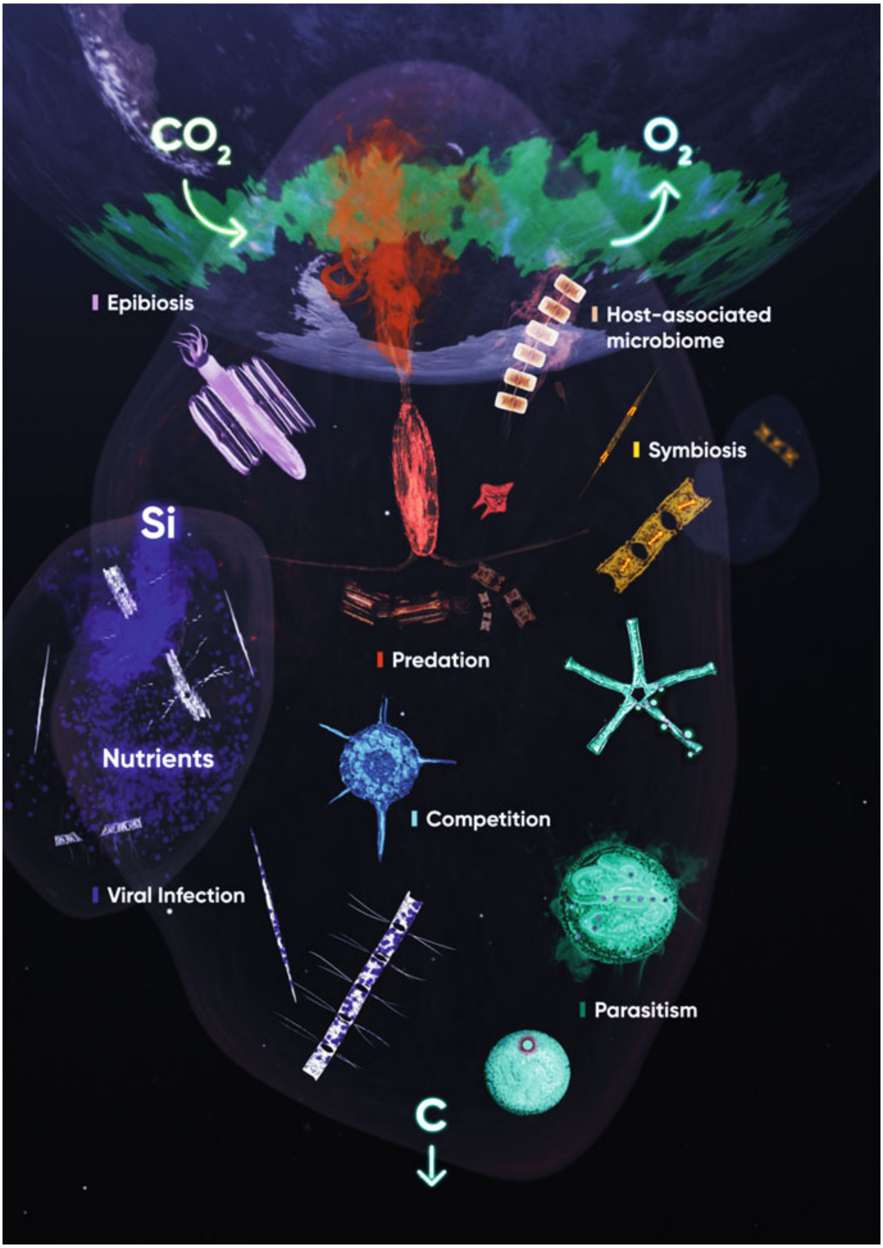

Fig. 9 An artistic view of the diversity of diatom interactions in the ocean and their link with larger scale processes. Authors: Adrien Bernheim & Flora Vincent

Excitingly, the reservoir of potential interactions involving diatoms seems to expand, as well as our capacity to study them at both mechanistic and ecosystem levels. Investigating microbial interactions involving one of the most important eukaryotic phytoplankton groups on the planet will likely shed light on novel key cellular mechanisms and provide clues about eukaryotic cell evolution.

References

Agatha S, Laval-Peuto M, Simon P (2013) The tintinnid lorica. In: Dolan J, Montagnes D, Agatha S, Coats W, Stoecker D (eds) The biology and ecology of tintinnid ciliates: models for marine plankton. West Sussex, pp 17–41

Alexander H, Jenkins B, Rynearson T, Dyhrman S (2015a) Metatranscriptome analyses indicate resource partitioning between diatoms in the field. Proc Natl Acad Sci U S A 112:E2182–E2190

Alexander H, Rouco M, Haley ST, Wilson ST, Karl DM, Dyhrman ST (2015b) Functional group-specifc traits drive phytoplankton dynamics in the oligotrophic ocean. USA. Proc Natl Acad Sci U S A 112:E5972–E5979

Armbrecht LH, Eriksen R, Leventer A, Armand LK (2017) First observations of living sea-ice diatom agglomeration to tintinnid loricae in East Antarctica. J Plankton Res 39:795–802

Armbrust EV (2009) The life of diatoms in the world's oceans. Nature 459:185–192

Assmy P, Henjes J, Klaas C, Smetacek V (2007) Mechanisms determining species dominance in a phytoplankton bloom induced by the iron fertilization experiment EisenEx in the Southern Ocean. Deep Res Part I Oceanogr Res Pap 54:340–362

Bachy C, Dolan JR, López-García P, Deschamps P, Moreira D (2013) Accuracy of protist diversity assessments: morphology compared with cloning and direct pyrosequencing of 18S rRNA genes and ITS regions using the conspicuous tintinnid ciliates as a case study. ISME J 7:244–255

Barberán A, Bates ST, Casamayor EO, Fierer N (2012) Using network analysis to explore co-occurrence patterns in soil microbial communities. ISME J 6:343–351

Bascompte J, Stouffer DB (2009) The assembly and disassembly of ecological networks. Philos Trans R Soc Lond Ser B Biol Sci 364:1781–1787

Briguglio A, Hohenegger J, Less G (2013) Paleobiological applications of three-dimensional biometry on larger benthic foraminifera: a new route of discoveries. J Foraminifer Res 43:72–87

Bronstein J (1994) Our current understanding of mutualism. Q Rev Biol 69:31–51

Brusca R, Richard C, Gilligan M (1983) Tongue replacement in a marine fish (Lutjanus guttatus) by a parasitic isopod (Crustacea: isopoda). Copeia 3:813–816

Buck KR, Bentham WN (1998) A novel symbiosis between a cyanobacterium, Synechococcus sp., an aplastidic protist, Solenicola setigera, and a diatom, Leptocylindrus mediterraneus, in the open ocean. Mar Biol 132:349–355

Calbet A, Landry M (2004) Phytoplankton growth, microzooplankton grazing, and carbon cycling in marine systems. Limnol Oceanogr 49:51–57

Campbell R (2009) Mesozooplankton prey preference and grazing impact in the Western Arctic Ocean. Deep Sea Res Part II Top Stud Oceanogr 56:1274–1289

Carotenuto Y, Dattolo E, Lauritano C, Pisano F, Sanges R, Miralto A et al (2014) Insights into the transcriptome of the marine copepod Calanus helgolandicus feeding on the oxylipin-producing diatom Skeletonema marinoi. Harmful Algae 31:153–162

Carpenter E (1999) Extensive bloom of a N_2-fixing diatom/cyanobacterial association in the tropical Atlantic Ocean. Mar Ecol Prog Ser 85:273–283

Carpenter E Foster R (2002) Marine cyanobacterial symbioses. Cyanobacteria in symbiosis., Netherlands, S. (ed)

Cermeño P, Falkowski PG, Romero OE, Schaller MF, Vallina SM (2015) Continental erosion and the Cenozoic rise of marine diatoms. Proc Natl Acad Sci 112:4239–4244

Chaffron S, Rehrauer H, Pernthaler J, von Mering C (2010) A global network of coexisting microbes from environmental and whole-genome sequence data. Genome Res 20:947–959

Chen M, Liu H (2011) Experimental simulation of trophic interactions among omnivorous copepods, heterotrophic dinoflagellates and diatoms. J Exp Mar Bio Ecol 403:65–74

Colin, S., Coelho, L.P., Sunagawa, S., Bowler, C., Karsenti, E., Bork, P., et al. (2017) Quantitative 3D-imaging for cell-biology and ecology of environmental microbial eukaryotes. elife in press: 1–15

Darwin, C. (1859) On the origin of species

Dick W (1999) Agroecology: ecological processes in sustainable agriculture. J Environ Qual 28: 354

Dunne JA, Lafferty KD, Dobson AP, Hechinger RF, Kuris AM, Martinez ND et al (2013) Parasites affect food web structure primarily through increased diversity and complexity. PLoS Biol 11: e1001579

Eiler A, Heinrich F, Bertilsson S (2011) Coherent dynamics and association networks among Lake Bacterioplankton taxa. ISME J 6:330–342

Faktorová D, Nisbet RER, Fernández Robledo JA, Casacuberta E, Sudek L, Allen AE et al (2020) Genetic tool development in marine protists: emerging model organisms for experimental cell biology. Nat Methods 17:481–494

Faust K, Sathirapongsasuti JF, Izard J, Segata N, Gevers D, Raes J, Huttenhower C (2012) Microbial co-occurrence relationships in the human microbiome. PLoS Comput Biol 8: e1002606

Fontaine C, Guimarães PR, Kéfi S, Loeuille N, Memmott J, van der Putten WH et al (2011) The ecological and evolutionary implications of merging different types of networks. Ecol Lett 14: 1170–1181

Foster RA, Kuypers MMM, Vagner T, Paerl RW, Musat N, Zehr JP (2011) Nitrogen fixation and transfer in open ocean diatom-cyanobacterial symbioses. ISME J 5:1484–1493

Foster RA, Zehr JP (2006) Characterization of diatom–cyanobacteria symbioses on the basis of nifH , hetR and 16S rRNA sequences. Environ Microbiol 8:1913–1925

Froneman P, Pakhomov E, Meaton V (1998) Observations on the association between the diatom, Fragilariopsis doliolus Wallich, and the tintinnid, Salpingella subconica Kofoid. S Afr J Sci 94: 202

Fuhrman, J. a (2009) Microbial community structure and its functional implications. Nature 459: 193–199

Fuhrman J, Steele J (2008) Community structure of marine Bacterioplankton: patterns, networks, and relationships to function. Aquat Microb Ecol:69–81

Fuhrman JA, Cram J, Needham D (2015) Marine microbial community dynamics and their ecological interpretation. Nat Rev Microbiol 13:133–146

Gärdes A, Iversen MH, Grossart HP, Passow U, Ullrich MS (2011) Diatom-associated bacteria are required for aggregation of Thalassiosira weissflogii. ISME J 5:436–445

Gómez F (2007) On the consortium of the tintinnid Eutintinnus and the diatom Chaetoceros in the Pacific Ocean. Mar Biol 151:1899–1906

Gómez F (2020) Symbioses of ciliates (Ciliophora) and diatoms (Bacillariophyceae): taxonomy and host–symbiont interactions. Oceans 1:133–155

Gowing MM, Garrison DL (1992) Abundance and feeding ecology of larger protozooplankton in the ice edge zone of the Weddell and scotia seas during the austral winter. Deep Res Part I Oceanogr Res Pap 39:893–919

Gsell AS, de Senerpont Domis LN, van Donk E, Ibelings BW (2013) Temperature alters host genotype-specific susceptibility to chytrid infection. PLoS One 8:e71737

Guillard RRL, Kilham P (1977) The biology of diatoms. Univ, California Press

Hamm C, Smetacek V (2007) Armor: why, when, and how. In: Evolution of primary producers in the sea, pp 311–332

Hamm CE, Merkel R, Springer O, Jurkojc P, Maier C, Prechtel K, Smetacek V (2003) Architecture and material properties of diatom shells provide effective mechanical protection. Nature 421: 841–843

Harder T (2008) Marine Epibiosis: concepts, ecological consequences and host Defence. In: Marine and industrial biofouling. Springer, Berlin Heidelberg, pp 219–231

Hardin G (1960) The competitive exclusion principle. Science 131:1292–1297

Harper H, Knoll A (1975) Silica, diatoms, and Cenozoic radiolarian evolution. Geology 3:175

Harvey H (1935) Plankton production and its control. J Mar Biol Assoc United Kingdom 20:407–441

Haywood AJ, Steidinger KA, Truby EW, Bergquist PR, Bergquist PL, Adamson J, MacKenzie L (2004) Comparative morphology and molecular phylogenetic analysis of three new species of the genus Karenia (Dinophyceae) from New Zealand. J Phycol 40:165–179

Hehenberger E, Burki F, Kolisko M, Keeling PJ (2016) Functional relationship between a dinoflagellate host and its diatom endosymbiont. Mol Biol Evol 33:2376–2390

Hendry KR, Marron AO, Vincent FJ, Conley DJ, Gehlen M, Ibarbalz FM et al (2018) Competition between Silicifiers and non-silicifiers in the past and present ocean and its evolutionary impacts. Front Mar Sci 5:1–21

Hilton JA, Foster RA, Tripp HJ, Carter BJ, Zehr JP, Villareal TA (2013a) Genomic deletions disrupt nitrogen metabolism pathways of a cyanobacterial diatom symbiont. Nat Commun 4:1767

Hilton JA, Foster RA, James Tripp H, Carter BJ, Zehr JP, Villareal TA (2013b) Genomic deletions disrupt nitrogen metabolism pathways of a cyanobacterial diatom symbiont. Nat Commun 4:1–7

Hutchinson G (1959) Homage to Santa Rosalia or why are there so many kinds of animals? Am Nat 93:145–159

Ings TC, Montoya JM, Bascompte J, Blüthgen N, Brown L, Dormann CF et al (2009) Ecological networks–beyond food webs. J Anim Ecol 78:253–269

Irigoien X (2005) Phytoplankton blooms: a “loophole” in microzooplankton grazing impact? J Plankton Res 27:313–321

Itoh K (1970) A consideration on feeding habits of planktonic copepods in relation to the structure of their oral parts. Bull Plankt Soc Japan 17:1–10

Jacobson DM, Anderson DM (1986) Thecate Heterophic dinoflagellates: feeding behavior and mechanisms. J Phycol 22:249–258

Jeong H, Yoo Y, Kim S, Kang N (2004) Feeding by the heterotrophic dinoflagellate Protoperidinium bipes on the diatom Skeletonema costatum. Aquat Microb Ecol 36:171–179

Kagami M, Arnout De Bruin AE, Bas AE, Ibelings W, Ellen AE, Donk V (2007) Parasitic chytrids: their effects on phytoplankton communities and food-web dynamics. Hydrobiologia:113–129

Karsenti E, Acinas SG, Bork P, Bowler C, De Vargas C, Raes J et al (2011) A holistic approach to marine eco-systems biology. PLoS Biol 9:e1001177

Kemp A, Villareal T (2018) The case of the diatoms and the muddled mandalas: time to recognize diatom adaptations to stratified waters. Prog Oceanogr 167:138–149

Kimura K, Tomaru Y (2013) Isolation and characterization of a single-stranded DNA virus infecting the marine diatom chaetoceros sp. strain SS628-11 isolated from western Japan. PLoS One 8:e82013

Kite GC, Dodge JD (2004) Structural Organization of Plastid DNA in two anomalously pigmented dinoflagellates. J Phycol 21:50–56

Kleppel G, Holliday D, Pieper R (1991) Trophic interactions between copepods and microplankton: a question about the role of diatoms. Limnol Oceanogr 36:172–178

Kress WJ, Erickson DL, Uriarte M, Garcı C (2015) DNA barcodes for ecology , evolution , and conservation. Trends Ecol Evol 30:25–35

Lafferty K, Kuris A (2002) Trophic strategies, animal diversity and body size. Trends Ecol Evol 17: 507–513

Lebour M (1922) The food of plankton organisms. J Mar Biol Assoc United Kingdom 12:644–677

Lee JJ (2011) Diatoms as endosymbionts. Springer, Dordrecht, pp 437–464

Lee JJ (1989) Identification and distribution of endosymbiotic diatoms in larger foraminifera. Micropaleontology 35:353–366

Lee JJ, Cervasco MH, Morales J, Billik M, Fine M, Levy O (2010) Symbiosis drove cellular evolution: Symbiosis fueled evolution of lineages of foraminifera (eukaryotic cells) into exceptionally complex giant protists. Symbiosis 51:13–25

Leel JJ, Correia M, Lee JJ, Correia M (2005) Endosymbiotic diatoms from previously Unsampled habitats. Symbiosis 38:251–260

Legrand C, Rengefors K, Fistarol GO, Granéli E (2003) Allelopathy in phytoplankton–biochemical, ecological and evolutionary aspects. Phycologia 42:406–419

Li C, Lim KMK, Chng KR, Nagarajan N (2016) Predicting microbial interactions through computational approaches. Methods 102:12–19

Lima-Mendez G, Faust K, Henry N, Decelle J, Colin S, Carcillo F et al (2015) Determinants of community structure in the global plankton interactome. Science 348:1262073–1262073

Malviya S, Scalco E, Audic S, Vincent F, Veluchamy A, Poulain J (2016) Insights into global diatom distribution and diversity in the world ’ s ocean. PNAS 113:1516–1525

Margalef R (1978) Life-forms of phytoplankton as survival alternatives in an unstable environment. Ocean Acta 1(1):493–509

Margalef R (1997) Turbulence and marine life. Sci Mar 61:109–123

Michels J, Vogt J, Gorb S (2012) Tools for crushing diatoms–opal teeth in copepods feature a rubber-like bearing composed of resilin. Sci Rep 2:465

Milici M, Deng ZL, Tomasch J, Decelle J, Wos-Oxley ML, Wang H et al (2016) Co-occurrence analysis of microbial taxa in the Atlantic Ocean reveals high connectivity in the free-living bacterioplankton. Front Microbiol 7:649

Miralto A, Barone G, Romano G, Poulet SA, Ianora A, Russo GL et al (1999) The insidious effect of diatoms on copepod reproduction. Nature 402:173–176

Modeo L, Petroni G, Rosati G, Montagnes DJS (2003) A multidisciplinary approach to describe Protists: Redescriptions of Novistrombidium testaceum Anigstein 1914 and Strombidium inclinatum Montagnes, Taylor, and Lynn 1990 (Ciliophora, Oligotrichia). J Eukaryot Microbiol 50:175–189

Morel F, Price N (2003) The biogeochemical cycles of trace metals in the oceans. Science 300:944–947

Nakayama T, Kamikawa R, Tanifuji G, Kashiyama Y, Ohkouchi N, Archibald JM, Inagaki Y (2014) Complete genome of a nonphotosynthetic cyanobacterium in a diatom reveals recent adaptations to an intracellular lifestyle. Proc Natl Acad Sci U S A 111:11407–11412

Paracer S, Ahmadjian V (2000) Symbiosis: an introduction to biological associations. Oxford University Press, New York

Pavillard J (1935) Péridiniens et diatomées pélagiques recueillis par Alain Gerbault entre les Iles Marquises et les Iles Galapagos. Bull Inst Océanogr Monaco 669:1–8

Pianka E (1970) On r-and K-selection. Am Nat 104:592–597

Pierella Karlusich JJ, Ibarbalz FM, Bowler C (2020) Phytoplankton in the *Tara* Ocean. Ann Rev Mar Sci 12:233–265

Pierella Karlusich JJ, Pelletier E, Lombard F, Carsique M, Dvorak E, Colin S, Picheral M, Cornejo-Castillo FM, Acinas SG, Pepperkok R, Karsenti E (2021) Global distribution patterns of marine nitrogen-fixers by imaging and molecular methods. Nat Commun 2(1):1–8

Platt T, George NW, Li Z, Shubha S, Shovonlal R (2009) The phenology of phytoplankton blooms: ecosystem indicators from remote sensing. Ecol Model 220:3057–3069

Pohnert G (2000) Wound-activated chemical defense in unicellular planktonic algae. Angew Chemie Angew Chem Int Ed 39:4352–4354

Pondaven P, Gallinari M, Chollet S, Bucciarelli E, Sarthou G, Schultes S, Jean F (2007) Grazing-induced changes in cell wall silicification in a marine diatom. Protist 158:21–28

Poulson-Ellestad KL, Jones CM, Roy J, Viant MR, Fernández FM, Kubanek J, Nunn BL (2014) Metabolomics and proteomics reveal impacts of chemically mediated competition on marine plankton. Proc Natl Acad Sci 111:9009–9014

Poulson K (2010) Allelopathic compounds of a red tide dinoflagellate have speciesspecific and context-dependent impacts on phytoplankton. Mar Ecol Prog Ser 416:69–78

Prince E (2008) Effects of harmful algal blooms on competitors: allelopathic oceanography, mechanisms of the red tide dinoflagellate Karenia brevis. Limnol Oceanogr 53:531–541

Proulx SR, Promislow DEL, Phillips PC (2005) Network thinking in ecology and evolution. Trends Ecol Evol 20:345–353

Rohr RP, Saavedra S, Bascompte J (2014) On the structural stability of mutualistic systems. Science 345:1253497–1253497

Rose J, Caron D (2007) Does low temperature constrain the growth rates of heterotrophic Protists? Evidence and implications for algal blooms in cold waters. Limnol Ocean Limnol Oceanogr 52: 886–895

Runge J (1988) Should we expect a relationship between primary production and fisheries? The role of copepod dynamics as a filter of trophic variability. Hydrobiologia 167:61–71

Schmidt C, Morard R, Almogi-Labin A, Weinmann AE, Titelboim D, Abramovich S, Kucera M (2015) Recent invasion of the symbiont-bearing foraminifera Pararotalia into the eastern Mediterranean facilitated by the ongoing warming trend. PLoS One 10:e0132917

Scholz B, Guillou L, Marano AV, Neuhauser S, Sullivan BK, Karsten U et al (2016) Zoosporic parasites infecting marine diatoms-a black box that needs to be opened. Fungal Ecol 19:59–76

Scoffin TP, Tudhope AW (1985) Sedimentary environments of the central region of the great barrier reef of Australia. Coral Reefs 4:81–93

Scognamiglio M, D'abrosca B, Esposito A, Fiorentino A (2015) Metabolomics: an unexplored tool for allelopathy studies. J Allelochem Interact J Allelochem 1:9–23

Shatwell T, Köhler J, Nicklisch A (2013) Temperature and photoperiod interactions with silicon-limited growth and competition of two diatoms. J Plankton Res 35:957–971

Sherr E, Sherr B (2009) Capacity of herbivorous Protists to control initiation and development of mass phytoplankton blooms. Aquat Microb Ecol 57:253–262

Sherr E, Sherr B (2007) Heterotrophic dinoflagellates: a significant component of microzooplankton biomass and major grazers of diatoms in the sea. Mar Ecol Prog Ser 352: 187–197

Smetacek V (2001) A watery arms race. Nature 411:745

Smetacek V (2012) Making sense of ocean biota: how evolution and biodiversity of land organisms differ from that of the plankton. J Biosci 37:589–607

Smriga S, Fernandez VI, Mitchell JG, Stocker R (2016) Chemotaxis toward phytoplankton drives organic matter partitioning among marine bacteria. Proc Natl Acad Sci 113:1576–1581

Sohn JH, Lee JH, Yi H, Chun J, Bae KS, Ahn TY, Kim SJ (2004) Kordia algicida gen. Nov., sp. nov., an algicidal bacterium isolated from red tide. Int J Syst Evol Microbiol 54:675–680

Strom S (2008) Microbial ecology of ocean biogeochemistry: a community perspective. Science 320:1043–1045

Strom SL, Macri EL, Olson MB (2007) Microzooplankton grazing in the coastal Gulf of Alaska: variations in top-down control of phytoplankton. Limnol Oceanogr 52:1480–1494

Sunagawa S, Acinas SG, Bork P, Bowler C, Acinas SG, Babin M et al (2020) Tara oceans: towards global ocean ecosystems biology. Nat Rev Microbiol 18:428–445

Teeling H, Fuchs BM, Becher D, Klockow C, Gardebrecht A, Bennke CM et al (2012) Substrate-controlled succession of marine bacterioplankton populations induced by a phytoplankton bloom. Science 336:608–611

Tippit DH, Pickett-Heaps JD (1976) Apparent amitosis in the binucleate dinoflagellate Peridinium balticum. J Cell Sci 21

Tomas RN, Cox ER (1973) Observations on the symbiosis of peridinium balticum and its intracellular alga. I. ULTRASTRUCTURE. J Phycol 9:304–323

Vancaester E, Depuydt T, Osuna-Cruz CM, Vandepoele K (2020) Comprehensive and functional analysis of horizontal gene transfer events in diatoms. Mol Biol Evol 37(11):3243–3257

Vázquez D, Aizen M (2004) Asymmetric specialization: a pervasive feature of plant–pollinator interactions. Ecology 85:1251–1257

Villareal TA (1991) Nitrogen-fixation by the cyanobacterial symbiont of the diatom genus Hemiaulus. Mar Ecol Prog Ser 76:201–204

Vincent F, Bowler C (2020) Diatoms are selective segregators in Global Ocean planktonic. Communities mSystems 5:e00444–e00419

Vincent FJ, Colin S, Romac S, Scalco E, Bittner L, Garcia Y et al (2018) The epibiotic life of the cosmopolitan diatom Fragilariopsis doliolus on heterotrophic ciliates in the open ocean. ISME J 12:1094–1108

Wasik A, Mikolajczyk E, Ligowski R (2000) Agglutinated loricae of some Baltic and Antarctic Tintinnina species (Ciliophora). J Plankton Res 18:1931–1940

Wootton J, Emmerson M (2005) Measurement of interaction strength in nature. Annu Rev Ecol Evol Syst:419–444

Wyatt T (2014) Margalef's mandala and phytoplankton bloom strategies. Deep Sea Res Part II Top Stud Oceanogr 101:32–49

Yamada N, Bolton JJ, Trobajo R, Mann DG, Dąbek P, Witkowski A et al (2019) Discovery of a kleptoplastic 'dinotom' dinoflagellate and the unique nuclear dynamics of converting kleptoplastids to permanent plastids. Sci Rep 9:1–13

Yamada Y, Tomaru Y, Fukuda H, Nagata T (2018) Aggregate formation during the viral lysis of a marine diatom. Front Mar Sci 5:167

Yeung LY, Berelson WM, Young ED, Prokopenko MG, Rollins N, Coles VJ et al (2012) Impact of diatom-diazotroph associations on carbon export in the Amazon River plume. Geophys Res Lett 39:L18609