Diatom–Bacteria Interactions in the Marine Environment

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Diatom–bacteria interactions evolved during more than 200 million years of coexistence in the same environment. In this time frame, they established complex and heterogeneous cohorts and consortia, creating networks of multiple cell-to-cell mutualistic or antagonistic interactions for nutrient exchanges, communication, and defence. The most diffused type of interaction between diatoms and bacteria is based on a win-win relationship in which bacteria benefit from the organic matter and nutrients released by diatoms, while these last rely on bacteria for the supply of nutrients they are not able to produce, such as vitamins and nitrogen. Despite the importance of diatom–bacteria interactions in the evolutionary history of diatoms, especially in structuring the marine food web and controlling algal blooms, the molecular mechanisms underlying them remain poorly studied.

marine diatoms
marine bacteria
microbial interactions
microbiomes

1. Introduction

Diatoms are among the most successful phytoplanktonic organisms, thriving in all aquatic environments [1], where they have to cope with competitors, pathogens, and grazers [2][3]. To defend themselves, they have developed different strategies, including the production of secondary metabolites affecting the reproduction, fitness, and viability of grazers, competing microalgal species, and bacteria. The interactions with bacteria living in their surroundings are particularly crucial to success in most environments [4]. Bacteria assimilate nutrients from the sea and sequester minerals with high efficiency, competing with microalgae, including diatoms, for resources while establishing positive collaborations with some other species based on the exchange of nutrients fundamental for both [5].

The interactions between diatoms and bacteria are fundamental in shaping population dynamics, are not only related to nutrient exchange, and are often complex and heterogeneous, spanning from mutualistic to antagonistic [6][7][8]. However, despite the importance of such interactions in the evolutionary history of diatoms, in structuring the marine food web, and in controlling algal bloom termination, the molecular mechanisms and factors underlying this crosstalk remain poorly studied [9]. The existence of an inter-kingdom mechanism of signalling between bacteria and diatoms has been confirmed only in the last decade [10]. In this interplay, bacteria communicate through the production and release of quorum sensing (QS) molecules, while diatoms produce pheromones possessing functionalities similar to bacterial QS molecules.

2. Diatom–Bacteria Niches of Interactions

The ocean is a heterogeneous environment in which nutrients are not uniformly distributed but are pumped into the water column by biotic and abiotic sources and spread by turbulence and currents, creating local nutrient patches [11]. Consequently, bacteria, microalgae, and other members of the marine plankton are aggregated in "hot spots" [11], in which nutrient exchanges, communication, and defence are facilitated [12][13]. In those spots, interactions between diatoms and bacteria may occur both through chemo-attraction and attachment to the cell surface, which are mediated by QS in the case of motile bacteria [14], or more rarely by random encounters and collisions due to water movements in the case of non-motile bacteria [4][15][16]. These microenvironments have different features, and the most common are marine snow in open waters [17] or biofilms on the surface of different substrates in the photic zones [12][18]. A relevant role in establishing interactions among diatoms and bacteria is played by the phycosphere [8][19].

2.1. Phycosphere

The phycosphere is the physical space surrounding the diatom's cell surface, in which nutrients and exudates are mostly concentrated and the exchanges between diatoms and bacteria occur to a greater extent [8][19] (**Figure 1**).

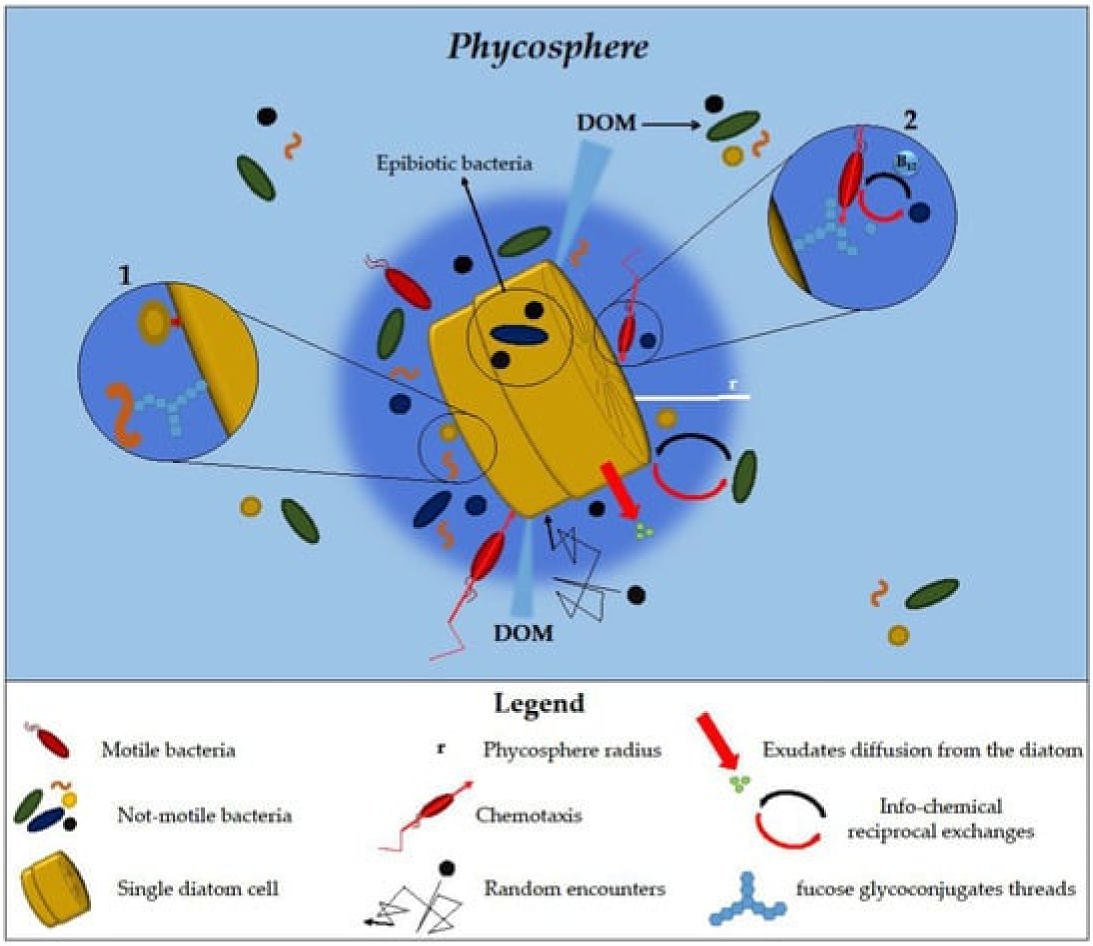

Figure 1. Phycosphere features and diatom–bacteria interactions occur in it. The phycosphere is represented as a dark blue gradient. The different types of interactions and types of contact are illustrated in the zoom-in circles (details in the text). Zoomed-in circle n° 1: bacteria attached to diatom cells by direct contact or to fucose glycoconjugate threads. Zoomed-in circle n° 2: bacteria unable to directly bind glycoconjugates benefit from their degradation by other bacteria possessing polysaccharide-degrading enzymes.

In general, phycosphere size depends on the size of phytoplankton cells, growth, and exudation rates that set different phytoplankton-phycosphere radii [8]. Since the turbulence is not able to influence water layers at a smaller scale, the transport of exudates from diatoms occurs mainly by diffusion [4]. However, when the phycosphere and cell radius are over a certain threshold size, mild to moderate turbulence can influence the diffusion rate and the phycosphere size itself by stirring and stretching its shape and mixing the exudate gradient [8]. Due to the diversified interactions occurring and the variability of its composition and structure, the phycosphere can be considered a very dynamic environment [20]. This milieu offers several advantages to the bacterial community associated with microalgae by providing them with easier access to organic matter released compared to those free living in the water column [14]. This may lead to an increased local concentration of bacteria in the phycosphere, as it was shown that richness in particulate organic matter may increase bacterial species diversity and abundance [21] (**Figure 1**).

The stability of the phycosphere and the interactions occurring in it are influenced by the chemical composition of exudates released by the diatoms. Indeed, a greater loss of small molecules compared to large ones generally occurs since the latter diffuse at a lower rate, which results in an increase in their residence time in the phycosphere, ultimately influencing its size and stability [8]. This may generate a chemotactic gradient, attracting coloniser bacteria that often form consortia with commensal or mutualistic relationships, degrading diatom-released compounds [22]. On the other side, bacteria may also influence the chemical composition of the phycosphere, with some differences related to the diversity of metabolism in different species [4][8][15].

Confocal laser scanning microscopy (CLSM) imaging showed that some bacteria stay in the phycosphere by either binding directly to the diatom cell surface or attaching to fucose glycoconjugate threads extending from diatom cells, as observed for bacteria associated with *Thalassiosira rotula* [23]. On the contrary, other bacteria associated with the same diatom are not able to directly attach to the diatom cell surface needing to interact with glycoconjugate-binding bacteria in order to colonise diatom cells. Bacteria possessing polysaccharides degrading enzymes can be attracted by threads and tufts of diatoms that can be used as carbon sources, favouring the establishment of cooperative association with other bacteria, as happens for *Gramela forsetii* that degrade the fucose glycoconjugate, making them available for *Planktotalea frisia* that in return produce vitamin B_{12}, for which *G. forsetii* is auxotroph (**Figure 1**, Zoomed-in circles n° 1 and 2).

Among bacteria interacting with diatoms, the epibiotic ones, that are attached to diatom cell surfaces, often have been found between and underneath a specific region of the diatom frustule, the cingulum, where they are more protected against several stressors while taking advantage of organic matter released by diatoms in the surroundings of this structure [24] (**Figure 1**).

Metagenomics and metaproteomics analysis of bacteria occurring during phytoplankton blooms in the North Sea revealed a “tight adherence (*tad*)” gene cluster codifying for the formation of pili, allowing the attachment on the diatom surfaces and the colonisation of the phycosphere in a subset of bacteria belonging to the order Rhodobacterales [25]. Those bacteria relied on *tad* in combination with QS, motility, and chemotaxis to colonise the phycosphere.

Diatoms also contribute to the selection of the bacteria species entering the phycosphere. This is the case of *A. glacialis*, which releases rosmarinic acid (RA) and azelaic acid (AA), which are able to selectively promote the motility and growth of specific bacteria, operating as a selection agent [26]. Transcriptomics, metabolomics, and co-expression network analysis revealed that *Phycobacter* was able to assimilate and catabolize AA using it as a carbon source, while *Alteromonas macleodii* showed the activation of a stress response mechanism based on the activation of cytoplasmic efflux and the downregulation of ribosome and protein synthesis pathways [27], confirming that AA is able to mediate microalgae-microbiome interactions.

The phycosphere displays some similarities with the plant rhizosphere, the interface between plant roots and soil [28]. As already reviewed by Seymour et al. [8], in both microenvironments, interactions with microorganisms are established and driven by the chemotactic perception of plant-released organic compounds, and some microbial taxa can be detected at both types of interfaces, such as *Rhizobium* and *Sphingomonas*.

2.2. Marine Snow

Diatom aggregation is one of the main driving forces in marine snow formation, occurring commonly at the end of diatom blooms due to the collision and aggregation of the cells with organic matter and, to a lesser degree, from the resuspension of benthic biofilms [29]. Marine snow patches, being rich in nutrients and widely distributed, transport organic matter from the upper to the lower layers [30] (**Figure 2**).

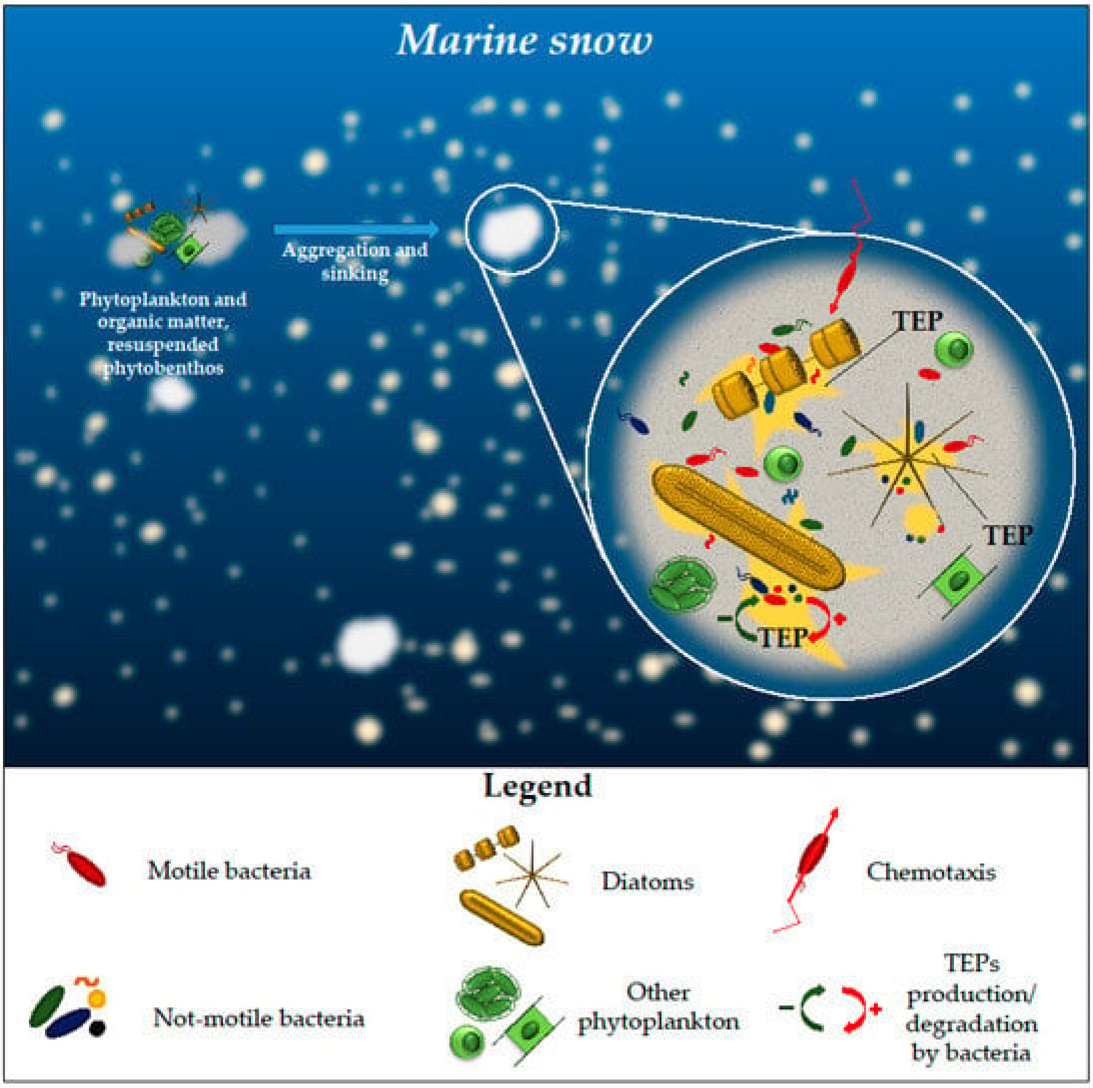

Figure 2. Marine snow formation and composition. The background gradient from light to dark blue indicates the sinking from the upper to the lower water layers occurring when diatoms, followed by other phytoplankton algae, aggregate with organic matter at the end of blooms. A zoom on a single particle highlights the presence of bacteria and of different phytoplankton groups. Bacteria can reach these aggregates by chemotaxis. Transparent exopolymeric particles (TEPs) released by diatoms and bacteria are responsible for the cohesion of the particles. Bacteria are also able to degrade TEPs produced by diatoms, influencing the aggregation process.

The quality and quantity of organic matter transported to the deep ocean by sinking particles are greatly influenced by bacterial succession [31]. In a network analysis conducted on a 3.5-year sampling dataset, it emerged that Flavobacteriia and some Gammaproteobacteria, among which *Pseudoalteromonas* and *Alteromonas* genera, use chemotactic motility to detect and rapidly reach diatom aggregates, contributing with other bacterial species to their degradation in the dark ocean.

One of the main agents training the aggregation are TEPs, principally released by diatoms [29] but also by bacteria and by phytoplankton in general [32] (**Figure 2**). TEPs are acid-rich polysaccharides that can be formed both abiotically and biotically through the condensation or exudation of extracellular polymeric substances (EPS) [33].

The production of diatom TEP precursors is species-specific. Different diatom species can produce them in low or high quantities, while others do not produce them at all [17]. For high TEPs producing diatoms, it seems that the aggregation of particles is part of their life cycle, contributing to their sinking at the end of the blooms. Polyunsaturated aldehydes (PUAs), released by diatoms in high quantities at the terminal phase of the blooms or through wound-activated mechanisms [34], have a dose-dependent effect on TEP formation [35] and on the community composition of the bacteria associated with sinking particles [36].

2.3. Biofilms

Biofilms represent one of the most widespread modes of aggregation among microorganisms, whose interaction actively regulates organic matter cycles and energy fluxes [12][18]. They represent a hub for microorganisms' aggregation where metabolic cooperation, cell-to-cell communication, genetic exchanges, protection against grazers, pathogens, toxins, and environmental stressors are favoured [12]. Diatoms are among the first colonisers of organic and inorganic surfaces in the marine environment, representing an important component of the biofouling community [37]. Pennate diatoms, having predominantly a benthic lifestyle, often dominate biofilms. Among them, the most widespread species belong to the genera *Navicula*, *Amphora*, *Nitzschia*, *Pleurosigma*, and *Thalassionema* [38]. Biofilms are composed of a matrix of EPS, mainly produced by bacteria and diatoms, that can be colonised by autotroph and heterotroph organisms, among which other bacteria, fungi, protozoa, and algae [39][40], all establishing connections among them and with the substrates [18] (**Figure 3**). EPS comprise different organic macromolecules, mainly polysaccharides but also glycoproteins and other organic polymers [39][41] and can be bound to the cells or released in the medium [18]. The EPS have a key function in mediating the initial attachment of cells to different substrata and provide protection against environmental stress [42].

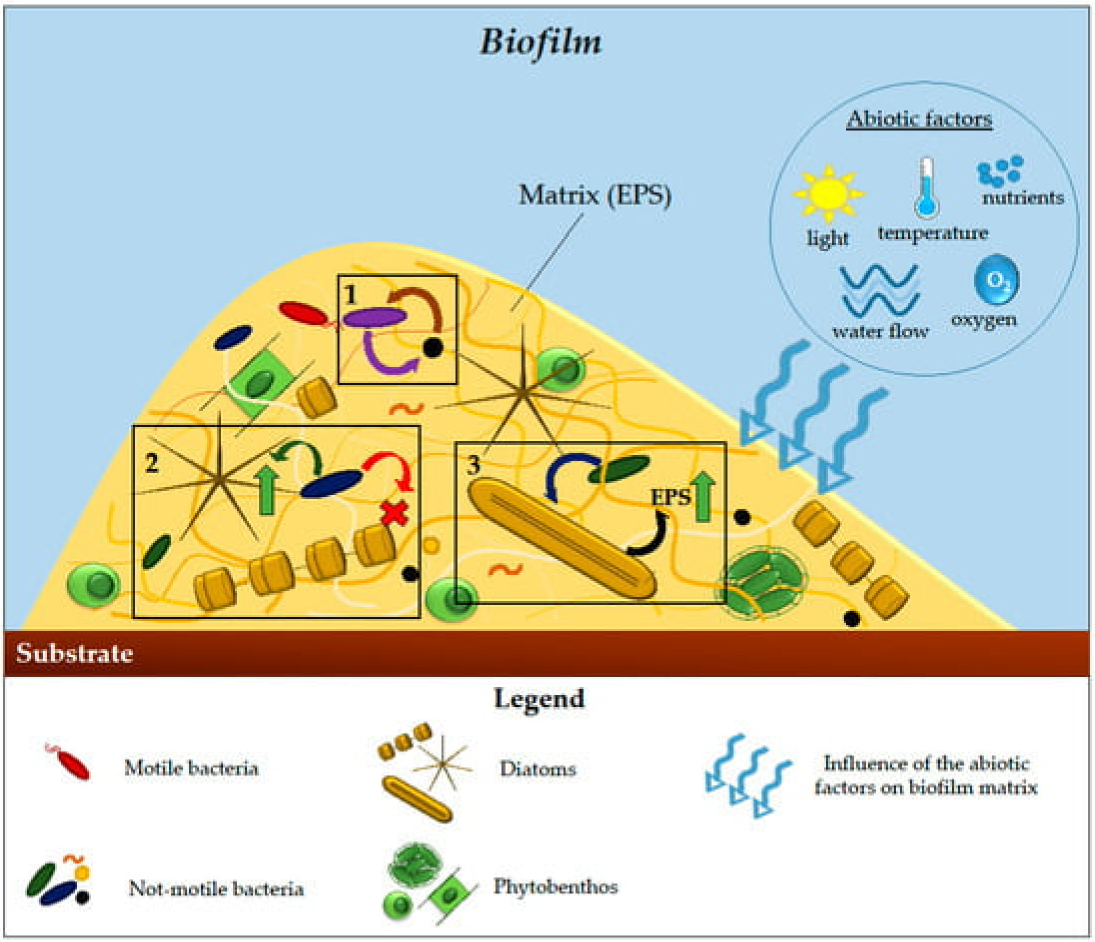

Figure 3. Biofilm structure and composition. The figure shows interactions that take place in biofilms. Curved arrows indicate the direction of the influence. The different types are grouped in black boxes: (1) bacteria influencing the behaviour of other bacteria living in the biofilm; (2) positive (green arrow) or negative (red cross) effect of bacteria on the dominance of different diatom species; (3) stimulatory effect (green arrow) on diatom extracellular polymeric substances (EPS) production. Abiotic factors, such as light, water flow, temperature, oxygen, and nutrient composition, are able to influence biofilm structure and stability.

The EPS matrix and its modifications occurring during diatom–bacteria interaction are involved in the biogeochemical cycle of carbon, nitrogen, and sulphur, and they are also relevant for a wide range of metal cations [33]. The binding of metals to EPS is considered fundamental for their vertical transport in the water column and their final accumulation into the sediments at the depth where they are transformed and finally re-enter the food chain [43]. Among the different diatom species, the polysaccharides present in the released EPS show high diversification in their molecule structures and branching [44]. The most frequently secreted ones are composed of galactose and glucose, but often also of xylose, rhamnose, mannose, and fucose [45][46][47][48] that can be used as carbon sources by bacteria [48][49]. These are able to influence the EPS composition of the biofilms as they secrete EPS themselves and may influence the formation and changes in the matrix composition through the release of chemicals, especially QS molecules [50].

Bacteria can also influence the species balance inside the biofilms (**Figure 3**). An example is the change in species prevalence when a mixed axenic co-culture of the three benthic diatoms *Navicula phyllepta*, *Seminavis robusta*, and *C. closterium* is added with a freshly prepared bacterial inoculum from marine sediments [51]. While in the axenic co-culture *C. closterium* was the dominant species, after the addition of bacteria isolated from intertidal surface mud, its growth and that of *N. phyllepta* were impaired, while *S. robusta* became the dominant species. Interestingly, each of those species cultivated individually with the same bacterial inoculum developed a specific bacterial community that became a combination of the three when the diatom species were cultivated together.

3. Diatom–Bacteria Types of Interactions

Diatom–bacteria interactions may occur through the exchange of metabolites, from small volatiles to complex molecules [8][52]. Such compounds are produced and released by both organisms to communicate, protect themselves, or impair the survival of their counterparts, ultimately contributing to the functioning of the ecosystem [53].

One example of metabolites produced by diatoms serving as defence strategy and also influencing the ecosystem equilibrium is the neurotoxin domoic acid (DA), produced in higher quantities during the stationary growth phase by some diatoms of the genera *Pseudo-nitzschia* and *Nitzschia* [54]. Silicate, phosphate, and iron limitation, as well as the change in nitrogen sources, seem to influence DA production [55][56][57][58]. There is also evidence that biotic factors, such as the presence of non-autochthonous bacteria able to utilise DA as a source of organic matter [24][59][60][61][62][63], may affect DA biosynthesis. However, the molecular mechanism underlying the influence of these bacteria on DA production has not yet been clarified [64].

Interactions between diatoms and bacteria may involve different mechanisms. The first is based on the exchange of nutrients and the release of growth factors that is beneficial for both partners; the second is based on the benefit for only one of the organisms involved in the relation without damage for the other [4][8]; the third implies the inhibition of growth or the release of algicidal compounds by bacteria [7][65], which leads to the death of co-occurring diatoms.

Diatom–bacteria interactions may be affected by several factors, such as the phase of the growth of both organisms involved and the cultivation conditions. A study of pairwise interactions between 8 diatom species and 16 bacterial strains highlighted that these relationships were strain-specific, with regards to bacteria, and may depend on the growth phase of the diatom. Overall, no universally positive or negative effects on diatom growth have been observed [66].

Nutrient availability can also influence bacteria–diatom population dynamics, as demonstrated by the capability of *A. macleodii* to have positive, negative, or neutral interactions with the diatom *P. tricornutum*, depending on nitrogen availability [67]. Specifically, *A. macleodii* establishes commensal relationships with *P. tricornutum* during its exponential growth, with no impact on diatom growth, when nitrogen is abundant, benefiting from the dissolved organic carbon (DOC) released by this diatom species. Later, during the stationary phase, both diatoms and bacteria continue to increase their cell numbers, suggesting the occurrence of a cooperative interaction with the bacteria providing the nitrate to the diatom for their growth, while diatoms provide the organic matter to bacteria. Conversely, the addition of DOC to the media at the diatom's early growth phase, before nitrate becomes depleted, triggers *A. macleodii* proliferation and reduces *P. tricornutum* growth, suggesting that in the presence of sufficient DOC, the bacterium competes with the diatom for nitrogen uptake.

3.1. Mutualistic Interactions

A typical mutualistic relationship is based on the exchange of cobalamin (vitamin B_{12}), for which many diatoms, as well as many other eukaryotic algae, are auxotrophs [68][69].

In exchange for organic carbon or nitrogen, selected bacteria and archaea establish symbiosis with diatoms by proving vitamin B_{12} that is produced de novo or through modifications of pseudo-cobalamin and other closely related compounds [70]. However, this system represents an active relationship and not a mere passive exchange of nutrients [71][72]. Indeed, to create a specific association with the bacterium *Ruegeria pomeroyi*, which supplies diatoms with vitamin B_{12}, *Thalassiosira pseudonana* releases 2,3-dihydroxypropane-1-sulfonate (DHPS). When in co-culture with *T. pseudonana*, *R. pomeroyi* shows an up-regulation of the genes involved in DHPS catabolism, while the diatom upregulates genes involved in the release of organic compounds, supporting bacterial growth. In a coastal environment in which iron and vitamin B_{12} limitations were found, the main vitamin B_{12} producer in plankton communities was found to be the Gammaproteobacteria *Oceanospirillaceae* ASP10-02a [73]. This bacterium showed high expression of genes related to organic matter acquisition and cell surface attachment, thus entertaining a mutualistic relationship with phytoplankton, among which diatoms, to fuel vitamin B_{12} production. Moreover, *Pseudo-nitzschia subcurvata* exuded organic matter that is used by *Sulfitobacter* sp. SA1 as a source of nutrients, while the bacterium provides biotin, vitamin B_{12}, and thiamine that support diatom growth in vitamin-limiting conditions [74]. SA1 also possesses a catalase that, similarly to what was previously observed in another diatom-*Sulfitobacter* association, can further improve *P. subcurvata* growth, supporting it in detoxification processes.

Similarly, diatoms unable to fix atmospheric N_2 establish symbiosis with nitrogen-fixing cyanobacteria, giving in return amino acids and organic carbon [8][75]. N_2-fixing cyanobacteria can be both obligate and facultative. As an example, *Richelia intracellularis* is an obligate symbiont adapted to live inside the *Rhizosolenia* and *Hemiaulus* genera frustules and is also transmitted to the host's next generation [76].

Certain bacteria use monomethyl amine (MMA), ubiquitously present in the ocean, as sources of organic carbon, energy, and nitrogen (or the sole nitrogen source) [65]. For example, the strain KarMa of the *Rhodobacteraceae Donghicola* sp. retrieves nitrogen in the form of ammonium from MMA degradation, providing it to *P. tricornutum*, thus sustaining its growth under photoautotrophic conditions. This interaction has a mutualistic character since KarMa growth, in turn, is supported by diatom-released organic carbon. This cross-feeding is widespread, since it was also observed when KarMa was co-cultured with the other two diatoms, i.e., *Amphora coffeaeformis* and *T. pseudonana* [77].

3.2. Facilitative Interactions

The beneficial effect of bacteria on diatom health and growth has been shown in many studies to occur through different mechanisms, always involving metabolite exchange [52][78][79][80][81][82]. Less is known about possible advantages for the bacterial community growing with diatoms, besides the already-ascertained advantage of benefiting from organic matter released by co-occurring diatoms.

Bacteria are able to influence the diatom metabolic profile by stimulating diatom cells towards the synthesis of amino acids and secondary metabolites. In a study conducted by co-culturing *T. pseudonana* with the bacterium *Dinoroseobacter shibae*, separated by a membrane that allowed only the exchange of chemical signals without any physical contact, diatom abundance was higher in comparison with the axenic algae [52]. Metabolic activity was also increased, especially with regards to the concentration of some intracellular amino acids and their derivatives, while the general health status did not change.

The bacterium *Bacillus thuringiensis*, following sporulation and mother cell lysis, releases compounds among which two diketopiperazines (DKPs), which are able to stimulate the growth of *P. tricornutum* as well as its content in neutral lipid [78].

3.3. Antagonistic Interactions

3.3.1. Inhibitory Effects of Bacteria on Diatoms

Not always the interactions between diatoms and bacteria are beneficial for one or both of them [4]. **Table 1** reports a simplified list of the inhibitory effects exerted by bacteria on diatoms.

Table 1. Examples of antagonistic interactions based on the inhibitory effects of bacteria on diatoms, including the compounds involved. Acronyms: NA = Not Available; OXO12 = N-(3-oxododecanoyl) homoserine lactone; TA12 = OXO12 tetramic acid; HHQ = 2-heptyl-4-quinolone; PHQ = 2-pentyl-4-quinolone; PQ = 2-n-pentyl-4-quinolinol.

Bacterial Species	Diatom Species	Bacterial Compounds	Effects on Diatoms	References
Croceibacter atlanticus	*Pseudo-nitzschia multistriata*	NA	induction of DNA fragmentation	[20]
Methylophaga	phytoplankton communities	NA	competition for vitamin B_{12}	[73]
Olleya sp. A30	*Pseudo-nitzschia subcurvata*	NA	growth impairment	[74]
Croceibacter atlanticus	*Thalassiosira pseudonana*	extracellular metabolites	inhibition of cell division, alteration of cell morphology, increase in organic matter release	[83]

Bacterial Species	Diatom Species	Bacterial Compounds	Effects on Diatoms	References
Maribacter sp. and *Marinobacter* sp.	*Seminavis robusta*	NA	negative influence on sexual reproduction rate by affecting diproline production	[9][84]
marine Proteobacteria	*Phaeodactylum tricornutum*	OXO12 and TA12	inhibition of growth	[85]
Pseudoalteromonas sp. and *Alteromonas* sp.	*Phaeodactylum tricornutum*	HHQ	Growth impairment by inhibition of photosynthetic electron transport and respiration	[86]
	Thalassiosira weissflogii and *Cylindrotheca fusiformis*	PHQ	inhibition of growth	[87]
	Amphora coffeaeformis, *Navicula* sp., and *Auricula* sp.	PQ	inhibition of motility	[88]

An example is given by the Flavobacter *Croceibacter atlanticus*, commonly associated with *Pseudo-nitzschia multistriata*, negatively affecting the growth of this and other diatom genera [20]. It colonises diatom cell surfaces, using their exudates to proliferate until diatoms reach the stationary growth phase. At this point, it leads to diatom death (likely to use the released organic matter), leaving the diatom cell surface before they sink.

Also, vitamin B_{12}-consumer bacteria can establish antagonistic interactions with diatoms, as in the case of *Methylophaga*, a gammaproteobacteria that competes for vitamin B_{12} while relying on phytoplankton carbon and energy to sustain its growth [73]. *Ollea* sp. A30, which possesses genes able to degrade diatom-derived organic compounds, seems be able to enter the frustules, consuming diatom organic matter from the inside [74]. When in co-culture with *P. subcurvata*, A30 negatively impacts the growth of this diatom by competing for vitamin B_{12}.

Some bacterial genera affect, in a species-specific way, the efficiency of sexual reproduction [84]. *Maribacter* sp. and *Marinobacter* sp. cells and their spent medium, for example, negatively affect the sexual reproduction rate of the biofilm-forming pennate diatom *S. robusta*, generally more efficient in axenicity. On the other hand, *Roseovarius* sp. increased the proportion of sexually active *S. robusta* cells.

Some marine proteobacteria frequently associated with diatoms use AHLs as signal molecules in QS [85]. In a biofilm matrix, AHLs can reach high local concentrations and be converted into tetramic acids (TAs). Using synthetic analogues, it was observed that both the N-(3-oxododecanoyl) homoserine lactone (OXO12) and its tetramic acid (TA12) inhibited the growth of the diatom *P. tricornutum*, with TA12 exerting this action at lower

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concentrations than 3OXO12; In addition, increasing concentrations of TA12, able to bind the quinone B (Q_B) binding site in the photosystem II (PSII), causes a decrease in the diatom's photosynthetic ability. On the other side, the diatom *Nitzschia* cf. *pellucida* seems to be able to disrupt bacterial β-keto-AHL signals using its haloperoxidase system to cleave its halogenated *N*-acyl chain [89]. Other than AHLs, other QS molecules, i.e., the quinolones, mediate diatom–bacteria interactions [86]. Quinolones are mainly produced by marine bacteria belonging to the *Pseudoalteromonas* and *Alteromonas* genera, but also by soil and freshwater bacteria belonging to the *Pseudomonas* and *Burkholderia* genera [86].

3.3.2. Algicidal Bacteria

Algicidal bacteria are important components in the determination of phytoplankton successions in marine environments since they can inhibit microalgal growth both through direct contact and the active release of diffusible factors to lyse cells [90][91]. The mode of action of algicidal bacteria ranges from high specificity for bacteria that kill only one species to universal for bacteria affecting a broad range of phytoplankton members [91]. For some bacteria, especially those living in biofilms, the algicidal activity is triggered by the perception of a certain microalgae density through a QS system [86], while others can switch on and off their algicidal activity depending on nutrient availability, with high nutrient concentrations stimulating the algicidal activity [92].

The most widespread algicidal bacteria belong to the genera *Saprospira*, *Vibrio*, *Alteromonas*, *Pseudomonas*, and *Pseudoalteromonas* [93]. Generally, *Alteromonas*, *Pseudoalteromonas*, and *Vibrio* kill diatoms, releasing diffusible substances, while other genera such as *Cytophaga* and *Flavobacterium* require direct contact with diatoms [94]. There are some exceptions reported, and one of them is *Kordia algicida*, a *Flavobacterium* that uses the QS-controlled release of diffusible proteases to kill a wide range of algal species, including the diatoms *S. costatum*, *T. weissflogii* [93], *C. socialis* [91], and *P. tricornutum* [94]. On the contrary, *Chaetoceros didymus* is not susceptible to *K. algicida* presence, and, surprisingly, the medium in which they are co-cultured is still active against *S. costatum* [94], a species susceptible also to the release of diffusible factors, like protease and DNAse activities from other algicidal bacteria [95].

3.3.3. Inhibitory Effects of Diatoms on Bacterial Growth

Some diatom species are able to activate defence mechanisms to deal with algicidal bacteria (simplified list of examples in **Table 2**) [4].

Table 2. Examples of antagonistic interaction based on diatom inhibition of bacterial growth and of the compounds involved. Acronyms: NA = Not Available; EPA = eicosapentaenoic acid; Pa = palmitoleic acid; HTA = (6Z, 9Z, 12Z)-hexadecatrienoic acid.

Bacterial Species	Diatom Species	Diatoms Compounds	Effects on Bacteria	References
Kordia algicida	*Chaetoceros didymus*	15-HEPE	inhibition of growth	[90]

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Bacterial Species	Diatom Species	Diatoms Compounds	Effects on Bacteria	References
Vibrio alginolyticus, *V. campbellii*, and *V. harveyi*	*Nitzschia laevis*, two *Nitzschia frustulum* strains, *Navicula incerta*, *Navicula* cf. *incerta*, and *Navicula biskanterae*	NA	inhibition of growth	[96]
marine and not-marine gram-positive and negative bacteria	*Phaeodactylum tricornutum*	EPA, PA, and HTA	death	[97][98][99]

The inhibitory effects of diatoms on bacterial growth are often mediated by compounds that, in some cases, have been isolated and characterised. PUAs, for example, affect diatom-associated bacterial communities when present in high concentrations [36][100]. Pure 2E,4E-decadienal, 2E,4E-octadienal, and 2E,4E-heptadienal tested on 33 bacterial strains at unnaturally high concentrations showed a variety of effects ranging from concentration-dependent growth inhibition to no effect or growth stimulation [34][100]. However, strain-specific effects on bacterial strains isolated from the Mediterranean Sea were also observed in laboratory experiments using PUA concentrations similar to those found in nature. Indeed, bacteria belonging to Gammaproteobacteria were less affected compared to *Rhodobacteraceae*, whose abundance decreased by 21%, suggesting a role for PUAs in the regulation of diatom-associated microbiome composition [101].

On the other side, oxylipins (oxygenated PUFA derivatives) are used by *C. didymus* against *K. algicida* attacks [94]. Indeed, differently from *S. costatum*, which is susceptible to the bacterial attack, *C. didymus* uses a wound-dependent defence mechanism to counteract the bacterial attack, which activates the synthesis and release of oxylipins [90], but also releases proteases [102]. The most abundant oxylipin released by *C. didymus* when attacked by *K. algicida* is the hydroxylated eicosapentaenoic acid 15-HEPE, which significantly inhibits bacterial growth [90].

P. tricornutum cell lysates showed antibacterial activity in vitro, which was attributed to the presence of eicosapentaenoic acid (EPA), palmitoleic acid (PA), and (6Z, 9Z, 12Z)-hexadecatrienoic acid (HTA), active against both marine and non-marine gram-positive and negative bacteria [97][98]. The analysis of the concentration of these fatty acids in the different *P. tricornutum* morphotypes highlighted higher production by fusiform cells with respect to the oval one [99].

4. Diatom-Associated Microbiomes

In the last few years, interest in studying the complexity of interactions established in nature between diatoms and their microbiome has increased, thus providing new information on their interplay [103], the stability of the associations and diatom species specificity [6], and the seasonality or geographical location influences [104]. As an example, a recent in situ study performed through metabarcoding of samples collected along the Australian coast in different seasons and locations allowed the characterization of the microbial community and reported that temperature and nutrient composition drive diatom community assemblages in different geographical locations. Moreover, they observed patterns of co-occurrence, conserved across space and time, among certain bacteria

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belonging to the *Roseobacter* and *Flavobacteria* clade with the diatoms of the genera *Skeletonema*, *Thalassiosira*, and *Cylindrotheca* [105], suggesting that species-specific interactions take place between these organisms and that those bacteria may significantly contribute to the seasonal and spatial variability of diatom communities.

In general, the structure of a diatom's associated microbiomes may be determined, in some cases, by selective processes that are both environmental and host-guided; in other cases, by neutral lottery-like processes, for which the possibility of a certain bacteria becoming part of a microbiome is proportional to its abundance in the environment [106].

Chemo-attractant and chemo-repellent compounds, but also secondary metabolites, released by diatoms in the phycosphere [4][8][15], can greatly influence the microbiome composition [59]. As an example, the analysis of the *P. tricornutum* exometabolome revealed the production of a pool of metabolites able to shape the associated microbiome composition, among which the 4-hydroxybenzoic acid selectively stimulated the growth of bacteria capable of metabolising and using it as a carbon source [107].

Axenic *A. glacialis*, when re-inoculated with its original microbiome, showed significant changes in its transcriptome and metabolome profiles and started secreting azelaic acid (AA) and rosmarinic acid (RA), able to favour the establishment of selected bacterial species while inhibiting the growth of unnecessary species [26].

On the other side, some bacteria species are able to control the composition of the microbiome associated with a certain diatom. This is the case of *Phaeobacter inhibens*, naturally occurring in association with *T. rotula*, which was shown to influence the microbiome assembly associated with the diatom [103].

Many of the cited studies have been conducted in laboratory conditions and revealed the long-term stability of the associated microbiomes, as for different strains of *Asterionellopsis glacialis* and *Nitzschia longissima*, which maintained a unique bacterial community for up to one year of growth in the laboratory [6]. In addition, species belonging to the *Roseobacter* clade were constantly present in all the analysed diatom strains and time periods. Also, the microbiomes of different *P. tricornutum* strains, despite belonging to different geographical locations, were very similar among each other and remained stable during laboratory cultivation, differing from the ones of other microalgal genera, i.e., *Entomoneis* and *Tetraselmis*, cultivated in the same conditions [108]. However, cultivation parameters could drive the microbiome composition; in the same *P. tricornutum* strains, it changed slightly when grown in a different medium with a higher nutrient concentration.

5. Most Used Approaches to Study the Bacterial Communities' Diversity

The technological advancement, especially in omics technologies, is greatly contributing to improving our understanding of microbial interactions, which are the subject of intensive investigations and projects based on the integration of big data coming from different approaches and omics techniques [109]. This approach integrates the analyses of meta-omics data to predict: (i) potential biotic interactions; (ii) reveal niche spaces; and (iii) guide more

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focused studies on possible relations and roles of compounds from different organisms composing the bacteria–diatom community. The co-occurrence pattern represents a useful tool to infer possible connections among microorganisms based on their abundances.

Another level of resolution is represented by the "trait-based" approach, which aims to reconstruct community biodiversity by tracking microorganisms' functional traits, ultimately inferring ecosystem functioning [110]. In particular, this approach uses functional annotations to cluster genomes by functions that co-evolved and are possibly connected, which allows grouping both known and unknown microorganisms. The use of clustered functions simplifies the analysis of enormous metagenomics datasets and allows the identification and unravelling of the intricate interconnected fluxes of functions at the base of complex communities [110][111].

The bioinformatics pipeline IDBac is a useful tool to integrate information on bacteria, proteins, and secondary metabolite profiles obtained through MALDI-TOF MS analysis [112]. This approach is based on the assessment of bacterial traits, the identification of phylogenetic relationships, and the comparison of metabolic differences among hundreds of clones in a short time.

At a lower scale, a community made up of a single diatom species and its associated bacteria can be studied by a combination of cell sorting techniques and metagenome sequencing of all the species composing the microbial community. Sequence clustering allows them to associate a set of genomic sequences with each species composing the consortium. Subsequent phylogenetic analysis can lead to identification at a species or genus level [113][114]. More specifically, this pipeline includes the utilisation of the NCBI database BLASwares by the Geneious® software [114] to identify and edit the 16S rDNA sequences found in the previous step and then the SILVA Incremental Aligner tool (SINA) to align the sequences [115]. ARB is also used to identify the taxonomical sequences not identified with the other tools and steps [116]. Mothur [117] and Usearch are useful tools to cluster the sequences based on their OTU and are used for network analysis and to visualise how communities are interconnected.

6. Potential Biotechnological Applications of Diatom–Bacteria Consortia

Bacteria have been considered for a long time as undesired contaminants in microalgae cultures grown for biotechnological purposes [118]. This view has now changed, and interactions between microalgae and their microbiome are being investigated for possible useful applications [119]. Nevertheless, most of the studies produced until now concern the use of consortia made of microalgal species in the *Chlorella*, *Scenedesmus*, *Tetraselmis*, and *Chlamydomonas* genera and their associated bacteria for the removal of nutrients from eutrophic waters, wastewater treatment, biofuel, and valuable compound production [118][120][121].

The beneficial cooperative interactions between diatoms and bacteria may provide useful tools to optimise the productivity of microalgae cultivation, since in most cases they culminate in an increase in diatom growth and consequently in their biomass [53], as for *T. pseudonana*, which increased cell density by 35% when cultivated in the presence of *D. shibae* [52]. The stimulatory effect of bacteria on diatom growth finds application mainly in

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wastewater treatment, bioremediation [120][122], and biofuel production [118]. In this regard, there is an increasing number of studies on the development of artificial consortia specific to each application based on the interaction mechanisms occurring in the consortia [121].

The presence of bacteria may positively influence the tolerance and performance of diatoms cultivated in presence of pollutants [123]. Indeed, it has been observed that the co-occurrence of free-living bacteria belonging to the hydrocarbon degrading genera *Marinobacter*, *Erythrobacter*, and *Alcanivorax* with the diatom *Nitzschia* sp. isolated from polycyclic aromatic hydrocarbons (PAHs)-contaminated sediments increased the growth rates and enhanced the tolerance of this microalga to PAHs compared to the performances of axenic diatom cultures, finally resulting in increased bioremediation of the PAHs fluoranthene (Flt) and benzo(a)pyrene (BaP) contaminated sites. This improvement in diatom tolerance to contaminants due to their associated bacteria has also been observed for *Thalassiosira delicatula* grown in the presence of metals and pesticide mixtures [124].

During the final steps of wastewater treatment, as well as in other industrial applications such as biofuel production, bacteria that increase microalgae flocculation through polysaccharides or protein production represents a sustainable, efficient, and cost-effective alternative to some toxic flocculation agents [119][122]. Nevertheless, the use of bacteria as flocculating agents in industrial applications is poorly explored for diatoms, but rather for other microalgae [125].

Biofilms dominated by diatoms and bacteria can be also applied in aquaculture to improve larval fish growth [126]. Indeed, biofilms formed naturally in *Seriola lalandi* culture cages, mainly composed of the diatom *N. phyllepta* and bacteria of the *Rhodobacteraceae* family, demonstrated the ability to control the proliferation of unwanted bacteria, especially when in combination with probiotic microorganisms, and to be a valuable nutritional source for the fish, being rich in carbohydrates. Biofilms can also be used as indicators of water quality because their composition and structure are susceptible to temperature increases and ocean acidification [127].

7. Conclusions

The interactions between marine diatoms and bacteria can have a substantial influence on ecosystem functioning, as they affect primary production, phytoplankton aggregation, and carbon and nutrient fluxes. Although the relevance of this interplay is gaining increasing attention from the scientific community, more studies are needed for a deeper understanding of the mechanisms involved. Due to the complexity of the interactions occurring, new approaches and methods are being developed to reveal the interactome network and identify compounds responsible for chemical communication among the organisms. The increasing level of knowledge in this field will have a pivotal role in establishing new approaches to answer questions related to environmental changes, but also in finding new solutions for a sustainable exploitation of diatom-microbiome consortia for biotechnological applications, from bioremediation strategies to the development of valuable products for human wellbeing.

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