



The Diatom Microbiome: New Perspectives for Diatom-Bacteria Symbioses

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Abstract

Since their relatively recent evolution, diatoms have come to dominate today's oceans, playing a critical role in major biogeochemical cycles, including carbon and silicon, and supporting coastal and polar food webs. A key factor underpinning diatom ecological success is their secretion of dissolved organic matter (DOM) that attracts a variety of heterotrophic bacteria in aquatic environments; in turn, these heterotrophs supply diatoms with nutrients and cofactors essential for their survival in different environmental regimes. These symbiotic exchanges occur in the diffusive boundary layer surrounding phytoplankton cells, including diatoms, known as the phycosphere. Research efforts over the past few decades have explored the nature and range of associations between diatoms and bacteria and illuminated the profound influence they can have on diatom physiology and ecology. Recent advances in genomics, microscopy, mass spectrometry, microbial cultivation, and microfluidic devices have revolutionized the study of diatom-bacteria symbiosis and promise to provide an unprecedented view of the importance of this microbial symbiosis to the oceanic ecosystem. In this chapter, we discuss DOM, alongside other nutrients, as major drivers of diatom-bacteria symbiosis, and outline new concepts in interkingdom signaling, exploring their role in diatom microbiome assembly and maintenance. We synthesize the current knowledge in light of new discoveries and highlight novel

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directions to further expand our understanding of diatoms and their success in the modern ocean living alongside bacteria.

1 Introduction

Despite their relatively recent evolution around 250 million years ago, diatoms represent a major lineage of eukaryotic phytoplankton with an estimated 200,000 species in today's oceans (Armbrust 2009; Kooistra et al. 2007). Their interactions with other microbes, particularly bacteria, have major influences on the oceanic ecosystem and beyond. This knowledge has been realized through many discoveries that cumulatively enhanced our understanding of interactions between diatoms and other microbes. More than a hundred years after the first illustrations of diatoms were published in the *Philosophical Transactions of the Royal Society in 1703*, thousands of diatom species were classified and extensively described by German botanist F.T. Kützing in a dedicated monograph in 1844 (Fig. 1). Approximately 50 years later, the first mono-algal diatom cultures were grown in the laboratory, and by then, the term “symbiosis” was coined by German mycologist De Bary to describe the phenomenon of different organisms living together. The first hint towards diatom-bacteria symbiotic interactions appeared in the early 1900s, and by the 1930s, the nature of interactions between diatoms and microbes was defined by the realization that surrounding bacteria were assimilating exudates released by living diatoms. The first positive and negative associations between diatoms and bacteria, represented by growth augmentation and algicidal effects, respectively, were reported in the early

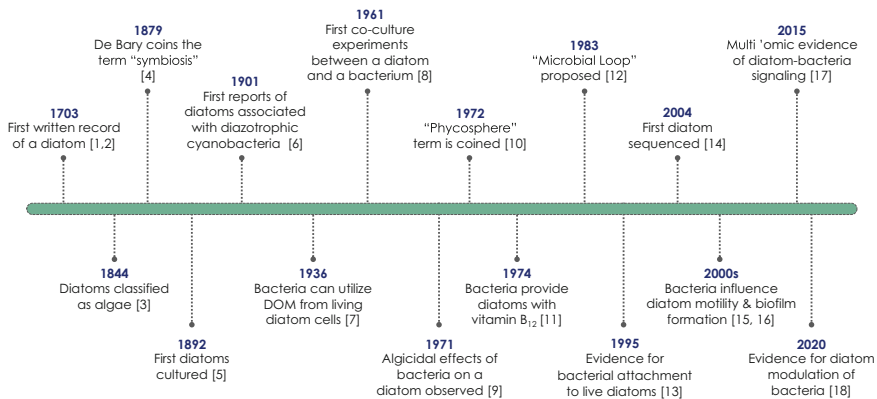


Fig. 1 A historical view of diatom–bacteria interactions. A schematic timeline illustrating major milestones in our understanding of diatoms and their interactions with bacteria. [1] Anonymous (1703); [2] Dolan (2019); [3] (Kützing 1844); [4] De Bary (1879); [5] Miquel (1892); [6] Ostenfeld and Schmidt (1901) [7] Waksman and Renn (1936); [8] Moskovits (1961); [9] Mitchell (1971); [10] Bell and Mitchell (1972); [11] Haines and Guillard (1974); [12] Azam et al. (1983); [13] Smith et al. (1995); [14] Armbrust et al. (2004); [15] Wigglesworth-Cooksey and Cooksey (2005); [16] Bruckner et al. (2008); [17] Amin et al. (2015); [18] Shibl et al. (2020)

1960s and 1970s. Evidence that diatoms and bacteria establish direct contact by attachment was reported in 1995, followed by findings in the early 2000s that proposed a strong influence of associated bacteria on the lifestyle of diatom species, in terms of motility and biofilm formation. The rise of genomics further revolutionized this field when in 2004 and 2008 the first two diatom genomes were publicly available. In the past decade, research on diatom-bacteria model systems, propelled by advances in the field of ‘omics, highlighted the exchange of metabolites and infochemicals that play important roles in this symbiosis. These milestones, and others highlighted in Fig. 1, paved the way for the field of diatom-bacteria symbiosis to flourish and opened new perspectives for how these associations influence today’s oceans.

2 Diatom DOM

After the “Microbial Loop” was first proposed in 1983 (Fig. 1; Box 1), diatoms were estimated to contribute ~20% of all primary productivity and generate a significant proportion of dissolved organic matter (DOM, Box 1) in aquatic environments (Nelson et al. 1995), sustaining heterotrophic microbial biomass and coastal marine food webs (Azam and Malfatti 2007; Buchan et al. 2014). Diatoms also secrete molecules that aggregate to form particulate organic matter (POM, Box 1), which serves as an anchor as well as a growth substrate for bacteria (discussed below).

A significant proportion of DOM generated by diatoms is released extracellularly. Although measurements of DOM release by diatom cells are highly variable, they typically range between ~2–40% of the cell’s total primary production, also known as percentage extracellular release (PER) (Thornton 2014). Mechanisms of release vary from cell leakage or passive diffusion across cell membranes, active transport/efflux, or via cell lysis and “sloppy feeding” by grazers. Diffusion across cell membranes is a common phenomenon often observed with gases (e.g., O₂, CO₂) and certain hydrophobic molecules (Hopkinson et al. 2011; Mykkestad 1995). Cell leakage frequently occurs in “unhealthy” or senescent diatom cells (Granum et al. 2002). Cell lysis is accompanied by a release of DOM and is mostly mediated through viral lysis (see chapter “Diatom Viruses”), algicidal bacterial activity (Mayali and Azam 2004), or sloppy grazing (Calbet and Landry 2004). Active efflux of metabolites from diatom cells plays an important role in DOM secretions and interactions with other microbes; however, characterization of this mechanism and distinction between it and other mechanisms is difficult. Several studies established that the extracellular DOM composition of diatoms is distinct from intracellular DOM (Granum et al. 2002; Mague et al. 1980; Puskaric and Mortain-Bertrand 2003), indicating that diatoms selectively secrete specific metabolites. Numerous recent studies involving diatom transcriptomics and metabolomics showed that diatoms upregulate biosynthesis of many metabolites, concurrent with their excretion, which indicates active efflux of these metabolites (Amin et al. 2015; Durham et al. 2015, 2017; Landa et al. 2017; Shibl et al. 2020). Active excretion is often manifested in the form of central metabolites, toxins, waste products, volatile

molecules, extracellular peptides and proteins, lipids, carbohydrates, infochemicals and signaling or defense metabolites [reviewed in Thornton (2014)].

3 Diatom's Backyard: DOM Accumulation in the Phycosphere

Once excreted outside the cell either by active export or passive diffusion/leakage, diatom-derived DOM accumulates into a diffusive boundary layer that surrounds diatom cells (Lazier and Mann 1989; Ploug et al. 1999; Richardson and Stolzenbach 1995). This physically sheltered microscale region, known as the phycosphere (Box 1; Fig. 2) (Bell and Mitchell 1972), is the aquatic equivalent of the well-studied terrestrial plant rhizosphere (Berendsen et al. 2012). The phycosphere is characterized by molecular diffusivity largely governing the transport of molecules and a negligible effect of turbulence on this microscale region (Guasto et al. 2012).

Consequently, small and hydrophilic molecules that have large diffusion coefficients disperse more rapidly away from the diatom cell surface than large and/or hydrophobic molecules that have smaller diffusion coefficients. In addition, the phycosphere size increases with diatom cell size, which plays a major role in the ability of bacteria to perceive diatom-derived DOM since larger phycospheres are more likely perceived by nearby bacteria (Amin et al. 2012; Seymour et al. 2017). These physicochemical features render the phycosphere a DOM-rich hub, where diatoms may release specific metabolites to attract bacteria that benefit them and complement their metabolic needs (Fig. 2).

Depending on environmental conditions, it is conceivable that diatoms alter the composition of DOM metabolites that they release to attract specific populations of bacteria that can help them survive nutrient limitations. For instance, a vitamin-limited diatom may release specific DOM metabolites that attract vitamin-producing bacteria, while the same cell may adjust its DOM secretions under iron limitation to attract bacteria that produce iron-chelating molecules. Indeed, numerous studies have shown that diatoms modify the composition of DOM under different nutrient regimes. For example, silicon (Si), N and P limitations influence diatom DOM lipid and carbohydrate secretions (Granum et al. 2002; Lombardi and Wangersky 1991; Magaletti et al. 2004; Pete et al. 2010). In fact, the rates of excreted DOM relative to total photo-assimilated carbon by many phytoplankton species, including diatoms, increase under nutrient limitation (Nagata 2000). While increases in extracellular DOM secretions under nutrient limitation are often interpreted as metabolic waste due to major changes in the metabolism of stressed diatoms, it is plausible to hypothesize that these increases in DOM secretion can also serve the purpose of attracting a beneficial microbiome to diatom cells that can alleviate such nutrient stresses. While we currently know a number of metabolites that play important roles in the phycosphere, most phycosphere metabolites are generally unknown. In addition, the concentrations of almost all phycosphere metabolites are obscured by the fact that we are unable to directly measure these molecules *in situ*. Our knowledge thus far is limited to modeling studies estimating phycosphere metabolite

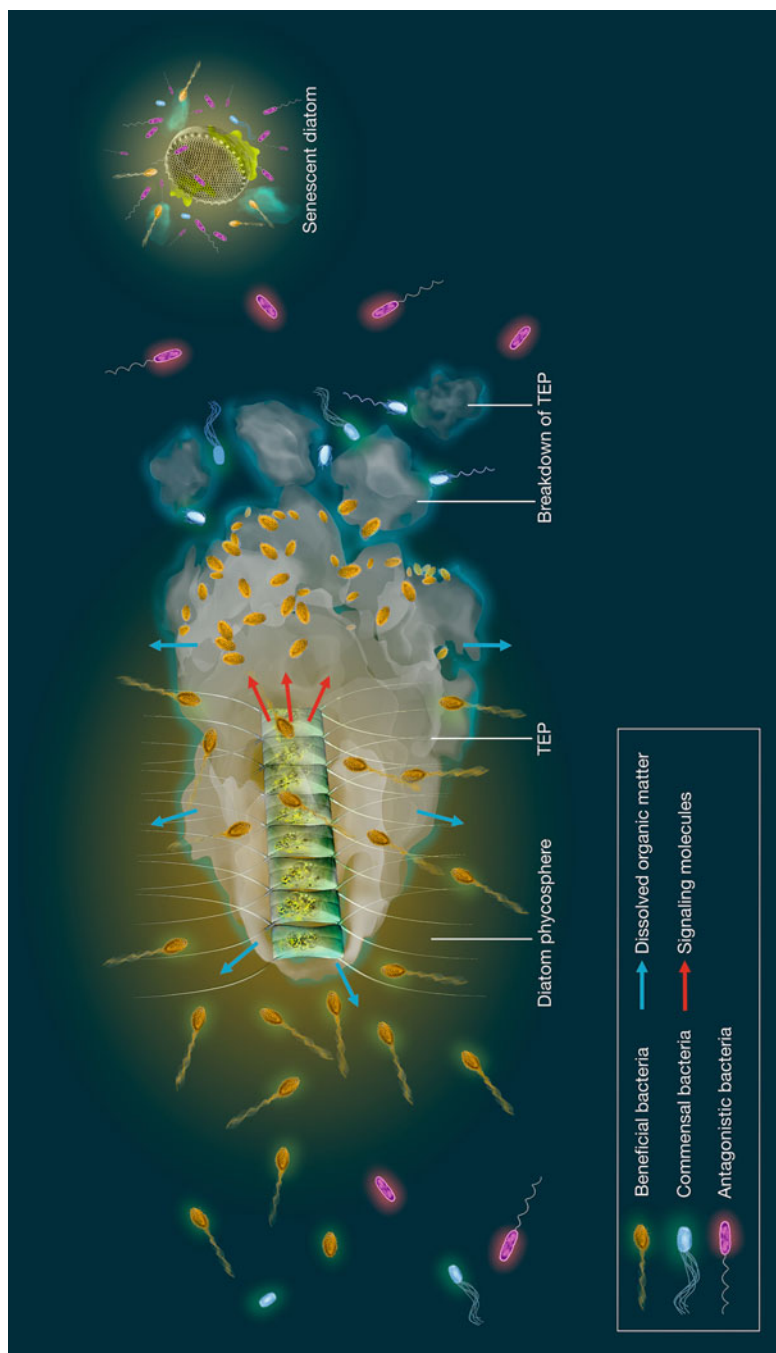


Fig. 2 A conceptual depiction of how diatoms establish and maintain their microbiome. (Left): Diatoms may release a unique composition of DOM (blue arrows) that attracts chemotactic bacteria into the phycosphere. Beneficial, commensal, and antagonistic chemotactic bacteria, as well as non-motile bacteria that encounter the diatom phycosphere, are attracted to these DOM secretions. Concurrently, diatoms release molecules that can aggregate to form gel-like particles

Fig. 2 (continued) known as transparent exopolymeric particles (TEP) that acts as an anchor for incoming bacteria. (*Rigit!*): Once in the phycosphere, bacteria induce diatoms to produce larger amounts of TEP. Beneficial bacteria may attach to TEP and use it as a growth substrate, the breakdown of which feeds other microbial communities. To maintain a healthy microbiome, diatoms release secondary metabolites (red arrows) in the phycosphere that act as signals/infochemicals and defense molecules to proliferate their symbionts while deterring antagonistic and algicidal bacteria. (*Background*): Under stress, senescent diatoms may not be able to maintain a healthy microbiome, which leads to the proliferation of antagonistic and algicidal bacteria that can lyse diatom cells. (Image credit: Glynn Gorick)

concentrations often using estimated excretion rates and diffusivity constants (Breckels et al. 2010; Karp-Boss et al. 1996; Seymour et al. 2017). Improvements to the sensitivity and ability to detect, measure, and identify diatom metabolites will significantly increase our knowledge about their role in shaping heterotrophic microbial communities and the contribution of these exchanges to the major biogeochemical cycles.

In response to DOM secretions by diatom cells, a wide range of bacteria are attracted to the phycosphere (Smriga et al. 2016; Stocker and Seymour 2012) (Fig. 2). Collectively, these concepts point to the phycosphere as a complex chemical and ecological environment and thus is the interface for symbiotic interactions between diatoms and bacteria (Amin et al. 2012; Seymour et al. 2017).

4 A Needle in a Haystack: Finding the Phycosphere in the Dilute Marine Environment

Establishment of associations between diatoms and bacteria requires physical proximity of both partners. Random encounters between planktonic diatoms and non-motile bacteria are estimated to be rare, with a bacterium encountering an algal cell 0.0035 times per day and an algal cell encountering 3.5 bacterial cells per day when considering the average density of phytoplankton and bacteria in the oceans (Seymour et al. 2017). In contrast, motile, chemotactic bacteria have a significant advantage over their non-motile counterparts. Motility increases the chance of a bacterium's encounter with an algal cell to 9 times per day while an algal cell will come in contact with 900 bacterial cells per day (Seymour et al. 2017). Cell size, diffusivity, and fluid flow, motility patterns, and swimming speed are essential to quantifying the probability of bacterial cells encountering floating particulate matter or potential algal cells (Słomka et al. 2020; Son et al. 2016; Taktikos et al. 2013; Xie and Wu 2014). Bacterial motility is energetically costly and different patterns and mechanisms of motility are ultimately governed by a cell's energy investment into this mechanism (Kempes et al. 2017; Mitchell 2002; Ni et al. 2020). Bacterial swimming speeds are influenced by turning angles and propulsive forces exerted by different motility patterns (Kiørboe et al. 2002; Mitchell et al. 1995). Algal motility also influences encounter rates, though this is mostly considered for flagellated taxa such as dinoflagellates and rarely for diatoms since most diatoms do not swim and those that do display gliding motility that is more relevant in benthic communities (Karp-Boss et al. 1996; Poulsen et al. 1999). Algal movements, whether through motility or sinking through the water column, disrupts the fluid flow around algal cells thereby disrupting the phycosphere. This disruption creates a plume of DOM and nutrients that enhance detection by bacteria (Stocker 2012). However, it remains challenging for motility calculations and encounter rate equations to incorporate other important bacterial components such as alternating swimming patterns, or chemotaxis.

Chemotaxis enables bacteria to track phycospheres by further boosting encounter rates compared to motility alone (Lambert et al. 2019). Once in the phycosphere,

chemotactic cells may attach to diatoms, or can continuously track the phycosphere using chemotaxis (Fig. 2). Laboratory experiments have shown that chemotactic bacteria can indeed swarm near and chase algal cells (Barbara and Mitchell 2003; Blackburn et al. 1998; Smriga et al. 2016). Bacteria that can achieve efficient chemotactic responses coupled with the ability to attach in the phycosphere once located likely gain an advantage over bacteria that must constantly track the phycosphere, since motility and chemotaxis are energetically demanding processes (Taylor and Stocker 2012). This dual mode has been observed in presumed diatom symbionts that can switch their motile lifestyle to an attached state (Fei et al. 2020) using bacteria–bacteria communication systems, known as quorum sensing (Daniels et al. 2004; Dobretsov et al. 2009) (Box 1).

5 Something Sticks: Bacterial Attachment, Aggregation, and Diatom-Bacteria Biofilms

Transparent exopolymeric particles (TEP, Box 1) are a complex “microgel” composed of polysaccharides secreted by diatoms and other phytoplankton. These polysaccharides coagulate in the phycosphere and serve as an important sticking agent and growth substrate for bacteria (Alldredge et al. 1993; Passow 2002a). Once in the phycosphere, bacteria may attach to diatoms or to their TEP (Fig. 2), a major constituent of diatom-derived POM (Passow 2002b). A “symbiotic” bacterium may then rely on vertical transmission of its offspring on TEP to remain in the phycosphere (Zehr 2015), or use reversible adhesion mechanisms (Van Loosdrecht and Zehnder 1990) that enable it to detach from the phycosphere during cell senescence or under unfavorable conditions. Upon attachment, bacteria can then induce alterations in the physical structure of diatom populations, including promoting the formation of diatom aggregates (Gärdes et al. 2011; Grossart et al. 2006b). Diatom aggregation is an important process in marine planktonic systems contributing to bloom termination, and driving significant sinking of POM in the form of marine snow (Alldredge and Gotschalk 1989; Grossart et al. 2006a; Smith et al. 1995). By influencing the onset, extent and dynamics of these aggregations, diatom-attached bacteria can play an important role in carbon export to the deep ocean (Leblanc et al. 2018; Tréguer et al. 2018). Moreover, this process can substantially alter the physical environment for diatom–bacteria interactions, promoting surface associations between these organisms.

Evidence for the role of bacteria in mediating diatom aggregation has been consistently demonstrated in the laboratory. Gärdes et al. (2011) reported that whereas axenic *Thalassiosira weissflogii* remained in uniform cell suspension, co-inoculation with diatom-attaching bacteria triggered aggregation. By comparison, free-living bacteria were unable to promote the formation of diatom aggregates. Aggregation was also dependent on the physiological state of diatom cells, whereby only photosynthetically active cells formed particles, suggesting that this was not a consequence of bacterial feeding on dead or decaying diatom cells. Aggregate-promoting bacteria rapidly divided following inoculation with *T. weissflogii* cells

while unattached bacterial isolates that were unable to promote diatom aggregation grew poorly, suggesting that they could not utilize diatom-derived organic substrates as efficiently. Furthermore, TEP concentrations of *T. weissflogii* aggregates far exceeded those of non-aggregating axenic cells, suggesting that diatom-attaching bacteria influenced TEP production (Gärdes et al. 2011). Certainly, particle-associated bacteria enhanced enzymatic hydrolase activity to access diatom surface mucus, compared to “free-living” bacteria (Smith et al. 1995). These experiments indicate the profound impact diatom-associated bacteria may have through attachment on their diatom host, including mediating aggregate formation and physical agglutination of these organisms (Gärdes et al. 2011; Grossart et al. 2006a). Thus, aggregation alters the physical microenvironment, which may increase colonization, sustained associations, and enable bacterial exploitation of diatom-derived resources.

Field studies suggest that the interactions of bacteria with diatom aggregates are environmentally relevant. While these associations undoubtedly can encompass non-specific bacterial scavenging of dead phytoplankton within the so-called detritosphere (Biddanda and Pomeroy 1988), accumulating evidence indicates that bacteria establish direct contact with live diatom aggregates in natural marine microbial communities too. Enumeration of free and aggregate-associated bacteria during progression of a diatom-dominated bloom of *Chaetoceros* and *Thalassiosira* in mesocosms demonstrated that particle-associated bacteria became more prevalent as the bloom progressed (Smith et al. 1995). These colonizing bacteria exhibited rapid growth and did not impede diatom growth, suggesting that aggregate-associated bacteria were actively metabolizing diatom-derived DOM in situ, via associations that go beyond detritus feeding (Smith et al. 1995). Thus, diatom–bacteria interactions appear to be important drivers of aggregate dynamics and sedimentation of organic matter in natural marine ecosystems.

Besides pelagic ecosystems, diatoms are also a major component of benthic intertidal and estuarine biofilms (Fig. 3a). These habitats constitute a distinct physical microenvironment for diatom–bacteria interactions. Microphytobenthic biofilms are highly-productive assemblages, which can contribute over 50% of total estuarine primary production (Joint 1978; Underwood and Paterson 2003). Composed of heterotrophic bacteria, cyanobacteria, and microalgae (predominantly diatoms), these environments are characterized by a matrix of cells and sediments that are stabilized by extracellular polymeric substances (EPS, Box 1) (Underwood and Paterson 2003). Spatial heterogeneity in biomass and species composition can drive resource patchiness. Moreover, the close spatial proximity between microbes can promote cell-to-cell interactions and communication. Similar to bacterial influences on diatom aggregate formation (Gärdes et al. 2011; Grossart et al. 2006a), several studies have observed bacterial induction of diatom biofilm formation (Bruckner et al. 2008, 2011; Windler et al. 2015). Transition of the planktonic fusiform morphotype of *Phaeodactylum tricorutum* to its benthic biofilm-forming oval form was triggered by inoculation with bacteria, and/or bacterial spent medium (Buhmann et al. 2016). Similarly, bacterial assemblages isolated from Lake Constance also induced biofilm formation of the pennate diatoms *Cymbella*

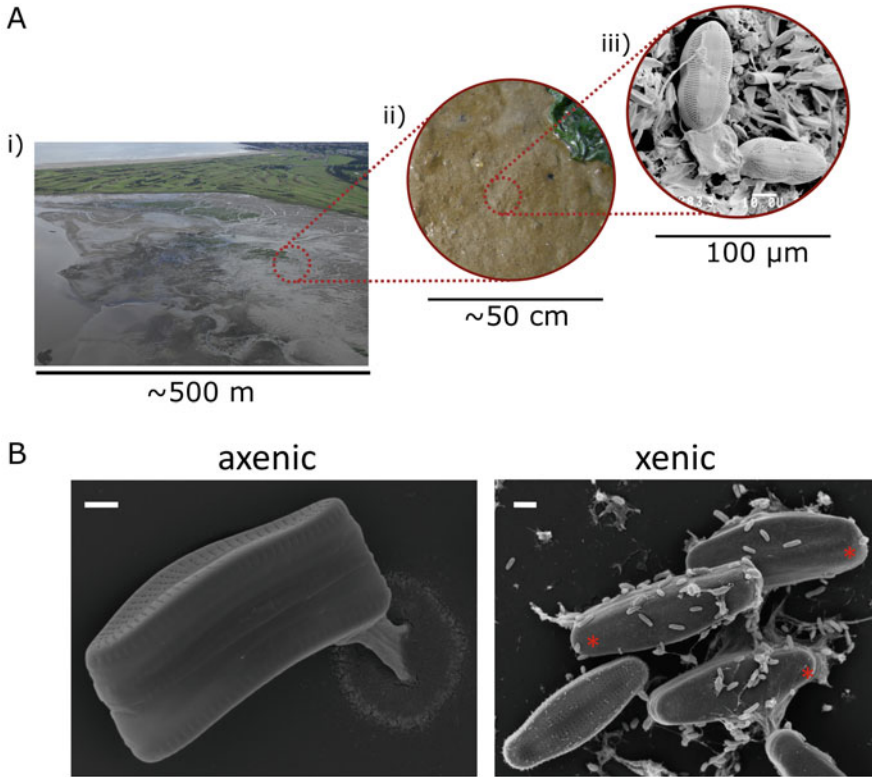


Fig. 3 Diatom–bacteria interactions in benthic environments. **(a)** Diatom biofilms growing on the surface of intertidal sediment, including a photograph of a spatially extensive intertidal mudflat (The Eden Estuary, St Andrews, Fife, UK) (i), and the sediment surface (ii). A low-temperature scanning electron micrograph of diatoms growing on the surface of the biofilm is also shown (iii). Images were kindly contributed by David M. Paterson (Sediment Ecology Research Group, University of St Andrews, UK) (Hubas et al. 2018). **(b)** Scanning electron micrograph of the benthic biofilm-forming freshwater diatom *Achnantheidium minutissimum* under axenic (left) and xenic conditions (right) (scale bar: 1 μm). In the presence of bacteria, *A. minutissimum* produces extracellular capsules (denoted by red asterisks) of extracellular polysaccharide (EPS). These capsules foster the attachment of bacteria, and thus promote diatom–bacteria interactions (Leinweber and Kroth 2015; Windler et al. 2015). By comparison, in axenic conditions the diatom frustule is clearly visible, due to the absence of an EPS capsule. A “stalk” like structure is also observable in the axenic cell, which is thought to mediate adherence in the early stages of biofilm formation (n.b. stalk structures are present both in axenic and xenic conditions) (Windler et al. 2015). Images were provided by Peter Kroth and Katrin Leinweber (University of Konstanz, Germany) and are licensed under CC-BY 4.0

microcephala and *Achnantheidium minutissimum* (Bruckner et al. 2008; Windler et al. 2015) and enhanced diatom EPS production, and free amino acid concentrations (Bruckner et al. 2008; Buhmann et al. 2016; Windler et al. 2015). In addition, these bacteria promoted the formation of specific extracellular structures that foster bacterial attachment. In particular, in the presence of a *Bacteroidetes*

bacterium, the diatom *A. minutissimum* produced extracellular “capsules” (Leinweber and Kroth 2015; Windler et al. 2015) (Fig. 3b). Since bacteria preferentially attach to encapsulated *A. minutissimum* cells, these capsules are likely important in mediating cell-to-cell interactions with diatom-associated bacteria. These studies add to the growing body of evidence that bacteria can influence both the morphologies and carbon flux of diatom communities. They also serve to highlight the breadth and diversity of habitats that diatoms have colonized, and how the physical features of such microenvironments may influence the nature of the interactions between diatoms and cohabitating bacteria.

6 Host Specificity in Diatom-Associated Bacteria: Towards a Diatom Microbiome?

Despite being classified as autotrophic (Box 1), many, if not most, diatom species require exogenous cofactors and nutrients (Fig. 4, top panel) that are often supplied by prokaryotes, such as bacteria (discussed below). This fact, coupled to many observations in laboratory diatom cultures and diatom-dominated blooms, has pointed to specific genera and species of bacteria that commonly co-occur with diatoms and display beneficial interactions with them (Amin et al. 2012). Indeed, the microbial communities associated with the diatoms *Asterionellopsis glacialis* and *Nitzschia longissima* appear to be consistent across strains of each species, regardless of culturing time in the laboratory (Behringer et al. 2018). Colonization experiments between the diatom *T. rotula* and marine microbial communities derived from seawater or other phytoplankton cultures yielded highly reproducible and specific microbial communities over time (Mönnich et al. 2020). Moreover, microbial communities associated with three species and 36 strains of the diatom *Leptocylindrus* genus did not display significant differences in composition between species (Ajani et al. 2018).

More specifically, two genera of nitrogen-fixing, symbiotic cyanobacteria, *Richelia* and *Calothrix* are known to associate with the diatoms *Rhizosolenia*, *Chaetoceros*, and *Hemiaulus* (Foster et al. 2011; Hilton et al. 2013; Villareal 1991) and are discussed in more detail in chapter “An Integrated View of Diatom Interactions”. Among the most frequently observed heterotrophic bacteria to co-occur and to interact with diatoms are members of the Rhodobacteraceae, Flavobacteriaceae, and various γ -proteobacterial groups. Rhodobacteraceae encompasses >70 genera that have diverse ecological adaptations and environmental niches (Simon et al. 2017). Several studies have described symbiotic interactions between diatoms and Rhodobacteraceae species or consistent associations between the two taxa, including *Silicibacter*, *Ruegeria*, *Sulfitobacter*, *Roseobacter*, *Roseovarius*, and *Donghicola* (Amin et al. 2012; Durham et al. 2015; Grossart et al. 2005; Hünken et al. 2008; Suleiman et al. 2016). Other groups of bacteria that have been shown to benefit diatoms or consistently associate with them include *Marinobacter*, Alteromonadaceae, Flavobacteria, Oceanospirillales, Sphingomonadaceae, and Bacteroides (Ajani et al. 2018; Amin et al. 2009;

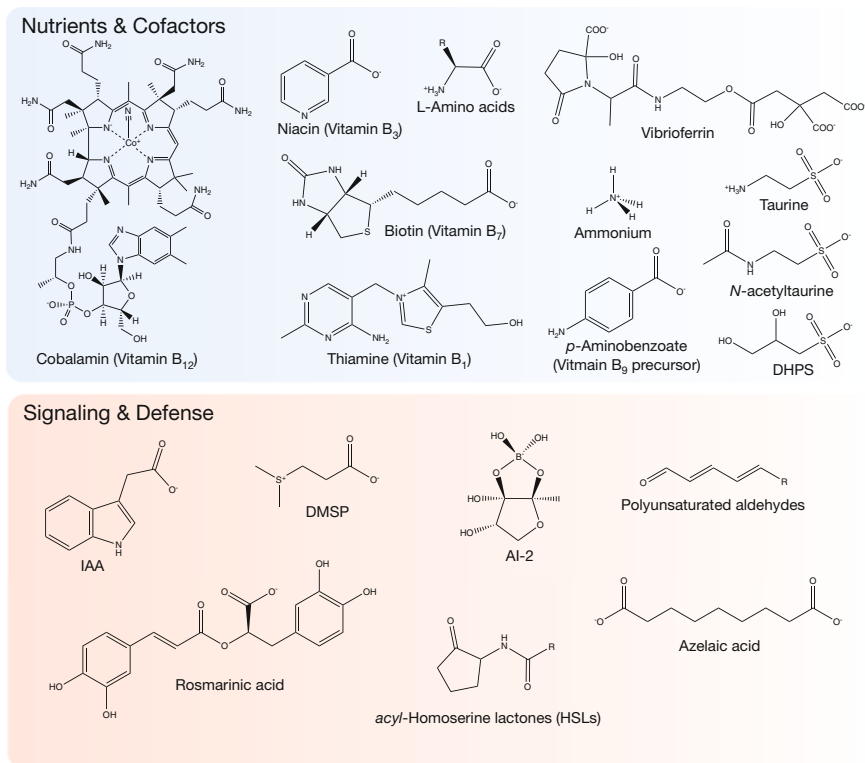


Fig. 4 Chemical structures of known picosphere metabolites. *Top*: Nutrients and cofactors shown to be required for diatom and/or bacterial growth in the picosphere. L-amino acids represent a variety of diatom-derived amino acids that have been shown to support the growth of picosphere bacteria. Vibrioferin is a cofactor (siderophore) that binds Fe(III) and renders it more bioavailable to diatoms. *Bottom*: Signaling and defense molecules shown to have major effects on diatom and/or bacterial behavior and transcriptional responses. DHPS = 2,3-dihydroxypropane-1-sulfonate, AI-2 = autoinducer-2, IAA = Indole-3-acetate, DMSP=Dimethylsulfoniopropionate. “R” in chemical structures denotes a variable chemical moiety/side chain

Johansson et al. 2019; Klindworth et al. 2014; Mönnich et al. 2020; Riemann et al. 2000; Schäfer et al. 2002; Teeling et al. 2012). While it is not clear whether diatoms have highly specific bacterial symbionts, similar to legumes (Poole et al. 2018), recently several strains of the Rhodobacteraceae bacterium *Sulfotobacter pseudotnitzschiae* have been isolated from the diatoms *A. glacialis* originating from the Persian Gulf (Fei et al. 2020), *Skeletonema marinoi* originating from the Baltic Sea (Töpel et al. 2019) and several cultures of the toxigenic diatom *Pseudonitzschia multiseriis* originating from the Atlantic and Pacific Oceans (Amin et al. 2015; Hong et al. 2015). These repetitive isolations of nearly identical bacteria (>99% average nucleotide identity, ANI) (Fei et al. 2020) from different diatom species originating from starkly different environments suggest this bacterium may be a highly specific symbiont of some diatoms. Several studies have also shown that

S. pseudonitzschiae and other *Sulfitobacter* spp. are attuned to diatom metabolites, enhance diatom growth, provide them with reduced nitrogen, and protect diatoms against viruses and oxidative stress (Amin et al. 2015; Fei et al. 2020; Hünken et al. 2008; Kimura and Tomaru 2014; Shibl et al. 2020), further highlighting a symbiotic role.

Cumulatively, these observations suggest that diatoms possess specific microbial communities, a so-called microbiome. However, current sampling methods for laboratory and field samples hinder our ability to define a specific diatom microbiome. For example, methods typically used to isolate and culture diatoms from field samples rely on isolating a single diatom cell or chain along with bacterial communities in $\sim 1 \mu\text{L}$ volume, while metagenomic studies that examine bacterial communities associated with diatom blooms rely on sampling liters of seawater. In contrast, phycosphere volumes of most diatoms vary between a few picoliter for small cells to hundreds of nanoliters for large cells. This large discrepancy in volume indicates that inadvertent inclusion of non-phycosphere bacteria in cultures and metagenomic samples is likely. Recent advances in fluorescence-activated cell sorting (FACS, Box 1) has aided in reducing some of the biases associated with traditional sampling methods (Baker and Kemp 2014; Crenn et al. 2018). However, FACS is mainly effective in capturing bacteria strongly attached to diatom cells or TEP and is mainly applicable to relatively small diatom cells and chains ($< 100 \mu\text{m}$). Loosely associated bacteria or ones that track the phycosphere without adhering, large diatoms and long diatom chains are not captured by this method. Thus, it has been difficult, to date, to define with a high level of certainty the true microbiome of diatoms and other eukaryotic phytoplankton groups. Further examination of microbial communities in the phycosphere using robust sampling methods coupled with advances in single-cell techniques, including genomics and metagenomics, will shed more light on the true diatom microbiome in the oceans.

7 Metabolic Attributes of Diatom Microbiomes: Metabolic Fitting or Coadaptation?

While defining the existence and nature of the “diatom microbiome” (Box 1) is a work in progress, so too is the development of ecological principles governing the assembly, stability, and maintenance of such communities. The apparent conservation of specific diatom-associated bacteria with certain diatom species implies that the diatom host likely plays an important role in driving the composition of its associated bacterial community. This observation coupled with evidence that diatom-associated bacteria can profoundly influence diatom ecology suggests that co-adaptive traits have arisen that underpin the association of diatoms with certain bacteria, and vice versa. On the other hand, the environment has an important role in shaping diatom microbiome composition as shown in *Leptocylindrus* species that generally displayed no significant differences in bacterial community composition across species, but large differences were found between strains collected at different locations and times (Ajani et al. 2018). Determining the extent of host versus

environment selection in driving diatom-associated bacterial communities thus remains a critical research question.

Host-driven regulation of diatom microbiome composition would require (i) host mechanisms to control the bacterial community composition (discussed below), and/or (ii) specific diatom metabolic attributes (e.g., auxotrophy) that select for bacterial taxa with specific functional traits. The ability of diatoms and their associated bacteria to satisfy each other's nutritional demands can be an important starting point to foster the establishment of specific interactions. However, whether such "metabolic fitting" drives the initiation of closer associations or arises as a consequence of persistent interactions between specific diatoms and bacterial taxa remains an open question (Kazamia et al. 2016). Functional redundancy between bacterial taxa may also mean that diverse bacteria have the necessary attributes to occupy a specific diatom phycosphere. In this scenario, coined "the lottery hypothesis," whoever gets there first (and has the necessary functional traits) will inhabit the diatom phycosphere. However, evidence against this hypothesis in microalgal community ecology has come from phytoplankton colonization studies. Exposure of axenic *T. rotula* cultures to compositionally different bacterial inocula derived from either seawater or phytoplankton hosts of varying degrees of relatedness converged to a stable and reproducible core community (Mönnich et al. 2020). Thus, no matter how diverse the starting community, the same taxa came to occupy the *T. rotula* microbiome, which suggests factors beyond potluck are at play. Similarly, microbiome recruitment was host-specific in a study of five green algal isolates (Jackrel et al. 2020). Further evidence for host-specific microbiomes is presented by a study of the bacterial communities associated with the toxic diatom *Pseudo-nitzschia*. Whereas native microbiomes of *P. pungens* promoted growth of the host, transplantation of the same microbiome to the related diatom species *P. australis* and *P. fraudulenta* either had no growth stimulatory effect, or in some cases decreased diatom growth rate (Sison-Mangus et al. 2014). Further investigation revealed that this effect was in part caused by the presence of the known algicidal bacteria Cellulophaga, which promoted the growth of *P. pungens*, but caused *P. australis* populations to completely crash. As marine bacteria are known to "switch on" and "off" their algicidal activity, e.g. through regulating enzyme activity (Skerratt et al. 2002), these results suggest that diatom-associated bacteria may recognize, respond, and adapt their behavior according to specific diatom hosts. This implies that coevolution between diatoms and their native bacterial microbiomes may have arisen and could play an important role in governing the assembly of diatom microbiomes. Specialization of native bacteria towards diatom host-derived exudates could also influence the nature of relationships of bacteria with diatoms (Sison-Mangus et al. 2014), discussed further below.

The findings above support the inference that diatom host-specific attributes, and metabolic specialization of bacterial taxa drive assembly of phytoplankton-specific consortia. As the primary interface for diatom–bacteria interactions, the phycosphere and its physical properties/chemical composition is likely a key constraint dictating the types of bacteria associating with diatoms. Evidence drawn from metabolomics approaches has demonstrated that the chemical composition of

phytoplankton-derived DOM varies according to phytoplankton taxonomy (Becker et al. 2014; Landa et al. 2017), which suggests that specialization in utilizing certain DOM compounds by bacteria can enable their phycosphere colonization. Indeed, evidence is beginning to emerge that host-derived resources can select for growth of specific bacterial taxa (Fu et al. 2020). Bacterial enzymes for accessing carbohydrate substrates are encoded by the “polysaccharide utilization loci” (PULs) (Krüger et al. 2019; Lombard et al. 2014). As PUL repertoire may vary between taxa (Krüger et al. 2019; Xing et al. 2015), the distribution of these genes in different bacteria could be an important mechanism tailoring certain species towards usage of phytoplankton-specific DOM compositions. As the major constituent of diatom-derived DOM, laminarin is of particular relevance to carbon utilization by diatom-associated bacteria (Becker et al. 2020). Notably, members of the Bacteroidetes, which are frequently found associated with diatoms (Amin et al. 2012), encode enzymes for laminarin degradation (GH16 laminarinases) (Krüger et al. 2019), suggesting that carbon utilization specialization could account for the observed associations between diatoms and Bacteroidetes bacteria. However, diatoms also produce specific polysaccharide compounds apparently resistant to bacterial enzymatic degradation, such as the recently identified fucose-containing sulfated polysaccharide, FCSP (Vidal-Melgosa et al. 2021). This compound accumulates on the surface of diatom cells, has antibacterial properties (Fitton et al. 2015), and so has been proposed to function as a defensive barrier against bacteria. These examples illustrate the importance of specific polysaccharide compounds that can promote or deter bacteria. Resource-driven assembly of host-associated communities almost certainly extends beyond carbon, and the roles of other nutrients and infochemicals in governing specific interactions between diatoms and bacteria are outlined further below. A persistent, close association between diatoms and certain bacteria could in itself drive the evolution of metabolic specializations and/or co-dependencies that cement closer ecological interactions (Helliwell et al. 2015; Kazamia et al. 2016). Specific environmental scenarios such as prolonged periods of nutrient limitation could provide the opportunity and time necessary to drive the evolution of more obligate associations (e.g., due to host loss of biosynthetic capacity for organic nutrients provided by associated bacteria). This raises the question of whether closer, more obligate associations are more resilient to environmental influences on microbiome composition, which requires further investigation. In any case, nutrient exchange is likely a critical factor initiating diatom–bacteria interactions in the short-term, but also in sustaining and developing them over evolutionary timescales.

8 Beyond Carbon: Cross-Feeding Between Diatoms and Bacteria for Other Vital Nutrients

Our major focus so far has been on the importance of diatom-derived DOM for instigating and sustaining diatom-bacteria symbioses (Fig. 2). For example, large quantities of dimethylsulfoniopropionate (DMSP) and glycolate are released by diatoms and other phytoplankton daily throughout the oceans (Schnitzler Parker

et al. 2004; Stefels et al. 2007) and these metabolites serve as carbon (and sulfur for DMSP) sources for specific groups of bacteria (Howard et al. 2006; Lau and Armbrust 2006; von Borzyskowski et al. 2019). However, a suite of other macronutrients (e.g., N, P and S), alongside inorganic and organic micronutrients (e.g., vitamins and iron) are necessary for the growth of diatoms and bacteria alike (Fig. 4, top panel). In fluid, turbulent, aquatic environments, diatoms frequently experience a range and combination of nutrient limitations (see chapters “Comparative and Functional Genomics of Macronutrient Utilization in Marine Diatoms” and “Molecular Mechanisms Underlying Micronutrient Utilization in Marine Diatoms”). Accumulating evidence suggests that diatom-associated bacteria play an important role in alleviating limitations for many of these nutrients, suggesting that the “diatom microbiome” must be dynamic and/or resilient to different environmental constraints over time. In the context of the diatom host, the capacity to recruit specific bacteria conferring distinct ecological functions relevant to the environmental conditions could thus confer a significant selective advantage. In this section, we will discuss the current understanding of the roles of bacteria in diatom nutrient provision and outline the types of bacteria recognized to be capable of fulfilling such roles.

An important class of organic micronutrients required by many diatoms are vitamins (Box 1, Fig. 4). Vitamins are necessary as cofactors for enzymes of central and secondary metabolism. Auxotrophs must therefore obtain an exogenous source of certain vitamins from their environment. While eight water-soluble B vitamins (thiamine, B₁; riboflavin, B₂; niacin, B₃; pantothenic acid, B₅; pyridoxine, B₆; biotin, B₇; folate, B₉ and cobalamin, B₁₂) are universally required for human nutrition, only three (B₁, B₇, and B₁₂) are added routinely to diatom media (Guillard and Ryther 1962). Compilation of the requirements of fifty-four diatom species demonstrated that 32, 7, and 0 species required cobalamin, thiamine, and biotin, respectively (Croft et al. 2005). As only certain prokaryotes are capable of its biosynthesis (Shelton et al. 2019), vitamin B₁₂ (Fig. 4, top panel) is considered to be a particularly pertinent exchange molecule mediating algal–bacteria interactions (Croft et al. 2005; Kazamia et al. 2012). This vitamin is necessary as a cofactor to the B₁₂-dependent isoform of methionine synthase (METH). As certain diatoms lack the B₁₂-independent isoform of methionine synthase (METE) (Helliwell et al. 2011) and cannot synthesize the vitamin themselves (Croft et al. 2005), they must obtain an exogenous source of this micronutrient for growth. The vitamin B₁₂ requirements of several marine diatoms can be satisfied in B₁₂-limited culture by heterotrophic bacteria, which utilize diatom DOM in return (Durham et al. 2015; Haines and Guillard 1974). In B₁₂-limited environments (Bertrand et al. 2015), diatoms may release a DOM composition particularly suited towards attracting B₁₂-synthesizing bacteria, thereby alleviating this limitation. A case in point is when the B₁₂-dependent diatom *T. pseudonana* was limited for B₁₂ it released a unique organic sulfur metabolite, 2,3-dihydroxypropane-1-sulfonate (Fig. 4, top panel), that supported the growth of the bacterium *Ruegeria pomeroyi* DSS-3, which in exchange alleviated the B₁₂ limitation of the diatom (Durham et al. 2015).

Environmental metatranscriptomics studies have predicted interactions between diatoms and bacteria governed by vitamin B₁₂, particularly in B₁₂-limited marine

ecosystems. In the Southern Ocean, where diatoms are the dominant primary producers, the γ -proteobacterium *Oceanospirillaceae* ASP10-02a contributed the most B₁₂ biosynthesis transcripts in this region (Bertrand et al. 2015). Concomitantly, elevated transcripts involved in cell-surface attachment and DOM acquisition in this group of bacteria are indicative of physical interactions that warrant further investigation. These findings highlight the importance of vitamin B₁₂ in chemical exchanges between diatoms and bacteria in large areas of the ocean. The evidence for the role of vitamin B₁₂ in underpinning a range of mutualistic interactions between bacteria and diverse algal taxa (Kazamia et al. 2012; Wagner-Döbler et al. 2010) emphasizes the importance of vitamin cycling in cross-kingdom microbial interactions more broadly.

Emerging evidence indicates that vitamin-based symbioses extend beyond vitamin B₁₂, and the unidirectional transfer of vitamins from bacteria to algae. Auxotrophy for biotin, niacin, and p-aminobenzoic acid (*p*-ABA, a precursor for folate, B₉; Fig. 4, top panel) is particularly common in marine Rhodobacteraceae (Cooper et al. 2019). As outlined in the section above, diatoms are commonly found in close association with members of the Rhodobacteraceae (Amin et al. 2012). Moreover, cultivated diatoms do not typically require an exogenous source of niacin, *p*-ABA, or biotin for growth and likely synthesize them by themselves (Croft et al. 2006; Guillard and Ryther 1962). It is therefore feasible that diatoms may be able to fulfill Rhodobacteraceae B-vitamin requirements, as has been observed with a model algal-bacterial system comprising the green alga *Ostreococcus tauri* and Roseobacter *Dinoroseobacter shibae* (Cooper et al. 2019). Given that vitamin auxotrophy can evolve rapidly when an external source of the vitamin is readily available (Helliwell et al. 2013, 2015), it is feasible that the widespread requirement of Rhodobacteraceae may be an evolutionary consequence of the tendency of members of this lineage to adopt lifestyles in close association with diatoms and other algae that synthesize such vitamins (Cooper et al. 2019).

Another critical micronutrient limiting diatom growth is iron. Iron is essential for a range of cellular processes, including photosynthesis, respiration, electron transfer, and nitrogen assimilation. However, due to the poor solubility of Fe(III), dissolved iron is present in extremely low concentrations in surface ocean waters (Johnson et al. 1997). In addition, most iron in the ocean is complexed with a variety of unknown organic ligands that further complicate its bioavailability to diatoms and other microbes (Gledhill and Buck 2012). Due to these challenges, microbes have evolved an array of strategies for iron acquisition (Boyd and Ellwood 2010). A common mechanism among some bacteria is the secretion of organic compounds known as siderophores that bind ferric iron, enabling its uptake via active transport mechanisms. Although bacteria and microalgae typically compete for iron (Hassler et al. 2011; Toulza et al. 2012), mutualistic bacteria that iron-limited diatoms may attract to the phycosphere via specific DOM metabolites can alleviate algal iron limitation. In particular, a number of γ -proteobacteria belonging to the *Marinobacter* genus that are found to be associated with dinoflagellates, diatoms and coccolithophores, produce an unusual siderophore known as vibrioferrin (Fig. 4, top panel). By comparison, non-algal associated close relatives produced other

siderophores to acquire iron (Amin et al. 2009). Once bound to Fe(III) and exposed to light, vibrioferrin undergoes a photochemical reaction that oxidizes the siderophore and renders it incapable of binding iron while simultaneously reduces Fe(III) to Fe(II), which is more soluble in seawater. Vibrioferrin is 10–20 times more photolabile than siderophores produced by free-living bacteria and has been shown to promote algal assimilation of iron (Amin et al. 2009), likely via mutualistic exchange for DOM.

Bacteria in the phycosphere can also improve the bioavailability of macronutrients for diatoms. Methylamines are ubiquitous organic nitrogen compounds in marine environments (Poste et al. 2014). Although nitrogen is a critical macronutrient limiting diatom growth (Tyrrell 1999), diatoms appear to be unable to degrade organic methylamine compounds (Suleiman et al. 2016). Coculture with bacteria harboring genes for methylamine catabolism was shown to fully support the growth of *P. tricornutum* on monomethylamine (MMA) as the sole nitrogen source, by remineralizing nitrogen and liberating bioavailable ammonium (Fig. 4, top panel). Given the widespread distribution of methylotrophic bacteria in marine waters (Sosa et al. 2015), the potential ecological significance of methylamine cross-feeding between bacteria and diatoms may only just be beginning to be recognized. Nitrogen is undoubtedly an important driver of diatom–bacteria interactions more broadly. Notably, diatom–diazotroph associations (DDAs) involve N_2 -fixing cyanobacteria that can fix atmospheric gaseous N_2 into biologically available ammonium for their symbiotic diatom hosts [reviewed in Foster and Zehr (2019)]. These relationships represent the most intimate symbioses between diatoms and bacteria described to date, and thus offer unique insight into the adaptations necessary to promote obligate and specific interactions with diatoms (outlined further in chapter “An Integrated View of Diatom Interactions”).

Clearly, bacteria are capable of alleviating the demands of diatoms for a range of nutrients. Given the dynamic environments in which diatoms thrive, this raises many questions over the versatility, assembly, and maintenance of the diatom microbiome. Are core microbiome members capable of satisfying a range of functional roles, and thus adaptable to prevailing environmental conditions? Alternatively, in addition to maintaining a core microbiome, must diatoms be flexible in their ability to attract distinct bacterial taxa, resulting in a microbiome that is partially dynamic depending on the environment? Or do specific environmental constraints drive highly variable bacterial communities, naturally selecting for certain ecotypes adept in the given conditions? Further work is undoubtedly required to determine how the diatom microbiome is shaped by different environmental stressors, versus by the diatom host itself.

9 Antagonistic Interactions Between Diatoms and Bacteria

While symbiotic and beneficial interactions have been discussed in detail above, parasitic or algicidal bacteria have been widely reported in culture and field studies. Exploitative algicidal bacteria can cause diatom cell lysis (Fig. 2), and thus

maximize bacterial access to diatom-derived resources. The activity of such harmful bacteria is likely to be critical in regulating diatom growth, productivity, and bloom dynamics in natural plankton assemblages (Mayali and Azam 2004). Mesocosm experiments have demonstrated that inoculation of the algicidal bacterium *Pseudomonas fluorescens* HYK0210-SK09 into a natural freshwater bloom of the small centric diatom *Stephanodiscus hantzschii* led to a 95% reduction in *S. hantzschii* growth (Jung et al. 2010). Termination of the *S. hantzschii* bloom occurred concomitantly with a proliferation of non-dominant algal species, alongside a significant increase in heterotrophic protists. This study provides compelling evidence that the presence and activities of algicidal bacteria in natural phytoplankton populations can have profound impacts on community structure and composition.

Mechanistically, algicidal bacteria can severely limit diatom growth, inhibit cell division, alter morphology, or hamper photosynthetic capabilities (Li et al. 2016; Paul and Pohnert 2011; Van Tol et al. 2017). These pathogenic effects are often mediated by excretion of small molecules and proteins, such as extracellular proteases, chitinases, or algicidal compounds (Lee et al. 2000; Li et al. 2016; Paul and Pohnert 2011). For instance, the algicidal bacterium *Chitinimonas prasina* LY03 will swim towards its diatom prey (*T. pseudonana*) and upon attachment produces chitinases to degrade the diatom cell wall, causing cell lysis and death (Li et al. 2016). Similarly, the algicidal activity of the bacterium *Kordia algicida* is mediated by extracellular proteases, the excretion of which is regulated in a bacterial density dependent manner (Paul and Pohnert 2011). While algicidal bacteria can clearly have pernicious effects, in some instances diatoms exhibit resistance towards these antagonistic agents, mediated by defensive mechanisms such as secretion of antibacterial compounds (Meyer et al. 2018). One class of molecules implicated in diatom defense against algicidal bacteria are the polyunsaturated aldehydes (PUAs) (Fig. 4, bottom panel), which have also been shown to suppress the reproduction of grazers (e.g. copepods) (Ianora et al. 2004; Miralto et al. 1999), and confer allelochemical effects against certain phytoplankton (Ribalet et al. 2007). The algicidal bacterium *K. algicida* induces production of the hydroxylated PUA eicosapentaenoic acid in *Chaetoceros didymus*, which confers growth inhibitory effects on *K. algicida* (Meyer et al. 2018). Examination of three other diatom-derived PUAs (2E,4E-decadienal, 2E,4E-octadienal, and 2E,4E-heptadienal) has demonstrated that this class of molecules can have antibacterial properties against other marine bacteria, inhibiting growth of 19 of 33 bacterial species surveyed (Ribalet et al. 2008). Albeit, interestingly, the majority of bacterial strains (14/16) isolated from diatom-dominated blooms (including *Sufitobacter* species) showed resistance to PUA exposure.

The efficacy of algicidal activity can also be dependent on the species composition and complexity of a given microbial community. For instance, while the PUA-producing diatom *C. didymus* is resistant to attack by *K. algicida* in coculture, this diatom becomes susceptible when a non-resistant diatom, *Skeletonema costatum*, is introduced (Bigalke and Pohnert 2019). Together, these findings suggest that a viable ecological strategy for diatoms could be to adopt mechanisms to

promote the close association of certain beneficial bacterial species, while deterring other less cooperative taxa.

10 Microbial Chatter: Communication and Signaling Between Diatoms and Bacteria

Signaling molecules are critical factors mediating microbe–microbe interactions in the oceans, and beyond. In the highly diverse marine ecosystem, perception and recognition of bacterial symbionts by diatoms most likely is initiated by the exchange of signaling molecules. Signals are typically needed at minute quantities, yet activate and regulate important metabolic pathways that in turn influence major biogeochemical cycles; therefore, although in many cases they are unlikely to constitute a major fraction of DOM in the oceans, they are indirectly responsible for a substantial proportion of DOM production and assimilation. Despite their importance, our knowledge of signaling molecules and their mechanisms of action between diatoms and other microbes is at its infancy. Because of their typically low effective concentrations needed to elicit responses in microbes, signaling molecules and infochemicals may be consumed directly in the phycosphere before they ever diffuse into bulk seawater, which may explain the scarcity of information on this important class of metabolites.

At the core of communication between diatoms and heterotrophic bacteria is the need for diatoms to attract specific “beneficial” bacteria that can satisfy their nutrient dependencies, while at the same time evade algicidal, parasitic, and opportunistic bacteria that can kill or compromise their cell health (Fig. 2). These subtle interkingdom mechanisms are likely carried out by infochemicals and defense molecules. While mechanisms of how multicellular eukaryotes nurture microbiomes are starting to be understood and typically take place in specialized compartments/organelles that can house such communities, diatoms and other eukaryotic phytoplankton are unable to differentiate and thus lack any such structures.

To decipher the mechanisms by which diatoms recruit and modulate their bacterial consortia, Shibl et al. (2020) used multi-omics techniques to study early transcriptomic and metabolic shifts following the re-introduction of axenic populations of *A. glacialis* to its natural bacterial community. This experiment identified two diatom secondary metabolites as likely signaling compounds, rosmarinic acid and azelaic acid (Fig. 4, bottom panel). Rosmarinic acid was shown to possess a quorum sensing-like (Box 1) effect on two putative symbionts belonging to the Rhodobacteraceae family (*Phaeobacter* sp. F10 and *S. pseudonitzschiae*) by facilitating their attachment to TEP produced by *A. glacialis*, while increasing the motility of a potential opportunist (*Alteromonas macleodii*). Coculture experiments between the diatom and these bacteria confirmed that while the potential symbionts colonized the diatom TEP, *A. macleodii* failed to attach in the phycosphere of the diatom. Azelaic acid was found to inhibit the growth of *A. macleodii*, while simultaneously promoting the growth of *Phaeobacter* sp. F10 and *S. pseudonitzschiae*. The only bacterial gene known to respond to azelaic acid, a

transcriptional regulator, was also restricted to a handful of bacterial orders and was geographically widespread at the surface and deep chlorophyll maximum in the oceans, despite not being abundant. These findings provide the first glimpse of a eukaryotic phytoplankton modulating specific bacterial growth and behavior within a microbial community, and suggest that unicellular eukaryotes like diatoms can nurture microbiomes in the phycosphere, similar to multicellular eukaryotes (Shibl et al. 2020). While this work highlights the role of two new infochemicals capable of regulating diatom microbiome composition, it is likely that there is a vast array of other cryptic metabolites present in the phycosphere that can, on the one hand, promote proliferation of bacterial symbionts, while, on the other, inhibit pathogens/opportunists.

Infochemicals are critical for initiating cell-to-cell communication and can mediate bacterial chemotaxis. Dimethylsulfoniopropionate (DMSP) (Fig. 4, *bottom panel*), an important diatom-derived organosulfur compound critical to climate processes, acts as a chemical cue to attract motile bacterial lineages to their host, in addition to being a carbon and sulfur source for some bacteria (Curson et al. 2011; Seymour et al. 2010). Bacteria able to metabolize DMSP as a carbon and/or sulfur source are especially responsive to these chemotactic infochemicals (Kiene et al. 2000; Seymour et al. 2010; Zimmer-Faust et al. 1996). In addition to inducing the upregulation of genes that putatively metabolize DMSP (Amin et al. 2015; Johnson et al. 2016), transcriptomic analysis of *R. pomeroyi* DSS-3 cultures treated with DMSP produced high levels of the quorum-sensing molecule *N*-(3-oxo-tetradecanoyl)-L-homoserine lactone, highlighting the multifaceted signaling role DMSP may play in the bacterial response to diatom products (Johnson et al. 2016).

Another example of a chemically-mediated signaling mechanism between diatoms and bacteria involves the *Roseobacter* group bacterium *S. pseudonitzschiae* strain SA11 and the toxigenic diatom *P. multiseriis*. In addition to organic carbon and sulfur metabolites, *P. multiseriis* releases the amino acid tryptophan to *S. pseudonitzschiae*, which in turn converts it to the hormone indole-3-acetate (IAA) (Amin et al. 2015) (Fig. 4, *bottom panel*). IAA promotes cell division of *P. multiseriis*, leading to an increase in photosynthesis and carbon fixation by the diatom. This presumably benefits *S. pseudonitzschiae* as it acquires more diatom-derived DOM. The discovery that *Roseobacter* group genes and transcripts responsible for converting tryptophan to IAA are widespread in the oceans suggests that IAA may be a common mechanism of signaling mediating *Roseobacter*-diatom interactions.

Quorum sensing (QS) is a bacterial communication system by which bacterial communities use small signaling molecules, known as autoinducers, to coordinate their gene expression as a function of cell density (Miller and Bassler 2001; Williams 2007). When cell density increases, excreted QS signals accumulate to a threshold and are subsequently sensed by QS response regulators, which in turn regulate the expression of genes involved in many processes, including bacterial defense, pathogenicity, siderophore production, attachment, biofilm formation, motility, and nutrient acquisition (Mukherjee and Bassler 2019). Several classes of QS molecules are

produced by a variety of bacteria: homoserine lactones (HSLs) (Fig. 4, *bottom panel*), autoinducers-2 (AI-2), 2-alkyl-4-quinolones (AQs), and long-chain fatty acids and their methyl esters, among others. N-acyl-HSL-mediated QS is arguably the most described system (Hmelo 2017), where HSL signal-producing bacteria are commonly associated with diatoms and other microalgal species (Gram et al. 2002; Mangwani et al. 2015; Zhou et al. 2016). Recent studies have examined the effect of QS signals on diatoms or on structuring of microbial communities in the phycosphere.

Because the repertoire of diatom-associated bacterial HSL signals is limited, studies have generally focused on the effects of common HSLs from marine bacteria on diatoms. For example, the HSLs C₁₀-HSL, 3-oxo-C₁₀-HSL, and 3-OH-C₁₀-HSL increased the chlorophyll *a* content and TEP production in the biofilm-forming diatom *Cylindrotheca* sp. (Yang et al. 2016). The benthic diatom, *Seminavis robusta*, exhibited differential physiological responses to structurally similar long-chain HSLs. C₁₄-HSL promoted growth of *S. robusta* while OH-C₁₄-HSL and oxo-C₁₄-HSL inhibited its growth. In addition to oxo-C₁₄-HSL, a tetramic acid derivative negatively affected the photosynthetic efficacy of *S. robusta* and triggered a downregulation of cell cycle-related proteins and shifts in its fatty acid metabolic profile (Stock et al. 2020). In field incubations, exposure of natural marine microbial consortia to 2-heptyl-4-quinolone (HHQ) restructured bacterial community composition to enrich microbes that produce or sense HHQ (Whalen et al. 2019). Recently, HHQ was shown to inhibit the growth of the diatoms *Cylindrotheca closterium*, *P. tricorntum*, and *A. minutissimum* (Dow et al. 2020). In contrast, other bacterial quinolone derivatives like 2-nonyl-4-quinolone and its *N*-oxide congener had weaker inhibitory effects. Similarly, a pentyl-quinolinol produced by an *Alteromonas* sp. displayed inhibitory properties on *Cylindrotheca fusiformis*, *Thalassiosira weissflogii*, and *Chaetoceros simplex* (Long et al. 2003).

A more direct role for bacterial AHLs in mediating diatom–bacteria interactions was recently shown with the ubiquitous diatom *A. glacialis*. Two potential bacterial symbionts belonging to the Rhodobacteraceae isolated from the microbial community associated with this diatom were shown to harbor complete QS systems, indicated by the presence of autoinducer synthase and an autoinducer response regulator genes that synthesize and perceive the autoinducer signal, respectively (Fei et al. 2020). In contrast, a potential opportunist, *A. macleodii*, lacked the ability to synthesize AHLs. Further experiments showed that the two Rhodobacteraceae isolates synthesize three AHL signals, one of which, 3-oxo-C_{16:1}-HSL, regulates bacterial biofilm formation. These findings correlate with the ability of these two bacteria to attach to diatom TEP, while *A. macleodii* was largely unresponsive to these AHLs and was unable to attach to the diatom (Fei et al. 2020). Cumulatively, these results suggest that AHL signals likely have a critical role in shaping the microbial consortia that can colonize diatom phycospheres. Additionally, these signals can influence physiological changes to diatoms and control their growth.

Diatoms can also produce signals, such as rosmarinic acid discussed earlier, that can interfere with HSL-mediated QS to promote attachment of specific bacteria, while preventing others from colonizing the phycosphere. Quorum-quenching

(QQ) is another process that is utilized by some eukaryotes to disrupt bacterial QS communication (Busetto et al. 2017; Natrah et al. 2011; Romero et al. 2011). Some algal species produce and secrete molecules structurally similar to QS signals to interfere with bacterial communication or release enzymes that inactivate QS molecules (Hughes and Sperandio 2008; Pietschke et al. 2017; Rajamani et al. 2008; Rolland et al. 2016). For example, the benthic diatom *Nitzschia cf. pellucida* produces a haloperoxidase enzyme that degrades a variety of bacterial AHLs (Syrpas et al. 2014). Like eukaryotes, some bacteria can also perform QQ presumably to compete with competitors; such a mechanism is commonly found across several groups such as *Bacillus spp.* and *Pseudomonas spp.* (Borges and Simões 2019; Romero et al. 2012), which can produce lactonases (Dong et al. 2001; Rémy et al. 2020; Romero et al. 2012), acylases (Lin et al. 2003; Sio et al. 2006), and oxidoreductases (Tang and Zhang 2014) that break down AHLs. Future work needs to focus on the molecular mechanisms that enable bacterial signals to influence diatom physiology and growth and the signaling mechanisms that enable diatoms to nurture a beneficial microbiome.

11 Future Outlook

Insights into the complex interactions between diatoms and bacteria have gained major traction (Fig. 1), particularly in the past decade, owing to significant advancements in sequencing and other ‘omics techniques. The development of several diatom-bacteria symbiosis model systems (Amin et al. 2015; Bruckner et al. 2008; Durham et al. 2015; Shibl et al. 2020) has provided an invaluable platform to gain a deeper understanding of the dynamics underpinning diatom microbiome assembly, nutrient exchange, and signaling. The employment and/or expansion of genetic tools for both diatoms and their symbionts, including in environmentally relevant systems, is now vital to gain further mechanistic understanding of the molecular machinery governing interactions between these organisms.

These developments coupled with improvements in sampling diatoms and their microbiomes from field samples using microfluidic techniques and advances in culturing of natural diatom-bacteria assemblages in the laboratory will yield critical insight that better represents the diatom-bacterial symbioses of natural marine ecosystems. Use of microscopy approaches, such as fluorescent in-situ hybridization, could also be a powerful tool for illuminating the nature of physical associations between diatom cells and associated bacteria in the environment. Devising more sensitive and high throughput methods for the extraction and identification of diatom DOM and bacterial metabolites in lab and field samples, as well as characterization of gene functions in model diatoms and their symbionts will significantly enrich our knowledge of the metabolic and genetic basis of these relations. In addition, advances to single-cell analyses will enable the study of microbe–microbe interactions at a relevant scale. This is particularly important if

some of the diatom-derived DOM is highly labile and does not diffuse away from the phycosphere into bulk seawater, due to rapid microbial assimilation.

In the past decade and until today, many studies have highlighted a variety of chemical exchanges between diatoms and specific species of bacteria. Future work needs to focus on how diatoms assemble and maintain beneficial microbial communities (Fig. 2) and whether these communities are conserved or variable, and if so, what controls this variability. Shedding light on these mechanisms will potentially explain the reason diatoms have arisen to dominance in the modern ocean, despite their relatively recent evolution relative to other phytoplankton lineages. In parallel with our growing understanding of the molecular life of diatoms (Falcatore et al. 2020), these directions represent the next critical steps in understanding diatom-bacteria symbiosis and interkingdom coevolution between ocean microbes.

Box 1 Glossary of Terms

Term	Definition
Autotroph	An organism that does not require an external source of organic molecules either because it can synthesize them itself or because it does not require them.
Auxotroph	An organism that requires an external source of organic molecules that it cannot synthesize.
Diatom diazotroph associations (<i>DDA</i>)	Planktonic symbiosis between several diatom genera and di-nitrogen (N_2)-fixing bacteria [reviewed in Foster and Zehr (2019)].
Diatom microbiome	The collection of microbes, mostly bacteria, that occupy the microenvironment surrounding diatom cells, known as the phycosphere. While the definition of a microbiome for multicellular eukaryotes encompasses symbiotic, commensal, and pathogenic microbes (Berg et al. 2020), here we define the diatom microbiome as mainly composed of symbiotic and commensal microbes, with pathogenic/antagonistic bacteria being foreign bacteria that may sometimes evade phycosphere defenses.
Dissolved organic carbon (<i>DOC</i>)	Organic carbon molecules that pass through a filter with pore sizes ranging from 0.2 μm and 1 μm (Verdugo et al. 2004).
Dissolved organic matter (<i>DOM</i>)	Organic matter that passes through a filter with pore sizes ranging between 0.2 μm and 1 μm (Verdugo et al. 2004).
Extracellular polymeric substances (<i>EPS</i>)	High molecular weight ($MW > 410,000$) mixture of different polymers, composed mainly of polysaccharides, proteins, nucleic acids, lipids, surfactants, and humic-like substances (Flemming and Wingender 2001; Toullec and Moriceau 2018). EPS can aggregate to form transparent exopolymeric particles (TEP).
Fluorescence-activated cell sorting (<i>FACS</i>)	A specialized type of flow cytometry for sorting a heterogeneous mixture of particles, including biological cells, based on the specific light scattering and fluorescent properties of each particle.

(continued)

Box 1 (continued)

Homoserine lactones (<i>HSLs</i>)	Acyl-homoserine lactones (also abbreviated as AHLs) are an important class of quorum sensing molecules mostly produced by the Proteobacteria.
Infochemicals/signaling molecules	Biomolecules mediating communication and interactions between organisms. Typically, these molecules are produced in minute quantities, yet they have major influences on the organisms that perceive them.
The microbial loop	Originally coined by Azam et al. (1983), this term stems from the increased recognition of the importance of bacteria, nanoflagellates, and microzooplankton in the consumption of phytoplankton-derived dissolved organic matter, which subsequently makes its way up to higher trophic levels.
Phycosphere	The diffusive boundary layer that surrounds phytoplankton cells and creates a microenvironment where transport of metabolites is mostly governed by diffusion.
Particulate organic matter (<i>POM</i>)	Organic matter retained on a filter with pore sizes ranging between 0.2 μm and 1 μm (Verdugo et al. 2004).
Quorum sensing (<i>QS</i>)	A type of mostly bacterial cell–cell communication that enables bacteria to coordinate their gene expression as a function of the population cell density. QS is mediated by diffusive small molecules, known as autoinducers (e.g., HSLs).
Quorum-quenching (<i>QQ</i>)	Defined as the disruption of QS by any means, e.g., inactivation of AHL signals with enzymes.
Transparent exopolymeric particles (<i>TEP</i>)	Defined as $>0.4 \mu\text{m}$ transparent particles that consist of mostly acidic polysaccharides and are stainable with the dye Alcian blue (Alldredge et al. 1993).
Vitamins	Organic micronutrients, necessary as cofactors for enzymes of central and secondary metabolism.

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