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Zooming in on the phycosphere: the ecological interface for phytoplankton–bacteria relationships

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By controlling nutrient cycling and biomass production at the base of the food web, interactions between phytoplankton and bacteria represent a fundamental ecological relationship in aquatic environments. Although typically studied over large spatiotemporal scales, emerging evidence indicates that this relationship is often governed by microscale interactions played out within the region immediately surrounding individual phytoplankton cells. This microenvironment, known as the phycosphere, is the planktonic analogue of the rhizosphere in plants. The exchange of metabolites and infochemicals at this interface governs phytoplankton–bacteria relationships, which span mutualism, commensalism, antagonism, parasitism and competition. The importance of the phycosphere has been postulated for four decades, yet only recently have new technological and conceptual frameworks made it possible to start teasing apart the complex nature of this unique microbial habitat. It has subsequently become apparent that the chemical exchanges and ecological interactions between phytoplankton and bacteria are far more sophisticated than previously thought and often require close proximity of the two partners, which is facilitated by bacterial colonization of the phycosphere. It is also becoming increasingly clear that while interactions taking place within the phycosphere occur at the scale of individual microorganisms, they exert an ecosystem-scale influence on fundamental processes including nutrient provision and regeneration, primary production, toxin biosynthesis and biogeochemical cycling. Here we review the fundamental physical, chemical and ecological features of the phycosphere, with the goal of delivering a fresh perspective on the nature and importance of phytoplankton–bacteria interactions in aquatic ecosystems.

Within the context of ecosystem function (Box 1), the ecological relationships between phytoplankton and bacteria arguably represent the most important inter-organism association in aquatic environments. The interactions between these two groups strongly influence carbon and nutrient cycling, regulate the productivity and stability of aquatic food webs, and affect ocean–atmosphere fluxes of climatically relevant chemicals[1–3]. Indeed, the shared evolutionary history of these organisms[4] has undoubtedly played an important role in shaping aquatic ecosystem function and global biogeochemistry.

Within aquatic ecosystems, phytoplankton are the dominant primary producers and the base of the food web. Consistent with their common functional roles, we here consider the phytoplankton to include both microalgae (for example, diatoms and dinoflagellates) and oxygenic phototrophic cyanobacteria (such as *Prochlorococcus*, *Synechococcus* and *Anabaena*). Together, these organisms are responsible for almost 50% of global photosynthesis and are consequently important regulators of global carbon and oxygen fluxes[5,6]. The abundance and metabolism of aquatic heterotrophic bacteria (Box 1), which represent about a quarter of all biomass in the euphotic zone of aquatic habitats[7] and the engine room for Earth's major biogeochemical cycles[8], are intrinsically linked to phytoplankton production and biomass[9,10]. Indeed, while phytoplankton and bacteria are both fundamental biotic features of aquatic habitats in their own right, the strong ecological coupling between these two groups demands that the nature and consequences of their synergistic influences are explicitly considered.

Phytoplankton–bacteria interactions are multifarious and often highly sophisticated[11,12], and can span the spectrum of ecological relationships from cooperative to competitive[13]. At the simplest level, the relationship between these organisms is based on resource provision and can be either reciprocal or exploitative in nature[2] (Fig. 1). Aquatic heterotrophic bacteria obtain a large, albeit variable, fraction of their carbon demand directly from phytoplankton[14], with up to 50% of the carbon that is fixed by phytoplankton ultimately consumed by bacteria[15]. Bacterial consumption of phytoplankton-derived organic material primarily involves the assimilation of the large quantities of typically highly labile, dissolved organic carbon (DOC) (Box 1) released by phytoplankton cells into the surrounding water column[16], but also includes consumption of more complex algal products (for example, mucilage and polysaccharides)[17,18] and senescent or dead phytoplankton biomass[19].

From the perspective of a phytoplankton cell, bacteria can be providers of limiting macronutrients via remineralization[20,21] (Box 1), but also competitors for inorganic nutrients[22]. When the allochthonous (Box 1) supply of nutrients is low, phytoplankton growth is predicted to particularly benefit from bacterial delivery of regenerated nitrogen and phosphorus[2]. Furthermore, evidence for the development of specific phytoplankton–bacteria interactions based on bacterial synthesis of vitamins (for example, vitamin B_{12})[12,23] and enhancement of micronutrient (for example, Fe) bioavailability[24] has begun to highlight the complex nature of the ecological links between these groups of aquatic microorganisms.

Evidence for intimate and selective associations between phytoplankton and bacteria is further provided by the consistent detection of particular bacterial species from phytoplankton cultures and algal blooms[11,24–28], which has led to the proposition that 'archetypal phytoplankton-associated bacterial taxa' exist[29].

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Box 1 | Glossary.

Ecosystem function. The collective influence of an ecosystem's biodiversity, physical properties and chemical features on the trophic and biogeochemical links, transfers and fluxes within the system, including the subsequent impacts of these processes on the wider biosphere.
Heterotrophic. An organism that must acquire organic carbon from its environment for sustaining growth and generating energy.
Dissolved organic carbon. The large reservoir of organic material found in aquatic ecosystems that is operationally defined as 'dissolved' by its ability to pass through a 0.22 μm filter (although sometimes this cut-off is defined at 0.45 μm).
Remineralization. The transformation of organic material into simple inorganic components.
Allochthonous. A material that is imported into an ecosystem from an external source.
Phycosphere. The region immediately surrounding a phytoplankton cell that is enriched in organic molecules exuded by the cell into the surrounding water.
Rhizosphere. The zone immediately surrounding the roots of a plant that is enriched in molecules secreted from the root into the soil, providing a key interface for the ecological relationships and chemical exchanges between plants and soil microorganisms.
Phytostimulator. An organism or chemical that promotes plant growth.
Bioavailability. The quality of a molecule or material that renders it metabolically utilizable to a living organism.
Diazotrophic. The capacity of some prokaryotes to fix atmospheric dinitrogen gas into more biologically available forms of nitrogen (such as ammonium).

These observations are corroborated by global surveys that show that phytoplankton-associated bacterial communities are often restricted to only a handful of groups[30], including specific members of the Roseobacter clade (Rhodobacteraceae), Flavobacteraceae and Alteromonadaceae[13,18,25,26,28,30]. These apparently universal patterns imply that the lifestyles of some bacteria within these groups are profoundly defined by their interaction with phytoplankton, and likewise there is evidence that phytoplankton can either benefit[12] or suffer[28] from the presence of these key bacterial groups.

In line with evidence for species-specific associations[29,31] and the often reciprocal nature of the metabolic exchanges between bacteria and phytoplankton[11,12,24], there is an emerging view that phytoplankton–bacteria interactions should often be considered within the framework of symbiosis[32]. Such an intimate relationship among planktonic cells would require the maintenance of close spatial proximity over substantial time frames—which is perhaps not intuitive in a habitat that is seemingly physically unstructured and often characterized by fluid flow[33]. Indeed, oceanographers and limnologists have traditionally examined the dynamics of phytoplankton and bacteria over large spatial scales (hundreds of metres to thousands of kilometres)[34] and long temporal scales (seasonal to annual)[35]. Even contemporary efforts to define the microbial ecology of the marine environment, such as the *Tara* Oceans programme (a global oceanographic expedition examining the biodiversity and biogeography of planktonic organisms)[36], still consider the ocean from this large-scale perspective. While clear correlations between phytoplankton productivity and bacterial abundance consistently demonstrated at these large scales are indicative of tightly coupled regional distributions and seasonal patterns[9], it has also long been acknowledged that phytoplankton–bacteria interactions will often be played out at the microscale[37], within the close quarters required to permit metabolic exchange and potential symbiotic associations. More recent advances in our understanding of phytoplankton–bacteria interactions at genomic[12], metabolic[11] and behavioural[38] levels have begun to confirm the importance of intimate cell–cell interactions between these two groups.

The physical interface for these close spatial interactions is the region immediately surrounding an individual phytoplankton cell, where metabolites are most readily exchanged in the face of the diluting effects of diffusion and turbulence. This region, coined the phycosphere[37] (Box 1), occupies only a minute fraction of the water column, but represents the key meeting place—or, in some cases, battleground—for many of the phytoplankton–bacteria interactions that ultimately mediate ecosystem productivity and biogeochemistry. In his seminal paper, Cole[2] suggested that "in considering bacterial–algal interactions, we should ask ourselves whether a phycosphere exists". Here, we consider not only the existence of the phycosphere, but also its significance within aquatic habitats, by first exploring the physical and chemical processes that control its formation and persistence within the environment, and then assessing its ecological importance by examining how it facilitates interactions between phytoplankton and bacteria.

The phycosphere as a fundamental ecological interface

Before examining the ecological relevance of the phycosphere, it is instructive to consider the inherent physical and chemical features of this unique aquatic microenvironment and relate these characteristics to other analogous systems.

The aquatic equivalent of the rhizosphere. In many ways, the phycosphere is the aquatic analogue of the widely studied rhizosphere (Box 1), where microorganisms interact with plants in terrestrial ecosystems (Fig. 2). The rhizosphere is the narrow zone adjacent to a plant root that is enriched in organic substrates exuded by the plant into the surrounding soil, and is considered one of the most complex ecological interfaces on the planet[39]. This zone harbours high numbers of microorganisms that exploit the elevated concentrations of labile organic material near to the plant root, while at the same time often influencing the plant's nutrient uptake and growth[40]. The best known interactions within the rhizosphere involve endosymbiotic associations between legumes and rhizobia, which form anoxic root nodules where they fix nitrogen; and arbuscular mycorrhizal fungi, which colonize the roots of most vascular plants, increasing the plants' access to water and phosphorus[41].

Although most marine bacteria do not commonly form endosymbioses with phytoplankton, some striking similarities exist between the phycosphere and the rhizosphere (Fig. 2). First, phytoplankton and plant roots both radically alter the chemical environment in their immediate vicinity. They modify oxygen and pH levels and release a large array of organic compounds[1,39], some of which can be detected and metabolized by bacteria[37,41,42]. Second, chemotaxis plays a central role at both interfaces. Root exudates stimulate the motility of soil bacteria, which enables microbial colonization of the rhizosphere[39], while marine bacteria exhibit chemotaxis towards a range of phytoplankton exudates[37,42–44], which may similarly enable colonization of the phycosphere. Third, some of the microorganisms associated with the two environments are phylogenetically similar. Plant-growth-promoting rhizobacteria produce phytostimulators (Box 1; for example, biologically available sources of nitrogen, phosphorus, hormones and volatile compounds) that improve plant growth[45], and some of these bacteria, such as *Rhizobium* and *Sphingomonas*, have been widely identified in green algae cultures[46].

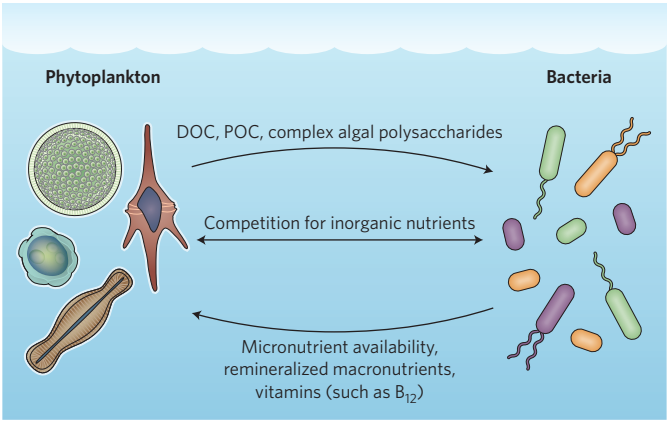


Figure 1 | Phytoplankton–bacteria interactions and exchanges. Interactions between phytoplankton and bacteria can range from the reciprocal exchange of resources required for growth (for example, nutrients and vitamins) to competition for limiting inorganic nutrients. POC, particulate organic carbon.

Fourth, some of the chemical 'currencies' exchanged are identical between the two cases. Besides primary metabolites such as sugars and amino acids, some more specific chemicals, including the organosulfur compounds dimethylsulfoniopropionate (DMSP) and 2,3-dihydroxypropane-1-sulfonate (DHPS), can be released at both interfaces and metabolized by bacteria[12,47] (Fig. 2).

Physicochemical features of the phycosphere. While both healthy and moribund phytoplankton cells exude metabolites into the surrounding water column[48–50], the release of photosynthates by healthy cells was initially attributed to an overflow mechanism by which cells excrete accumulated organic molecules when carbon fixation rates exceed the rate of carbon incorporation into biomass[51]. This explanation would, however, imply that exudation should decrease or even stop at night, but constant exudation rates have been measured over diel cycles[52,53]. Instead, exudation by healthy cells occurs through both passive and active transport. Gases, solvent molecules and many small hydrophobic compounds can passively diffuse through the cell membrane[49], while large macromolecules, such as proteins, are synthesized as they are translocated to the extracellular space[54]. In contrast, small polar and charged organic molecules (for example, monosaccharides and amino acids) need to be actively transported across cell membranes[55]. The deliberate release of specific compounds would impose a significant cost for phytoplankton in terms of both carbon and energy[56], which could be justified if these molecules enable the establishment of beneficial associations with bacteria.

In addition to affecting diffusion across membranes, molecular polarity plays an important role in determining diffusivity within the phycosphere. Hydrophilic molecules (for example, polar amino acids) diffuse more rapidly in water than hydrophobic molecules. Interestingly, many intercellular signalling molecules (such as diatom pheromones and bacterial homoserine lactones) are hydrophobic[13] and should exhibit limited diffusion away from cell surfaces.

The nature of the compounds exuded by a phytoplankton cell is influenced by the cell's health. During early growth phases, phytoplankton cells release soluble and generally highly labile, low-molecular-weight molecules, such as amino acids, carbohydrates, sugar alcohols and organic acids[29,49,50]. Notably, many of these low-molecular-weight compounds are also potent chemoattractants for bacteria[42,57]. When cells senesce, higher-molecular-weight molecules, including polysaccharides, proteins, nucleic acids and lipids, are released through exudation or cell lysis[29,48,58,59]. The different sizes and lability of these molecules have potentially important implications for the physical dynamics of the phycosphere, as well as the metabolism of phycosphere-residing bacteria and potential colonizers. Large molecules diffuse more slowly than small ones, which increases their residence time in the phycosphere, limits their loss to the bulk seawater, and ultimately influences the size and stability of the phycosphere.

The size of the phycosphere is primarily governed by the size of the phytoplankton cell. Given that cell size varies by more than two orders of magnitude across phytoplankton taxa, a large range of phycosphere sizes is expected (Box 2). The phycosphere size further depends on phytoplankton growth rate and exudation rate, along with the diffusivity of the exuded compounds and their background concentration (see Supplementary Information for an extended discussion and calculations).

An inherent difference between the rhizosphere and the phycosphere is that the interactions between phytoplankton and bacteria occur within a turbulent environment, which can affect the shape and size of phycospheres. For small phytoplankton cells or mildly turbulent conditions (for example, cells smaller than 70 μm in radius or a turbulent dissipation rate of 10^{-8} W kg^{-1}; Box 2), the stirring of the phycosphere by turbulence is negligible, with molecular diffusion instead leading to a symmetric spreading of the phycosphere rather than complex stirring and mixing (Fig. 3). For intermediate phycosphere sizes or turbulent conditions, turbulence will stretch the phycosphere and somewhat reduce its size, but will not significantly disrupt gradients (Fig. 3). Deformation increases with the intensity of turbulence and the size of the phycosphere, until the phycosphere is so large, or the turbulence so strong, that the chemical plume is stirred into a tangled web of filaments[60] and ultimately mixed. These scenarios are discussed quantitatively in the Supplementary Information.

Mechanisms for bacterial colonization of the phycosphere

After evaluating the theoretical considerations above, we suggest that Cole's question regarding the existence of the phycosphere[2] can be answered in the affirmative. Next, we consider whether bacteria can gain access to this potentially important microenvironment, and, if so, how. There are three potential mechanisms by which this can occur: random encounters, chemotaxis and vertical transmission (Fig. 4).

Random encounters. The abundance of phytoplankton and bacterial cells in the water column, as well as the diffusivity of these cells, governs the occurrence of random encounters between them. For non-motile bacteria and phytoplankton, encounters occur randomly by Brownian motion and are relatively rare. In a scenario of 10^6 bacteria per ml (each with a diameter of 1 μm) and 10^3 phytoplankton per ml (each with a diameter of 15 μm), a bacterium will encounter 0.0035 phytoplankton cells per day (or only one every 286 days), while a phytoplankton cell will encounter 3.5 bacteria per day (see Supplementary Information for calculations). After this initial random encounter, bacteria may maintain their position within the phycosphere if they can attach to either the surface of the phytoplankton cell[61] or the matrix of extracellular polymeric materials surrounding some phytoplankton species[62].

Motility and chemotaxis. Beyond random encounters, bacteria may use motility and chemotaxis to actively gain access to the phycosphere. Given the seemingly homogenous, turbulent and dilute nature of the pelagic environment, it is perhaps not immediately intuitive that motility and chemotaxis should be important properties for planktonic bacteria. However, many marine bacteria exhibit these behaviours[63], which provide a fitness advantage[38] within a habitat that is in fact sometimes highly heterogeneous at the microscale and awash with localized hotspots of organic material[64–67]. Indeed,

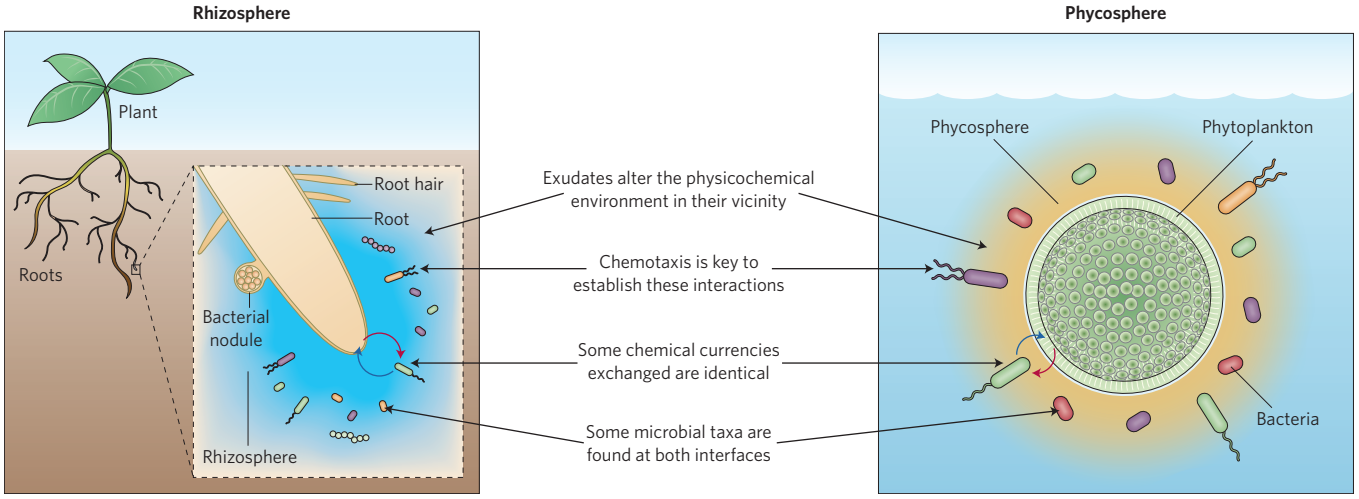


Figure 2 | The rhizosphere and the phycosphere are analogous microenvironments. The phycosphere, defined as the region surrounding a phytoplankton cell that is enriched in organic substrates exuded by the cell, is an important microenvironment for planktonic aquatic bacteria. It is the aquatic analogue of the rhizosphere, which is the key ecological interface for plant–microorganism interactions in terrestrial habitats.

relative to the enteric bacteria traditionally used as model organisms for chemotaxis[68], many planktonic marine bacteria exhibit high-performance motility[63], with swimming speeds that are typically several times faster than *Escherichia coli*[69]. This motility alone will greatly enhance a bacterium's chances of coming into contact with the phycosphere, because it increases the diffusivity of cells by more than 2,000-fold. So while a non-motile bacterium will only come into contact with 0.0035 phytoplankton cells per day, within a scenario of 10^5 motile bacteria per ml (when considering the proportion of motile cells to be 10%), each motile bacterium will encounter 9 phytoplankton cells per day. In this case, the number of bacteria with which a phytoplankton cell will come into contact will increase from 3.5 to 900 per day (see Supplementary Information for calculations). This increase in contact is solely driven by motility and ignores chemotaxis, which will further enhance contact rates. Many marine bacteria indeed exhibit highly sensitive and extremely directional chemotaxis[70–72], as well as exquisite abilities to modulate their swimming speed[71], allowing them to rapidly migrate into localized chemical hotspots within the short time frames required to exploit the often fleeting existence of substrate gradients in the water column[67].

For a chemotactic bacterium inhabiting the water column, the phycosphere makes an ideal target that is rich in labile, low-molecular-weight organic substrates. Indeed, the existence of the phycosphere was first proposed after the observation that marine bacterial isolates exhibit chemotaxis towards phytoplankton exudates[37]. It has since been demonstrated that marine bacteria exhibit chemotaxis towards the exudates of a wide variety of phytoplankton species[42–44] and a range of phytoplankton-derived substrates, including glycolate, acrylate, specific amino acids, and DMSP[37,57,73,74]. The importance of chemotaxis in the initiation of phytoplankton–bacteria interactions has been confirmed within laboratory model systems. For example, the capacity of *Marinobacter adhaerens* to perform chemotaxis was shown to fundamentally control the nature of microscale associations between this bacterium and the diatom *Thalassiosira weissflogii*[31].

Experimental approaches employing simulated phycospheres—generated using 10–40 μm diameter beads loaded with organic substrates[75] or with microfluidic channels designed to produce microscale chemical patches[43,72,76]—have revealed that many marine bacterial isolates indeed employ chemotaxis to exploit chemical gradients characteristic of phycospheres. More direct evidence has come from microscopic observations of marine bacteria swarming around phytoplankton cells[38,65] and even 'chasing' motile phytoplankton as they swim past[77] (although the latter may have been caused by the bacteria being swept along in the wake of the phytoplankton cell[78]).

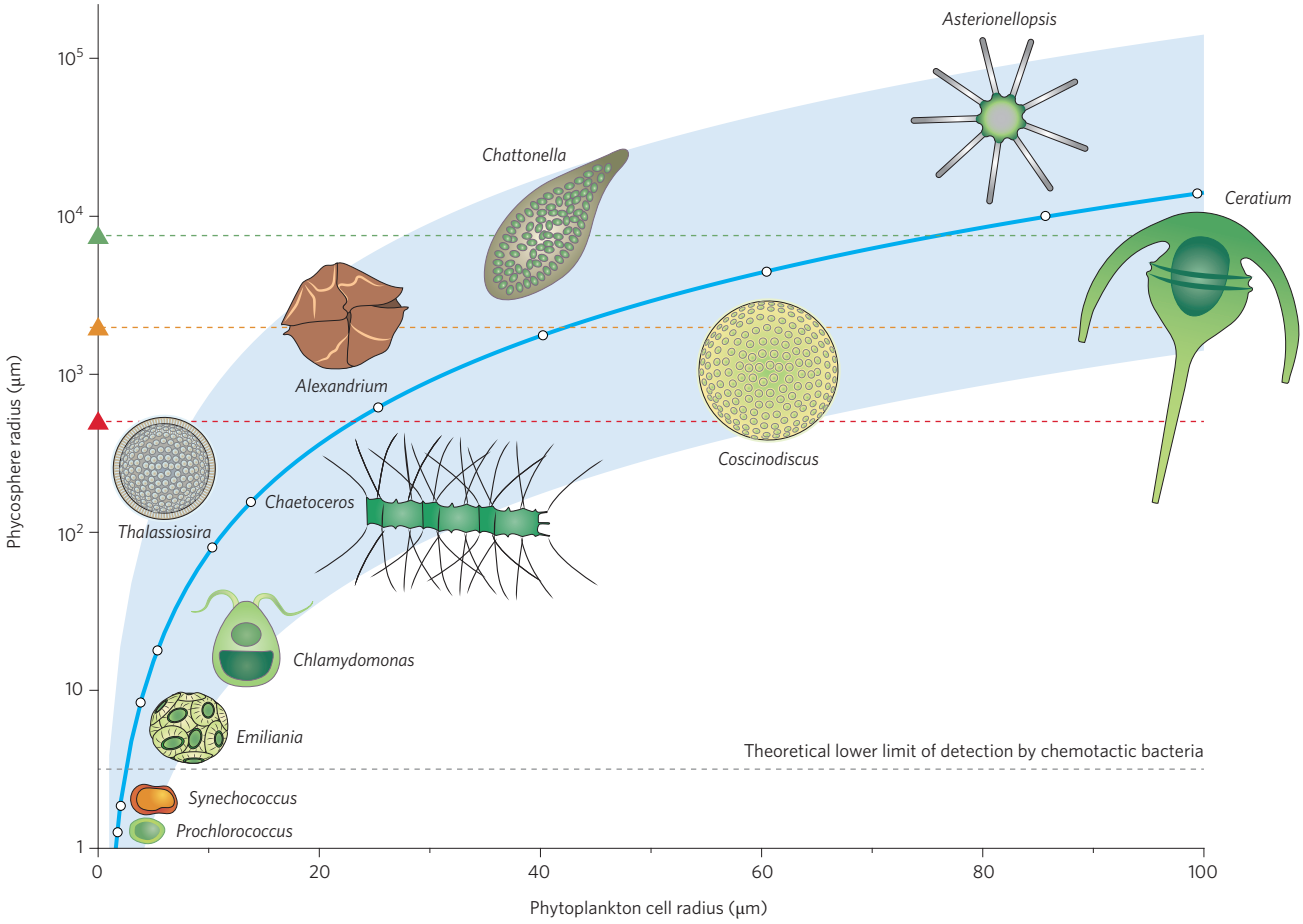
The ability of bacteria to use chemotaxis to exploit the phycosphere has also been widely examined from a theoretical perspective[38,79–81]. Early numerical approaches suggested that marine bacteria can use chemotaxis to cluster within the phycosphere of sufficiently large and leaky phytoplankton cells[80], but with only modest gains in nutrient exposure, and only under quiescent conditions[81]. However, these studies calculated bacterial responses to phycospheres using motility and chemotaxis parameters derived from *E. coli*, because equivalent parameters were not available for marine bacteria. As mentioned above, it is now clear that many chemotactic marine bacteria markedly outperform *E. coli*, with higher swimming speeds and directionality resulting in more efficient chemotactic responses[63,71,72,82]. Indeed, models that have incorporated motility characteristics that are more representative of marine bacteria have indicated a much greater potential for bacterial clustering within the phycosphere, even within mildly turbulent conditions[79,83]. A recent model indicated that while environmental conditions regulate the relative importance of the phycosphere to the overall bacterial consumption of phytoplankton-derived DOC, chemotaxis always strongly enhances bacterial uptake, and motile bacteria dominate phycosphere consumption under most scenarios[38].

Maintaining spatial proximity. Given the above theoretical, experimental and observational perspectives, it is perhaps appealing to envisage the phycosphere as a microenvironment characterized by swarming masses of chemotactic bacteria. However, it is noteworthy that the proportion of motile bacteria within pelagic marine environments is often low[84], and evidence for intimate reciprocal chemical exchanges between phytoplankton and bacteria has also come from model systems where the bacterial partner is in fact not motile or chemotactic. The apparently mutualistic relationship between the Roseobacter clade member *Ruegeria pomeroyi* and the diatom *Thalassiosira pseudonana*[12] does not rely on chemotaxis, as the *R. pomeroyi* genome lacks all known chemotaxis genes[85]. While it is possible that interactions of this type might persist via the bulk diffusive transport of substrates between phytoplankton and bacterial partners, such a relationship would be somewhat constrained by the sharp decay in concentration of molecules away from the cell surface (see Supplementary

Box 2 | Phycosphere size.

The size of the phycosphere is strongly determined by the size of the phytoplankton cell. For a 50 μm diameter diatom (assumed spherical for simplicity), with a typical growth rate of one per day, the concentration of small molecules exuded at a rate of 5% of the cell's carbon content per day[149] will be 240 nM of carbon at the cell surface. Concentration varies inversely with distance from the cell, so that at a distance of 10 times the cell radius, the concentration is 10% of that occurring at the cell surface, and at a distance of 100 radii, the concentration drops to 1%. Assuming the background concentration of the compound is 10 nM of carbon, this implies a ~1,200 μm radius phycosphere (defined here as the region with concentration more than 50% greater than the background). Higher exudation rates, higher growth rates and higher-molecular-weight compounds can result in considerably larger phycospheres (see Supplementary Information).

On the other hand, for a small phytoplankton cell, such as *Prochlorococcus*, which has a diameter of 0.8 μm, the size of the phycosphere will be negligible (<1 μm). Indeed, previous predictions based on motility and chemosensory parameters from *E. coli* indicate that the phycosphere associated with phytoplankton cells smaller than 4 μm in diameter are undetectable by chemotactic bacteria[80]. This prediction does not entirely rule out the possibility of chemotactic associations between heterotrophic bacteria and small cyanobacteria, for three reasons: marine bacteria exhibit chemotactic capabilities that substantially exceed those of *E. coli*[63,71]; chemotaxis of marine bacteria towards the exudates of *Prochlorococcus* and *Synechococcus* has been observed[42]; and physical associations between these small cyanobacteria and heterotrophic bacteria have been reported[150]. However, these potential physical constraints on the size of the phycosphere must be taken into account when considering the relative ecological significance of the phycosphere within a given environment, particularly because the bulk of photoautotrophic biomass and production within many marine ecosystems (for example, the oligotrophic open ocean) is comprised of small phytoplankton cells that are likely to generate a negligibly sized phycosphere.



Phycosphere radius as a function of cell radius. The baseline case (blue line) corresponds to a phytoplankton growth rate (μ) of one per day, a leakage fraction of 5% (f = 0.05), a leaked compound with n = 6 carbons, a molecular diffusivity of $D = 0.5 \times 10^{-9}$ m^2 s^{-1} and a background concentration of C_B = 10 nM. The phycosphere is defined as the region where the concentration is >50% above background (q = 1.5). Also shown are two further cases in which either μ, f, $1/D$, $1/C_B$ or $1/(q-1)$ by themselves, or the product of these five terms overall, is tenfold greater (upper boundary of the blue shaded region) or tenfold smaller (lower boundary) than in the baseline case. The grey dashed line corresponds to the theoretical lower limit for phycosphere detection by chemotactic bacteria as calculated using *E. coli* parameters[63] (it is, however, noteworthy that the chemotactic performance of marine bacteria appears to be substantially greater than *E. coli*[64]). The triangles on the y axis and the corresponding red, orange and green dashed lines denote the points where turbulence will have an effect on phycosphere shape and size, with the different coloured lines corresponding to turbulence levels of $\varepsilon = 10^{-6}$ (red), 10^{-7} (yellow) and 10^{-8} (green) W kg^{-1}. Threshold values were computed for the case of small molecules (diffusivity $D = 0.5 \times 10^{-9}$ m^2 s^{-1}) and assuming a Peclet number of Pe = 1. See Supplementary Information for calculations.

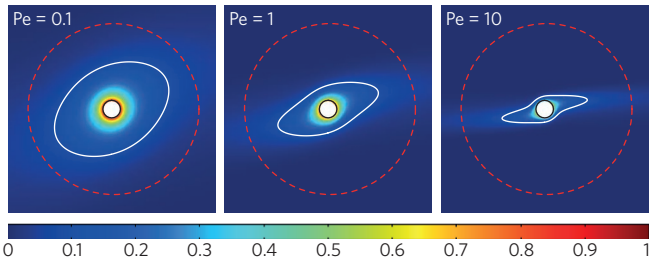


Figure 3 | The effect of mild to moderate turbulence on the phycosphere. Shown is the concentration of a given chemical (colour scale: 1 corresponds to the maximum concentration in the quiescent case) around a phytoplankton cell, assumed spherical (central white circle bordered in black). Three different Peclet numbers are shown. Pe = $a^2(\varepsilon/\nu)^{1/2}/D$ is a dimensionless number that accounts for the combined effect of cell radius a, turbulent dissipation rate ε, kinematic viscosity of water ν, and diffusivity of the exuded compound D. The larger the Pe, the stronger the deformation of the phycosphere. The white curve denotes the location where the concentration is 10% of the maximum concentration in the quiescent case. The red dashed line, included for reference, denotes the region computed for the quiescent case where the concentration is 10% of the maximum. Calculations were performed in three dimensions, but a two-dimensional view is shown.

Information). Such constraints are particularly pertinent within the context of molecules being transferred from bacteria to phytoplankton cells. While significantly elevated concentrations of molecules may occur up to hundreds of micrometres away from a phytoplankton cell, the plume of substrates surrounding a bacterial cell will drop 10-fold at only ~5 μm from the bacterium and 100-fold at ~50 μm (see Supplementary Information for calculations). This, together with the three-dimensionality of the environment, implies that a great majority of the metabolites that leak from bacteria will diffuse into bulk seawater and only a minute fraction will reach nearby phytoplankton cells. Therefore, in the absence of bacterial motility and chemotaxis to maintain spatial proximity between phytoplankton and bacterial cells, the persistence of interactions based on reciprocal chemical exchanges will often require close spatial coupling.

Close spatial associations among phytoplankton and bacterial cells may occur when the bacterial partner resides intracellularly within the phytoplankton cell or is attached to the external surface of the phytoplankton cell. Intracellular bacteria have been shown to be abundant in some phytoplankton species[86], while attachment of bacteria to the surfaces of phytoplankton cells is commonly observed[87,88], with phytoplankton-attached bacterial communities often exhibiting specific phylogenetic signatures that differ markedly from free-living assemblages and between phytoplankton host species[89]. In each of these scenarios, vertical transmission of bacterial associates might permit the prolonged preservation of close spatial associations in the absence of bacterial motility. An example of such a scenario is provided by the obligate symbiotic relationship that takes place in the pelagic ocean between the diazotrophic cyanobacterium *Atelocyanobacterium thalassa* (UCYN-A) and its prymnesiophyte phytoplankton host, whereby vertical transmission of the bacterial partner preserves the spatial association[90].

Random encounters, chemotactic behaviour and vertical transmission of attached cells are all likely to allow bacteria to retain contact with the phycosphere, albeit to different extents. Physical constraints (for example, the diffusion of metabolites) and the ecological nature of the interaction (obligate versus opportunistic; transient versus enduring) undoubtedly govern the manner in which spatial associations between phytoplankton and bacteria are established and maintained (Fig. 4). The fact that many aquatic bacteria exhibit strong chemotaxis to phytoplankton-derived chemicals[37,57,73,74], and that specific phytoplankton–bacteria symbioses relying on vertical transmission have a long evolutionary history[91], suggests that these scenarios have probably played a significant role in shaping the microbial ecology of aquatic ecosystems.

A marketplace for the exchange of chemical currencies

Phytoplankton–bacteria interactions involve the exchange of diverse chemical currencies that include both growth resources and infochemicals. The sensing or metabolism of these currencies underpins relationships between the two groups, spanning obligate mutualism, commensalism, competition and antagonism (Fig. 5). The phycosphere has been widely anticipated to represent the forum for the exchange of these chemical currencies, but technological barriers (related to difficulties in directly sampling the phycosphere microenvironment) have so far hampered confirmation of this hypothesis. However, given theoretical considerations regarding the requirement for close proximity of partners for chemical exchange—particularly within scenarios of specific or selective relationships—we propose that the phycosphere is the most likely setting for these interactions to occur.

Competition and antagonism. Phytoplankton–bacteria interactions have been most extensively considered within the context of competitive or antagonistic relationships[2,13,52,92–94], often involving competition for inorganic nutrients[52] or the algicidal activities of bacteria and related defence mechanisms of phytoplankton[95–98]. For example, the Bacteroidetes *Kordia algicida* infects diatoms and causes cell lysis using extracellular proteases[96] (Fig. 5), while in response to this attack the diatom *Chaetoceros didymus* has evolved a defence mechanism based on the secretion of algal proteases[99]. Another member of the Bacteroidetes, *Croceibacter atlanticus*, infects diatoms by attaching to their surface and inhibiting cell division, resulting in cell elongation and plastid accumulation[28] (Fig. 5). In this case, it appears that direct cell attachment and transfer of (as yet unidentified) molecules leads to increased exudation of organic matter that is used by the bacteria[28]. Moreover, some bacteria exhibit temperature-dependent virulence, such as the Rhodobacteraceae member *Ruegeria* sp. R11, which kills phytoplankton at 25 °C but not at 18 °C (ref. 100).

Mutualism. Recent demonstrations of widespread mutualistic associations have challenged the view that competition and antagonistic interactions dominate the relationships between phytoplankton and bacteria[11,12]. In fact, it may be argued that mutualistic interactions between these organisms are just as prevalent, or perhaps even more common, than antagonistic interactions[29]. Indirect support for this view comes from the frequent observation that prolonged culturing of phytoplankton in the absence of bacteria can negatively influence phytoplankton physiology and growth[101,102].

Among the most widely studied mutualistic interactions are obligate relationships between vitamin-synthesizing bacteria and phytoplankton species that require these vitamins[103–105]. Many eukaryotic phytoplankton cannot synthesize several of the vitamins that they require for growth. For example, among 326 phytoplankton species examined in one study, ~50% were found to require vitamins B_1, B_7 or B_{12} (ref. 23), with most species that form harmful algal blooms (HABs) requiring vitamins B_1 and B_{12} (ref. 106). Prokaryotes that synthesize these vitamins sustain phytoplankton growth in exchange for organic carbon[12,23,103,104].

Akin to interactions between nitrogen-fixing rhizobia and legumes[107], another common obligate mutualism is that between nitrogen-fixing cyanobacteria and diatoms or prymnesiophytes, whereby the cyanobacteria provide fixed nitrogen to the phytoplankton in exchange for amino acids and organic carbon[108–110]. A

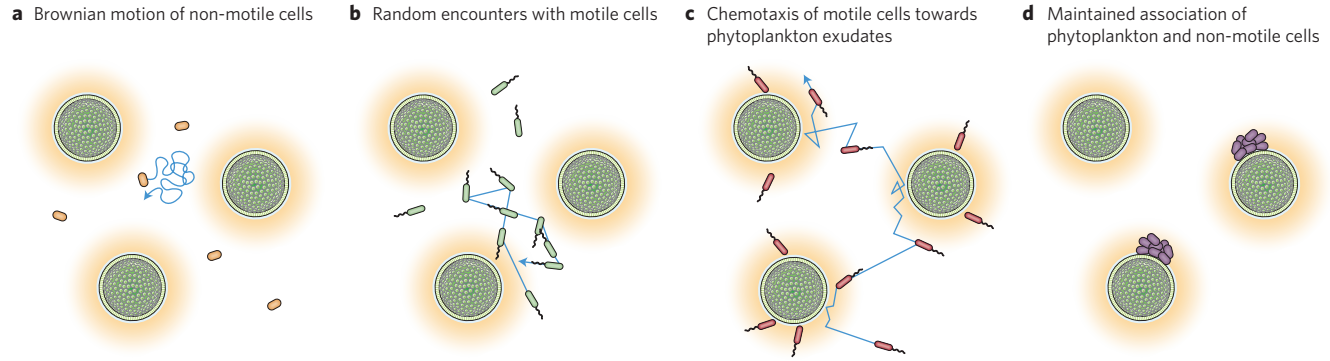


Figure 4 | Bacteria may encounter and, in some cases, retain contact with the phycosphere through several means. a, Non-motile cells, moving through the environment randomly via Brownian motion, will infrequently 'bump into' a phytoplankton cell at a rate of 0.0035 phytoplankton cells per day. **b**, The increased diffusivity of motile bacteria substantially increases their random encounter rate to 9 phytoplankton cells per day. **c**, Many motile marine bacteria also exhibit chemotaxis towards phytoplankton exudates, further increasing their capacity to migrate into, and then retain contact with, the phycosphere. **d**, Populations of non-motile bacteria that become attached to phytoplankton cells may retain prolonged contact via vertical transmission.

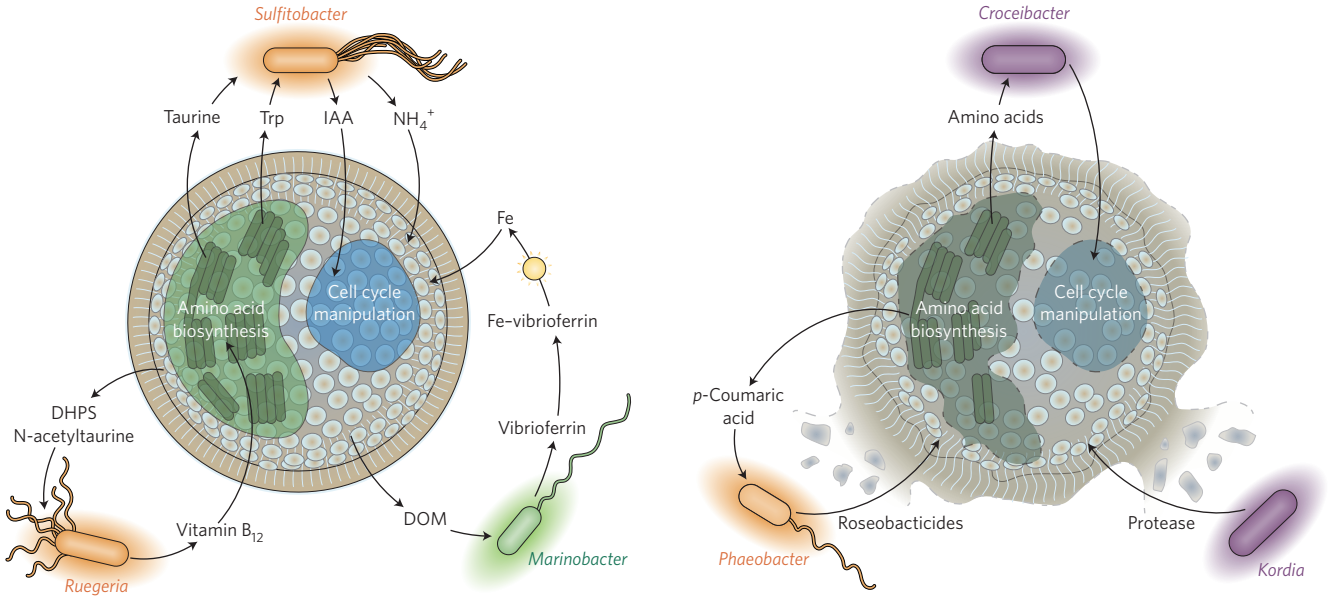


Figure 5 | Depiction of mutualistic (left) and algicidal (right) phytoplankton–bacteria interactions expected to occur in the phycosphere. Bacteria are coloured according to phylogeny: Rhodobacteraceae in orange, Alteromonadaceae in green and Flavobacteriaceae in purple. A generic phytoplankton cell is portrayed to represent multiple species. Shading around phytoplankton and bacteria represent gradients of molecules diffusing out of cells. Mutualistic interactions (left) occur between phytoplankton and *Sulfitobacter*, *Ruegeria* and *Marinobacter*. *Sulfitobacter* enhances the growth of the diatom *P. multiseries* by converting diatom-secreted tryptophan (Trp) to the growth-promoting hormone indole-3-acetic acid (IAA), which is released and subsequently taken up by the diatom to increase its cell division. *Sulfitobacter* also provides ammonium to *P. multiseries* in exchange for the diatom-secreted carbon source taurine. *R. pomeroyi* provides the diatom *T. pseudonana* with vitamin B_{12}, which is used in biosynthesis of the amino acid methionine in exchange for several carbon sources, including N-acetyltaurine and 2,3-dihydroxypropane-1-sulfonate (DHPS). *Marinobacter* secretes the siderophore vibrioferrin to acquire iron in the dark; in sunlight, the iron–vibrioferrin complex is highly photolabile and degrades, releasing bioavailable iron that is taken up by phytoplankton in exchange for DOM. Algicidal interactions (right) occur between phytoplankton and *Croceibacter, Phaeobacter* and *Kordia*. *C. atlanticus* attaches to diatom cell surfaces and releases an as yet unidentified molecule that arrests diatom cell division and increases diatom secretion of organic carbon, including amino acids. *P. gallaeciensis* senses secretion of *p*-coumaric acid from the coccolithophore *E. huxleyi* during senescence, which activates the bacterial production and release of the algicidal molecules roseobacticides A and B, which lyse *E. huxleyi* and release DOM. *K. algicida* produces extracellular proteases that lyse diatom cells in order to acquire DOM.

further example involves phytoplankton that depend on nearby bacteria to detoxify reactive oxygen species (such as hydrogen peroxide)[111–113], although it remains unclear what benefit bacteria reap from this interaction.

In contrast to early views that phytoplankton–bacteria interactions involved only recycling of algal detritus by bacteria[114], recent evidence has revealed far greater complexity in chemical exchange. For example, in exchange for bacterially derived ammonium, the diatom *Pseudo-Nitzschia multiseries* supplies the Rhodobacteraceae member *Sulfitobacter* sp. SA11 with organosulfur molecules, including taurine and DMSP (Fig. 5). The diatom also secretes the amino acid tryptophan, which is converted by the bacterium into the hormone indole-3-acetic acid (IAA)—which is then transferred from the bacterium back to the diatom to promote its cell division and increase its carbon output[11]. The importance of this multifaceted and mutualistic infochemical exchange is corroborated by the ubiquitous production of IAA by Rhodobacteraceae in the ocean[11,115] and by widespread growth responses of microalgae to IAA[116,117].

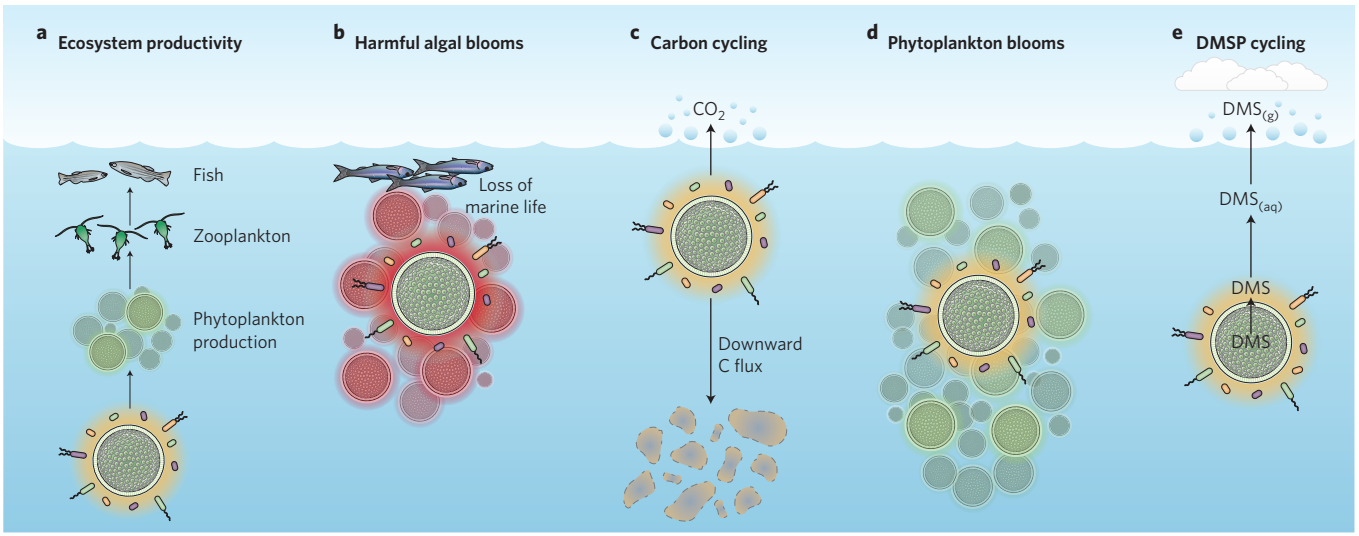


Figure 6 | Potential large-scale implications of processes taking place within the phycosphere. a, Ecosystem productivity: increased phytoplankton production supported by bacterial provision of remineralized nutrients, vitamins or micronutrients in the phycosphere supports heightened food web productivity. **b**, Harmful algal blooms: some bacteria promote the growth of toxic phytoplankton and their production of toxins[130,131]. **c**, Carbon cycling: phytoplankton–bacteria interactions within the phycosphere can manipulate the level of aggregation of phytoplankton biomass, which subsequently controls downward flux of C. Increased aggregation of cells will lead to increased export to depth[133], while decreased aggregation will reduce downward C flux[132], leading to increased respiration and CO_2 production in the upper water column. **d**, Phytoplankton blooms: bacterial provision of limiting nutrients and vitamins will influence phytoplankton competition and bloom dynamics. **e**, DMSP cycling: pathways of bacterial DMSP degradation in the phycosphere may influence DMS production and flux of this volatile into the atmosphere.

Interestingly, these molecular exchanges bear resemblance to interactions that dominate the rhizosphere. For example, nitrogen-fixing bacteria provide ammonium to legumes in exchange for organic carbon. In addition, multiple signals are exchanged between legumes and bacterial symbionts, including IAA[107,118] and tryptophan[119].

Another example of a complex, and apparently mutualistic, chemical exchange involves the Roseobacter clade bacterium *R. pomeroyi*, which sustains the growth of the diatom *T. pseudonana* by secreting vitamin B_{12} in exchange for a suite of diatom-derived molecules, including sugar derivatives, organic nitrogen compounds[120] and most significantly, the organosulfur molecule DHPS[12] (Fig. 5). Because DHPS catabolism is restricted to limited groups of marine bacteria[12], its secretion suggests a preferential selection of specific bacteria by diatoms. In addition, *T. pseudonana* differentially regulates more than 80 genes homologous to those used by plants to recognize external stimuli, pointing towards further parallels between rhizobial and phytoplankton–bacteria interactions[120].

Iron and carbon exchange between several *Marinobacter* species and a wide range of phytoplankton, including diatoms, dinoflagellates and coccolithophores, is also suggestive of a mutualistic interaction[24] (Fig. 5). Iron is an important micronutrient for most microorganisms, yet its acquisition in the marine environment is hampered by its scarce bioavailability[121,122]. Many marine bacteria, including *Marinobacter* species, alleviate iron limitation by excreting small organic molecules with exceptionally high affinity for iron, called siderophores[123]. Phytoplankton-associated *Marinobacter* species produce the siderophore vibrioferrin[124], which forms an iron complex that is highly photolabile. Vibrioferrin supplies *Marinobacter* with iron in the absence of light, but once exposed to sunlight the vibrioferrin–iron complex degrades within minutes, releasing inorganic soluble iron. This labile form of iron is then quickly taken up by the bacteria as well as the phytoplankton host, which releases DOC to sustain bacterial growth[24].

Adapting to market conditions. Phytoplankton–bacteria interactions can also change dynamically according to the physiological state of the partners. For example, the Rhodobacteraceae member *Phaeobacter gallaeciensis* establishes a potentially mutualistic relationship with healthy cells of the coccolithophore *Emiliania huxleyi*[125] by producing the growth-promoting hormone phenylacetic acid and the antibiotic tropodithietic acid, which may kill algicidal bacteria, in exchange for organic carbon. However, when *E. huxleyi* cells become senescent, the bacterium shifts its lifestyle to become an opportunistic pathogen. Upon detection of *p*-coumaric acid, an algal by-product released during senescence, *P. gallaeciensis* releases roseobacticides A and B, algicidal molecules that lyse *E. huxleyi*[125] (Fig. 5). This 'Jekyll and Hyde' strategy allows *P. gallaeciensis* to maximize access to algal organic matter, first by a steady association with healthy phytoplankton cells and then by killing the cells when they become senescent. Similar interactions have also recently been documented between another member of the Rhodobacteraceae, *Dinoroseobacter shibae,* and the dinoflagellate *Prorocentrum minimum*[126], suggesting that these types of strategies might be widespread.

Clearly, the chemical ecology of the phycosphere is sophisticated and complex, and it is even possible that participating microorganisms exploit the different physical properties of molecules in the phycosphere to their advantage. Many of these chemicals are small charged molecules that are highly soluble and diffusible (for example, ammonium, taurine and DHPS), and will provide broadcast cues, whereas others are non-polar and extremely insoluble (such as roseobacticides) and will have more localized effects. This could lead to spatial partitioning within the phycosphere, with attached bacteria utilizing poorly diffusible substrates on the surface of the phytoplankton cell and free-living chemotactic bacteria responding to more highly soluble and diffusible molecules from a greater distance. Or one might alternatively envisage a cascade of cues, whereby a phytoplankton cell could, for example, use rapidly diffusing molecules such as taurine to attract bacteria from a distance, and then less diffusible molecules as a second layer of selectivity in attracting true mutualists closer to the cell. Such a sophisticated chemical exchange is plausible given that a similar scenario has

been reported in rhizobial symbiosis, whereby legumes secrete flavonoid molecules that attract diverse bacteria, and then a complex signalling mechanism leads to the establishment of symbiosis with only selected partners[118].

A microscale environment with global significance

While bacteria–phytoplankton interactions in the phycosphere occur within an inherently microscale context, they may often have cascading bottom-up influences on ecosystem-scale processes (Fig. 6).

Primary productivity and algal blooms. The overall productivity of aquatic habitats is overwhelmingly governed by phytoplankton primary productivity, which in turn is controlled by the availability of key limiting nutrients, minerals and vitamins. While the provision of these limiting resources often comes from large-scale physical processes, in some cases more localized resource inputs from the phycosphere are predicted to help sustain phytoplankton productivity, particularly when allochthonous nutrient inputs are low[2]. Bacterial remineralization within the phycosphere has been proposed to provide phytoplankton cells with locally elevated concentrations of macronutrients[20], although this would lead to 'regenerated' rather than 'new' production[127]. On the other hand, some phytoplankton species acquire newly bioavailable (Box 1) nitrogen through intimate associations with symbiotic diazotrophic (Box 1) bacteria[90]. Furthermore, interactions played out in the phycosphere can also enhance phytoplankton access to key limiting micronutrients, including iron[24] and vitamins[12]. When these latter examples are extrapolated from the single-cell level to the scale of the phytoplankton community, phycosphere-based interactions may play a significant role in governing bulk rates of primary production, which subsequently influence aquatic food web structure and fishery yields.

The localized mediation of phytoplankton growth by bacteria in the phycosphere will also influence competitive interactions among phytoplankton species, which in turn could shape phytoplankton bloom dynamics. Indeed, specific bacterial taxa are consistently associated with phytoplankton bloom events[29]. However, in addition to the possible stimulatory influences of bacteria residing within the phycosphere, other algicidal species have been implicated in bloom collapse by lysing phytoplankton cells[94]. These bloom regulation processes are particularly important within the context of HABs, whereby some phytoplankton species produce toxins that can accumulate through the food chain[128]. While only 2% of all phytoplankton species produce HABs[128], these phenomena are occurring with increasing frequency and can have a disproportionately large impact on natural ecosystems, public health and local economies[129]. Bacteria can both augment and buffer the influence of HABs. There are examples of algicidal bacteria lysing toxic phytoplankton species, leading to HAB termination[130]. On the other hand, some bacterial species enhance the growth of HAB-forming species[130] and even increase the production of toxins[131].

Biogeochemical cycling. The phycosphere also represents an important hotspot for biogeochemical cycling. Within the context of carbon cycling, bacteria within the phycosphere will experience organic matter concentrations that are orders of magnitude higher than in the surrounding water, with the nature of this organic material playing a large role in determining its ultimate fate. Bacteria that use chemotaxis to exploit the elevated concentrations of photosynthates within phycospheres have been shown to substantially enhance DOM exposure rates[72], but whether this translates into increases in the amount of cycled carbon remains unknown[67]. A recent modelling study revealed that the proportion of DOM that is consumed by bacteria in the phycosphere can be high (up to 92%), but is very sensitive to environmental conditions, particularly bacterial abundance[38]. When the phycosphere is enriched in more complex organic materials, such as transparent exopolymer particles (TEP) often found associated with diatom phycospheres[13], bacterial colonization can have a direct effect on the amount of carbon that is respired in the upper ocean. Indeed, an enhancement of bacterial degradation of these sticky polysaccharides decreases the aggregation of phytoplankton cells and reduces the amount of carbon transported to depth[132]. A complicating factor is that some bacteria associated with the surfaces of diatoms enhance the production of TEP[133], which increases diatom aggregation and carbon export.

Interactions occurring within the phycosphere are also likely to play a significant role in the marine sulfur cycle, which may subsequently exert an influence on climatic processes. Marine phytoplankton produce large quantities of the sulfur compound DMSP, which accounts for up to 10% of the carbon fixed by phytoplankton photosynthesis[134,135]. DMSP also provides a substantial fraction of the carbon and sulfur requirements of heterotrophic marine bacteria[136,137], and for many it acts as a potent chemoattractant and thus potentially an important cue for bacterial colonization of the phycosphere[57,73]. However, not all marine bacteria metabolize DMSP in the same way, with the relative strength of two competing degradation pathways determining the proportion of DMSP that is ultimately converted into dimethyl sulfide (DMS)[138], a volatile gas accounting for 90% of biogenic sulfur emissions to the atmosphere and a major precursor of cloud condensation nuclei[139]. The identity and DMSP degradation capacity of the bacteria inhabiting the phycosphere and/or the chemical conditions (for example, DMSP concentration or other chemical cues) within the phycosphere might regulate the direction of DMSP transformation and thereby influence the amount of DMS released to the atmosphere. Given the climatic significance of DMS, these microbial-scale ecological interactions, played out within the phycosphere, would have important implications for regional-scale climate regulation.

Perspectives

Evidence for substantial complexity and sophistication in the chemical exchanges between phytoplankton and bacteria is suggestive of a requirement for close spatial proximity of the protagonists. This points to the fundamental role of the phycosphere as a key meeting place for shaping phytoplankton–bacteria partnerships and antagonisms, and supports the proposition that the phycosphere's importance might be akin to that of the rhizosphere in plant–microorganism relationships[2]. However, while the concept of the phycosphere has been widely adopted, there is in reality little direct experimental evidence for its occurrence or the extent of its role within phytoplankton–bacteria associations. This is largely a consequence of the challenges associated with examining exchanges and interactions within the minute volumes occupied by phycospheres. While the coupling of ecogenomics and analytical chemistry has recently provided important new perspectives on the nature of phytoplankton–bacteria interactions[11,12], the next step must be to extend these approaches from the level of bulk, culture-flask analyses to the scale of the phycosphere microenvironment. While achieving this will be far from trivial, new tools and approaches are beginning to provide previously unattainable capacity to zoom in on the phycosphere. Microsensors and microelectrodes[140] have been used to measure microscale chemical features of the rhizosphere[141], while micromanipulation techniques have recently been used to examine microbial communities within specific microenvironments, such as the termite gut[142]. Approaches of this kind could also be applied to sample the microscale chemical and microbiological features of the phycosphere. New tools to examine the genomic characteristics of microbial assemblages at the microscale, including the development of low-volume metagenomic[143], along with single-cell genomic[144] and transcriptomic[145] approaches, provide an avenue for characterizing

microbial processes at the molecular level inside the phycosphere. Other technologies including microfluidics[146] and nanoscale secondary ion mass spectrometry (NanoSIMS)[147,148] also provide capacity to interrogate microbial interactions and chemical transfers within a microscale context. A further, significant, challenge will then be to take these approaches out of artificial laboratory settings and into the natural aquatic environment. These targeted approaches for zooming in and teasing apart the dynamics of the phycosphere will ultimately provide a clearer perception and a greater recognition of the importance of this specific microenvironment within phytoplankton–bacteria interactions, helping to deliver more robust insights into the basal function of aquatic ecosystems.

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Author contributions

J.R.S., S.A.A., J.-B.R. and R.S. conceived the study, researched the literature and wrote the manuscript.

Additional information

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The authors declare no competing financial interests.