

Contents lists available at [ScienceDirect](http://ScienceDirect)

# Biotechnology Advances

journal homepage: [www.elsevier.com/locate/biotechadv](http://www.elsevier.com/locate/biotechadv)

Research review paper

## Algae–bacteria interactions: Evolution, ecology and emerging applications

Rishiram Ramanan<sup>a</sup>, Byung-Hyuk Kim<sup>a</sup>, Dae-Hyun Cho<sup>a</sup>, Hee-Mock Oh<sup>b,c</sup>, Hee-Sik Kim<sup>a,c,\*</sup><sup>a</sup> Sustainable Bioresource Research Center, Korea Research Institute of Bioscience and Biotechnology (KRIBB), Yuseong-gu, Daejeon 305-806, Republic of Korea<sup>b</sup> Bioenergy and Biochemical Research Center, KRIBB, Yuseong-gu, Daejeon 305-806, Republic of Korea<sup>c</sup> Green Chemistry and Environmental Biotechnology, University of Science & Technology, Yuseong-gu, Daejeon 305-806, Republic of Korea

### ARTICLE INFO

#### Article history:

Received 22 June 2015

Received in revised form 1 December 2015

Accepted 2 December 2015

Available online 3 December 2015

#### Keywords:

Algae  
Bacteria  
Cyanobacteria  
Coevolution  
Symbiosis  
Industrial use  
Microbial ecology  
Biogeochemical cycling

### ABSTRACT

Algae and bacteria have coexisted ever since the early stages of evolution. This coevolution has revolutionized life on earth in many aspects. Algae and bacteria together influence ecosystems as varied as deep seas to lichens and represent all conceivable modes of interactions – from mutualism to parasitism. Several studies have shown that algae and bacteria synergistically affect each other's physiology and metabolism, a classic case being algae–roseobacter interaction. These interactions are ubiquitous and define the primary productivity in most ecosystems. In recent years, algae have received much attention for industrial exploitation but their interaction with bacteria is often considered a contamination during commercialization. A few recent studies have shown that bacteria not only enhance algal growth but also help in flocculation, both essential processes in algal biotechnology. Hence, there is a need to understand these interactions from an evolutionary and ecological standpoint, and integrate this understanding for industrial use. Here we reflect on the diversity of such relationships and their associated mechanisms, as well as the habitats that they mutually influence. This review also outlines the role of these interactions in key evolutionary events such as endosymbiosis, besides their ecological role in biogeochemical cycles. Finally, we focus on extending such studies on algal–bacterial interactions to various environmental and bio-technological applications.

© 2015 The Authors. Published by Elsevier Inc. This is an open access article under the CC BY-NC-ND license (<http://creativecommons.org/licenses/by-nc-nd/4.0/>).

### Contents

1.	Introduction . . . . .	15
2.	Evolution of bacteria and algae . . . . .	15
2.1.	Bacterial evolution benefitted algae . . . . .	15
2.2.	Evolution of multicellularity in algae – do bacteria play a part? . . . . .	16
3.	Ecology of algal–bacterial interactions . . . . .	18
3.1.	Defining types of association . . . . .	18
3.1.1.	Mutualism . . . . .	18
3.1.2.	Commensalism . . . . .	18
3.1.3.	Parasitism . . . . .	19
3.2.	Habitats . . . . .	19
3.2.1.	Phycosphere – an intimate microenvironment . . . . .	19
3.2.2.	Lichens . . . . .	20
3.2.3.	Corals . . . . .	20
3.2.4.	Extreme environments . . . . .	20
3.2.5.	Marine phytoplankton . . . . .	21
3.3.	Mechanism of interactions . . . . .	21
3.3.1.	Omics approach to illuminate interactions . . . . .	22
4.	Emerging applications . . . . .	22
4.1.	Environmental mitigation . . . . .	22

\* Corresponding author at: Sustainable Bioresource Research Center, KRIBB, Yuseong-gu, Daejeon 305-806, Republic of Korea.  
E-mail address: [hkim@kribb.re.kr](mailto:hkim@kribb.re.kr) (H.-S. Kim).

4.1.1.	Nutrient removal and wastewater treatment	22
4.1.2.	Bioremediation	23
4.1.3.	Bloom control	23
4.2.	Biotechnological potential	23
4.2.1.	Biorefineries – cultivation systems	23
4.2.2.	Biorefineries – microalgal harvesting	24
4.2.3.	Advanced biorefineries	24
4.2.4.	Sustainable aquaculture system	24
5.	Present & future prospects	25
	Acknowledgments	26
	References	26

## 1. Introduction

Algae are the undisputed primary producers in the aquatic ecosystem and contribute approximately half of the global net primary productivity (Field et al., 1998). These photosynthetic organisms along with cyanobacteria live in the planktonic region of the aquatic habitat and are collectively called phytoplankton (Buchan et al., 2014). Phytoplankton and bacterioplankton numerically dominate the ocean and freshwater planktonic community (Sarmiento and Gasol, 2012). These plankton communities together influence the global carbon cycle and ultimately the climate. Therefore, the interactions between these two groups of plankton and the influence of their interaction on each other and on a global scale are areas of recent research interest (Amin et al., 2015; Landa et al., 2015). Several studies show that heterotrophic bacteria play a ubiquitous role in algal growth and survival (Amin et al., 2015; Gonzalez and Bashan, 2000; Kim et al., 2014a; Seyedsayamdoost et al., 2011). Thus, it opens the possibility for revisiting the global carbon cycle and other biogeochemical processes (Amin et al., 2012, 2015; Landa et al., 2015). Similarly, decades earlier in terrestrial ecosystem, it was proven that heterotrophic bacteria not only decompose plant and animal organic matter, but also promote plant growth by complex communication mechanisms and nutrient exchange (Philippot et al., 2013). In this context, evidence of prominent rhizosphere bacteria associated with algae casts light on the possibility of coevolution (Cooper and Smith, 2015; Goecke et al., 2013; Kim et al., 2014a; Ramanan et al., 2015). Therefore, mass cultivation in algal biotechnology should integrate the essence of evolutionary and ecologically relevant relationship between algae and bacteria. Together they not only influence ecosystems but also could potentially influence the growth of future biotechnology industry (Subashchandrabose et al., 2011; Wang et al., 2015). Thus, this review attempts to articulate algal–bacterial interactions in totality, from ecology and evolution, to the use of this knowledge to invigorate their combined biotechnological potential.

Evolution of life was transitional where self-replicating molecules and chemicals formed the basis of prokaryotes. Subsequently, aggregation of prokaryotes led to eukaryotes. Cyanobacteria, a prokaryote, and their association with eukaryotes evolved into algae. A group of single-celled algae and other ancestors led to multicellular organisms (Herron and Michod, 2008). In this evolutionary hierarchy of life, a significant step is that of association of algae and bacteria. To completely understand the ecophysiology and symbiosis between algae and bacteria, thousands of years of time scale needs to be breached to reach their evolution. This evolutionary journey of algae and bacteria and their symbiosis taken together shall be a fair opening deliberation in this review.

## 2. Evolution of bacteria and algae

The evolution of life is one of the most intriguing research questions that is still in shade. But a prominent bright spot in the overarching shade is a general agreement on the role played by algae and bacteria in earth's evolution. One of the most potential reasons for existence of human or multicellular organisms on earth is due to the presence of

archaea, bacteria, cyanobacteria and subsequently eukaryotic algae. These prokaryotic organisms (bacteria and cyanobacteria), which are the linchpin in the formation of eukaryotic algae and their subsequent interaction with each other, are discussed vividly in the subsequent sections.

### 2.1. Bacterial evolution benefitted algae

Earth is 4500 million years old and Earth's atmosphere was devoid of oxygen at origin. Oxygenic photosynthesis is the main reason for the present day atmosphere (Blankenship and Hartman, 1998). According to Earth scientists, life would have originated approximately 3800 million years ago (mya) in a hyperthermal environment as Earth and its oceans were boiling at about 100 °C. But whether life originated in oceans (Nisbet and Sleep, 2001), hydrothermal vents (Martin et al., 2008), rock environment or anoxic terrestrial geothermal fields (Mulikidjanian et al., 2012) is a question under serious debate. Nonetheless, it is clear that first organisms in Earth were perhaps prokaryotic thermophiles capable of living in a methane and sulfur atmosphere, crucially a life without oxygen (Gribaldo and Brochier-Armanet, 2006; Sleep, 2010). By 3500 mya, Earth has stabilized considerably from multiple explosions and bombardment resulting in photosynthesis, first anoxygenic and much later, oxygenic (Arndt and Nisbet, 2012; Sleep, 2010; Zahnle et al., 2010). This early phase in evolution could be understood from tracking the availability of atmospheric oxygen. Geological features suggestive of oxygen, such as red beds, lateritic paleosols, and sedimentary sulfate deposits, indirectly provide ample proof for atmospheric oxygen (Kopp et al., 2005; Rasmussen et al., 2008; Tomitani et al., 2006). The accumulation of oxygen occurred in two phases. Atmospheric oxygen increased gradually from void to 1–2% around 2400–2000 mya (Rasmussen et al., 2008). Scrutiny of oldest morphological fossils suggests that cyanobacteria originated around 2150 mya coinciding with the great oxygenation event (GOE). Although eukaryotes are known to have emerged 1780–1680 mya ago, levels of oxygen were stable perhaps due to trapping of oxygen by ferrous forming magnetite and other formations even by 850 mya (Holland, 2006). The second subsequent rise in oxygen to ~20% observed in today's atmosphere is credited to the emergence of photosynthetic eukaryotes such as algae and increased photosynthetic productivity by lichens colonizing land masses. This eventually accelerated the degradation of rocks, thereby releasing fertilizing minerals around 800 mya which increased oxygen concentration in the Carboniferous era (360–300 mya) coinciding with the existence of vascular plants and increased carbon sink (Holland, 2006; Rasmussen et al., 2008). It is also widely accepted that cyanobacteria have played a major role in evolution of eukaryotic algae through the primary endosymbiosis (PE) event, in addition to their contribution to GOE. In PE, a heterotrophic eukaryotic ancestor engulfed a cyanobacterium and retained it as an organelle thereby enabling photosynthesis in eukaryotes (Curtis et al., 2012; Yoon et al., 2004). The host cell which received the cyanobacterium was earlier thought to have originated from bacteria, but increasing evidence suggests that, it was indeed an archaea

(Williams et al., 2013). Cyanobacteria were directly responsible for this oxygenic environment as well as for the birth of photosynthetic eukaryotes, and indirectly responsible for evolution of various aerobic organisms, including humans. Hence, from the perspective of this review, the paleo- and meso-proterozoic eras are of utmost relevance, where primary and secondary endosymbiosis (SE) is believed to have taken place (Yoon et al., 2004).

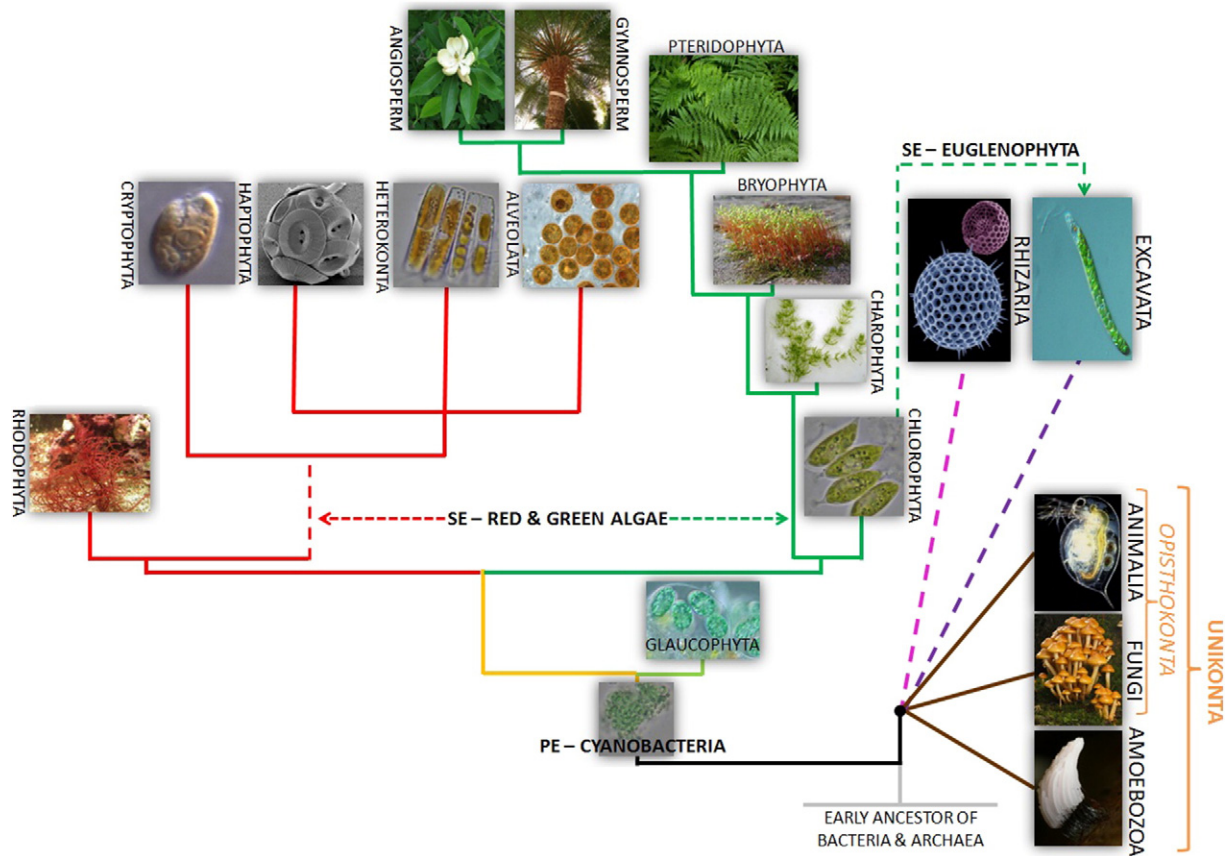
Cyanobacteria are considered to be algae by phycologists because of phenotypic similarities but the advent of molecular phylogeny and polyphasic studies proved their bacterial ancestry. Hence, the term cyanobacteria was previously used interchangeably with the term blue-green algae (Wilmotte, 2004), but the correct term is now accepted to be cyanobacteria. Apart from cyanobacteria, other prokaryotes which perform tetrapyrrole-based photosynthesis are proteobacteria (purple bacteria), heliobacteria, chloroflexi (green non-sulfur bacteria) and chlorobi (green sulfur bacteria). Cyanobacteria possess two types of photosystems (type I & II) and perform oxygenic photosynthesis as mentioned earlier. The other four groups have either of these two photosystems and perform anoxygenic photosynthesis. The defining moment in photosynthesis is the ability to use water as a source of hydrogen in the photosynthetic reaction, not the evolution of oxygen. Thus, photosynthesis originated in the anoxygenic form, perhaps in archaea, using a primitive photosystem I-like reaction center. Oxygenic photosynthesis is believed to have originated in the cyanobacterial lineage under ultra-violet light conditions prevailing then, in addition to depletion of electron donors. From this ancestor, photosynthesis possibly spread to other lineages through lateral gene transfer.

A simplistic view of algal–bacterial evolution and their role in endosymbiosis events is portrayed in Fig. 1. Cyanobacterium was retained as

primary plastid over time in three distinct evolutionary lineages – red algae, green algae and glaucophytes. Study of plastid multi-gene phylogeny using molecular clock analyses placed the origin of first alga before 1558 mya (Parfrey et al., 2011; Yoon et al., 2004). Later, a series of secondary endosymbiosis events led to diversification of this ancestor (Curtis et al., 2012; Li et al., 2006). Therefore, the role of bacteria in this ancestral algal genesis is not questioned. But considering the fact that heterotrophic bacteria are always associated with algae in nature, the role of these bacteria during various secondary endosymbiosis events needs to be questioned. The interplay between cyanobacteria, algae, bacteria and protists in a series of endosymbiotic events has been discussed in several excellent reviews (Decker and Holde, 2011; Keeling, 2009; Prechtel et al., 2004; Thompson et al., 2012; Tomitani et al., 2006; Vaishnav and Striepen, 2006). Moreover, evidence of horizontal gene transfer from bacteria and archaea to algae to help adapt to extreme environments is also emerging (Schönknecht et al., 2013). Hence, the holistic role of ectosymbiotic heterotrophic bacteria which surround the present-day algae in these endosymbiosis events is not well documented, apart from a few studies reviewed below.

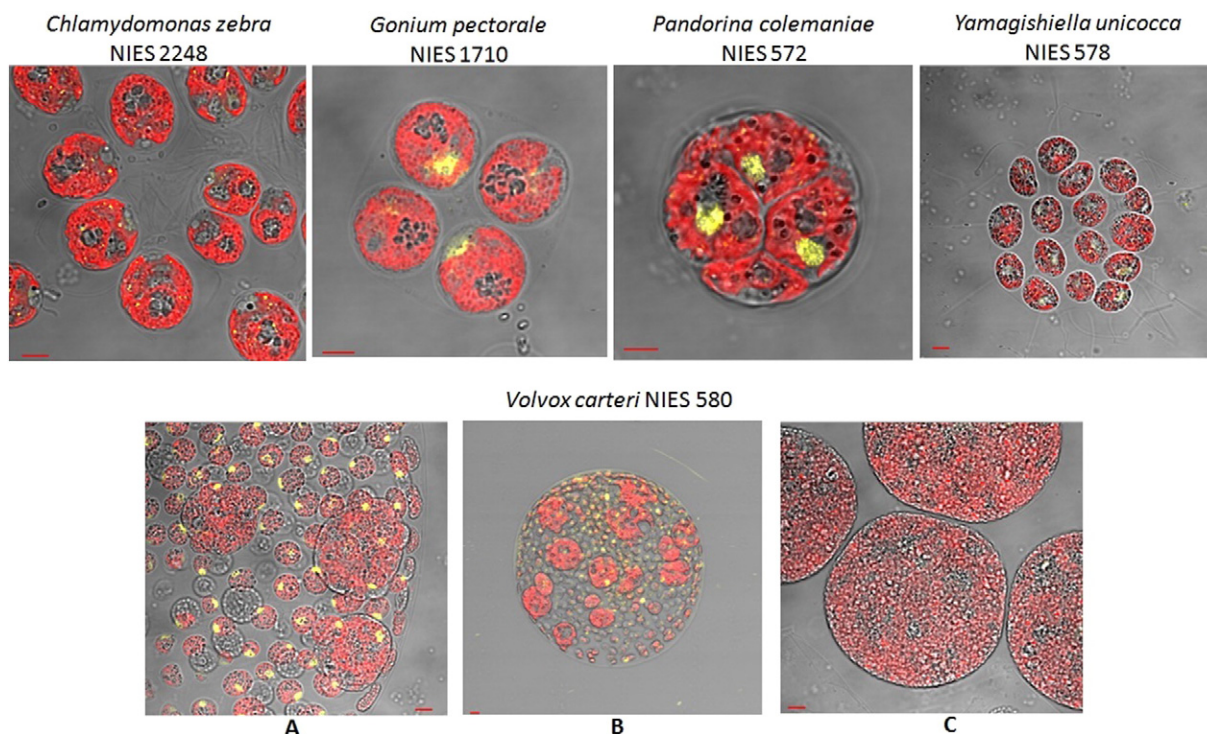
## 2.2. Evolution of multicellularity in algae – do bacteria play a part?

After these endosymbiotic series, algae moved a level higher in complexity from cellular autonomy to cellular cooperation, i.e. division of labor within cells (Herron et al., 2009; Kirk, 2005). Although various studies were conducted to elucidate each step towards multicellularity in volvocine algae (Herron et al., 2009; Kirk, 2001), there are hardly any studies on the role of ectosymbiotic bacteria which inhabit the cell wall and cell sheath in these algae. Fig. 2 shows the overwhelming presence of bacteria associated with various multicellular algae and



**Fig. 1.** A pictorial representation of evolution of algae after primary (PE) and secondary endosymbiosis (SE) events. The green branches indicate the green lineage while the red branches indicate the red lineage respectively. The dashed lines indicate the presence of sub-groups within the respective lineages where primary and/or secondary endosymbiosis is known to have occurred. The individual images used in this figure are only representative and some of these images are accessed through Creative Commons Attribution License.





**Fig. 2.** Confocal laser scanning images merged with differential interference contrast microscopic images of several multicellular algae and their closest unicellular relative. The strains were stained with SYBR green and pseudo-colored in yellow. The images reveal the presence of bacteria in all strains, including *V. carteri* (B), especially in flagellates and outer layers of ECM (A & B) whereas the gonidia do not have significant bacterial presence on their outer surface (C). The scale bar represents 5  $\mu$ m.

their closest unicellular relative, *Chlamydomonas*. Recently, Kawafune and colleagues showed the presence of bacterial endosymbionts in two volvocine green algae: unicellular *Carteria cerasiformis* and multicellular *Pleodorina japonica*. Definitive evidence on the identity and molecular phylogenies of endosymbionts were unknown earlier although they were discovered within the cytoplasm of *Volvox* and other volvocaleans, as early as 1970 in case of *Volvox*. The endosymbionts belong to hydra group within the Rickettsiaceae family, the perennial endosymbionts of non-arthropod hosts (Kawafune et al., 2012, 2014). Members of Rickettsiaceae family also include the bacterial genus *Rickettsia* that are associates of invertebrates like blood-feeding arthropods and become pathogenic when transmitted to vertebrates (Andersson et al., 1998; Perlman et al., 2006). It is also well-known that the members of Rickettsiaceae family serve as the origin of mitochondria in eukaryotes, a defining event in their evolution (Andersson et al., 1998; Emelyanov, 2001; Gray et al., 1999). Considering the increasing evidence of bacterial endosymbionts in multicellular algae, the role of bacteria in multicellularity can no longer be ignored. This leads us to question the theory of evolution of multicellularity. For example, one of the crucial steps in evolving to multicellularity is the conversion of cell wall structures to extracellular matrix (ECM), which constitutes 99% of cell volume in *Volvox*. This evolution not only gave an advantage of hosting large gonidia (reproductive cells) inside ECM, but also the competitive advantage over smaller algae for better access to nutrients (Kirk, 2005). Since bacteria are always associated with algae in the cell wall surface, corroborating with the evidence of bacterial endosymbionts, several questions arise. Were bacteria engulfed during the inversion process where cytoplasmic bridges play a critical role? Did cell-wall adhering bacteria help in creating specializations which keep individual *Gonium* cells together, that later transformed into ECM in *Pandorina* and *Volvox*? These are some of the unanswered questions in evolutionary biology of algal–bacterial interactions in algal multicellularity (Kirk, 2005; Nozaki, 1990).

These questions could be answered if the diversity of algae-associated bacterial community is ascertained in these lineages. Multicellular volvocine algae, red algae, brown algae, and plantae have independent origins for multicellularity, which occurred about 1000 mya. However, the bacteria associated with most green algae and plants consist of core group of genera called the Plant Growth Promoting Bacteria (PGPB). This term was first used by Kloepper and colleagues as Plant Growth Promoting Rhizobacteria (PGPR), which was subsequently expanded for other bacteria as well (Bashan and Holguin, 1998; Kloepper et al., 1980). Earlier studies show that specific bacterial genera are associated with each green alga vindicated by the diversity of secretory products. Our phylogenetic study demonstrates that an overarching clade of bacteria such as proteobacteria and bacteroidetes are more likely to be associated with green algae than other bacterial phylotypes. Moreover, these bacteria are also functionally equipped to be associated with green algae (Ramanan et al., 2015). This clade of bacteria associated with green algae (PGPR & Bacteroidetes) are similar and even in some cases identical, as in the case of *Rhizobium* (Kim et al., 2014a), and perform similar functions to that of plant–bacteria interactions. In the meantime, it is widely known that algae are ancestors of land plants, which originated relatively recently at approximately 450 to 470 million years ago (mya) (Bhattacharya and Medlin, 1998; Palmer et al., 2004). Algae have also played a defining role in animal evolution (Ni et al., 2012). Hence, another compelling query to be answered on coevolution is that whether some of the bacterial genera like *Rhizobium* and *Rickettsia*, for instance, continued to associate with the highly evolved descendant of algae and arthropods, respectively. Even though the role of algae and bacteria in evolution has never been questioned, their collective role is yet to be determined. In conclusion, both algae and bacteria conceivably coevolved from prokaryotes to form unicellular eukaryotes to multicellular higher plants and animals. In this context, studying both organisms and their interactions in unison from ecology to present day

applications is more enriching and fulfilling than engaging in their own individual subsistence. As bacteria and algae have coevolved, along the way they have formed a diversity of interactions, some of which define their respective habitats (Ashen and Goff, 2000). For more detailed discussion on evolution of algae and bacteria, the readers are requested to refer on Refs. Bhattacharya and Medlin (1998), Blankenship and Hartman (1998), Herron and Michod (2008), Keeling (2009), Li et al. (2006), Ni et al. (2012), Rasmussen et al. (2008), Tomitani et al. (2006), Vaishnava and Striepen (2006), Williams et al. (2013), and Yoon et al. (2004).

### 3. Ecology of algal–bacterial interactions

#### 3.1. Defining types of association

Algal–bacterial interactions cover the whole range of symbiotic relationships which are deemed possible. Algae, heterotrophic bacteria and archaea are the primary producers and decomposers, respectively, making them the structural pillars of the ecosystem and its foremost functional entities. However, most types of interactions between algae and bacteria in the planktonic zone are scantily studied and those studied often reflect the importance of taking up such studies. This is because of the onerous task of separating the partners which are naturally bound to each other. Axenic cultures of algae are difficult to isolate, maintain and study because of their completely different physiology and metabolism compared to their xenic counterparts, which are always laden with bacteria (Amin et al., 2015; Cho et al., 2013, 2015b).

Therefore, direct evidence on the amount of carbon and nitrogen exchange that takes place between a cyanobacterium and a nanoplankton was established only by 2012. This relationship is believed to be as important to vertical flux of carbon and nitrogen as their ancient, omnipresent mutualism (Thompson et al., 2012). Although the primary function of heterotrophic bacteria is decomposition, it is now accepted that some bacteria also play a part in algal growth promotion, establishing mutualistic interactions. This paradoxical dual function often complicate such studies on interactions, requiring a complex study on the complete set of ecological functions of each partner in the aquatic food chain. The emerging studies on the modes and factors influencing interactions also question conventional wisdom, with most studies pointing to relation continuum. Hence, this section will dwell on those emerging studies on algal–bacterial modes of interactions which would have enormous ecological significance in the future, as well as relevance for the algal biotechnology industry.

##### 3.1.1. Mutualism

There are many examples of mutualism between algae and bacteria, the one mentioned before is the first study to conclusively prove single cell interactions. Other studies have also revealed the role of mutualism, in some cases obligate relationships, for each other's subsistence. Croft et al. (2005), made a strong case for mutualism in Vitamin B<sub>12</sub> auxotrophs, when they proved that bacteria supplied Vitamin B<sub>12</sub> to algae in exchange for fixed carbon. Further studies by this group validated the evolutionary importance of this mutualism (Helliwell et al., 2011). Facultative relationship was also observed between *Chlamydomonas reinhardtii*, the model green alga encoding both Vitamin B<sub>12</sub>-dependent (METH) and -independent (METE) methionine synthases, and heterotrophic bacteria which delivers Vitamin B<sub>12</sub> whenever required, indicating a widespread distribution of such relationship (Kazamia et al., 2012b). The supply of Vitamin B<sub>12</sub> by an associated bacterium results in repression of *C. reinhardtii* METE gene expression and subsequent utilization of Vitamin B<sub>12</sub> supplied, indicating an opportunistic relationship. *C. reinhardtii* exuded photosynthetic carbon is not taken up by the bacterium, therefore the nature of the relationship is still unclear. But mutualism is not limited to micronutrient supply from bacteria alone (Droop, 2007).

Many studies have highlighted the role of *Mesorhizobium* and *Azospirillum* in algal growth promotion and vice-versa (Gonzalez and Bashan, 2000; Hernandez et al., 2009; Watanabe et al., 2005). One of the most important implications of these studies, especially by Bashan and colleagues, is that algae are dependent on macronutrients such as nitrogen (N) since they do not possess nitrogen fixing mechanism and that is supplemented by bacteria, especially in oligotrophic environment. A recent study conclusively proved the case of mutualism between a well-known PGPB, *Rhizobium* sp. and wastewater derived algae, *Chlorella vulgaris*, highlighting the importance of this mutualism in freshwater (Kim et al., 2014a). However, considering the ecological structure and function, the major question which arises is the need for bacteria to benefit algal growth, while being a decomposer. Mutualism, as the word indicates is not a one way exchange, rather the bacteria stand largely benefitted by being associated with algae, a blessing in oligotrophic environment. We demonstrated that algae supply fixed organic carbon to an artificial consortium of mutualistic bacteria, mostly belonging to PGPB, and bacteria in return, supply dissolved inorganic carbon and low molecular organic carbon for algal consumption (Cho et al., 2015b). Mutualism is not limited to unicellular microalgae but also prevalent in macroalgae, in some cases they are endosymbiotic (Hollants et al., 2011). Such exchanges between biotic communities in aquatic ecosystems have a huge role in cycling of nitrogen, sulfur, carbon and phosphorus (Amin et al., 2009; Ask et al., 2009; Azam, 1998; Cho et al., 2015a; González et al., 2000; Grossart et al., 2006; Grover, 2000; Oh et al., 2001b). The mechanism of such mutualistic exchanges is covered extensively in Section 3.3.

##### 3.1.2. Commensalism

Commensalism is a relationship in which only one partner benefits unlike mutualism. However, there is a very thin line that separates mutualism and commensalism. It is now understood with most cases of commensalism, mutualism, and parasitism that the thin line which not only delineates but also determines these relationships is environmental factors. And these interactions are a continual and not discrete interface (Ewald, 1987; Hu et al., 2010; Johnson et al., 1997; Karst et al., 2008; Neuhauser and Fargione, 2004; Valiente-Banuet and Verdú, 2008; van Ommereen and Whitham, 2002). From this perspective, most algal–bacterial associations studied till date are either mutualistic or parasitic; the intertwining relationship is almost deficient in literature. Although there are numerous studies which describe the change in community structure of algae and/or bacteria depending upon environmental factors (Bruckner et al., 2008; Carrillo et al., 2006; Cole, 1982; Interlandi and Kilham, 2001; Klepac-Ceraj et al., 2012; Mayali and Doucette, 2002; Sher et al., 2011), specific algal–bacterial interactions are viewed as discrete interactions and the continuum concept has not been applied. Only a handful of studies demonstrate, only partially, the role of nutrient availability in determining the relationship between algae and bacteria (Gurung et al., 1999; Kudela and Dugdale, 2000; Leung and Poulin, 2008; Liu et al., 2012; Sherr et al., 1988). An excellent early treatise on algal–bacterial competition and commensalism reveals the role of phosphorus (Bratbak and Thingstad, 1985). Other studies have indicated that phosphorus limited algae outcompete themselves allowing bacterial commensals to outnumber algae. Similarly, the role of nutrients, N:P ratio, carbon and light intensity in regulating the growth of these organisms in association have been partly discussed (Grover, 2000; Gurung et al., 1999; Currie and Kalf, 1984). However, mechanism or factors behind an apparent shift from mutualism to parasitism and vice versa via commensalism remains just a theory, although algae and bacteria serve as an excellent model system. Besides, there is a strong debate on whether mutualistic relationships become parasitic over time and later live autonomously, challenging the continuum concept (Sachs and Simms, 2006). In any case, commensalism has not been in the forefront in algal–bacterial interactions, which in itself raises the question of whether the moment is too fleeting. Or as an article pointed out, commensals could be



considered as non-interacting partners and therefore difficult to prove absence of interaction (Zapalski, 2011). Our latest study on the phycosphere bacterial diversity shows evidence of certain bacteria which might be commensals harboring the algal sheath for carbon and shelter (Cho et al., 2015b). From the studies available it can be speculated that commensalism though an integral part of the relationship continuum is totally determined by environmental factors, and hence not highlighted while documenting algal–bacterial interactions (Hirsch, 2004; Zapalski, 2011). Therefore, studying algal–bacterial commensalism might as well shed light on true validity of the continuum concept.

### 3.1.3. Parasitism

Unlike mutualism and commensalism, parasitism is relatively well-studied. Many bacteria are known to negatively affect algae and hence very encouraging for scientists studying microalgae and cyanobacterial bloom control (Kim et al., 2008; Lee et al., 2010; Lovejoy et al., 1998; Wang et al., 2010). Moreover, algae also are parasitic, often to their higher taxa or their own counterparts (Goff and Coleman, 1984; Goff et al., 1996; Sachs and Wilcox, 2006). In fact, red algae are considered to be model parasites (Goff et al., 1996). About 10% of known red algae are parasitic and the mechanism of this parasitism is adequately established (Hancock et al., 2010). However, very few studies have been conducted on algal parasitism on bacteria and vice-versa, their mechanism of elimination and its ecological reasoning. These studies demonstrate that the algal cell lysis is achieved through a mechanism similar to plant–pathogen interaction. Glucosidases, chitinases, cellulases and other enzymes that help degrade plant cell wall are also involved in the lysis of algal cells (Afi et al., 1996; Arora et al., 2012; Wang et al., 2010). In fact, this phenomenon of algal cell wall lysis is not only limited to bacteria, but also to fungal and mollusk enzymes (Nikolaeva et al., 1999). Apart from actual lysis of cells and utilizing the intracellular compounds as nutrients by bacteria and fungi, second form of parasitism is competition for existing nutrients with algae resulting in slower growth rates of algae, eventually after several generations, outcompeting algal existence in that environment. Yet another version of parasitism and competition is altruism, either self-driven or driven by the beneficiary, which would then closely resemble competition (Doncaster et al., 2013). Both parasitism and competition were manifested in a recent study on algal-associated fungi and bacterium, respectively (Cho et al., 2015b). Besides, such parasites are useful for many applications in algal and industrial biotechnology, which will be discussed in detail in following sections (Bhat, 2000; Dahiya et al., 2006). Hence, it is imperative to specifically learn the ecological and evolutionary significance of such degradation, and algal–bacterial parasitism, in general.

A general agreement for most associations is that they often happen in close proximities. For example, parasitic bacteria are usually present in the algal cell wall or its associated sheaths, to facilitate cell wall degradation (Wang et al., 2010). Besides, any association is a function of its microenvironment and the surrounding macroenvironment, which also strongly supports the continuum concept (Ewald, 1987; Johnson et al., 1997; Karst et al., 2008; Sachs and Wilcox, 2006). Hence the habitats play an important role in ecophysiology of these organisms in an association.

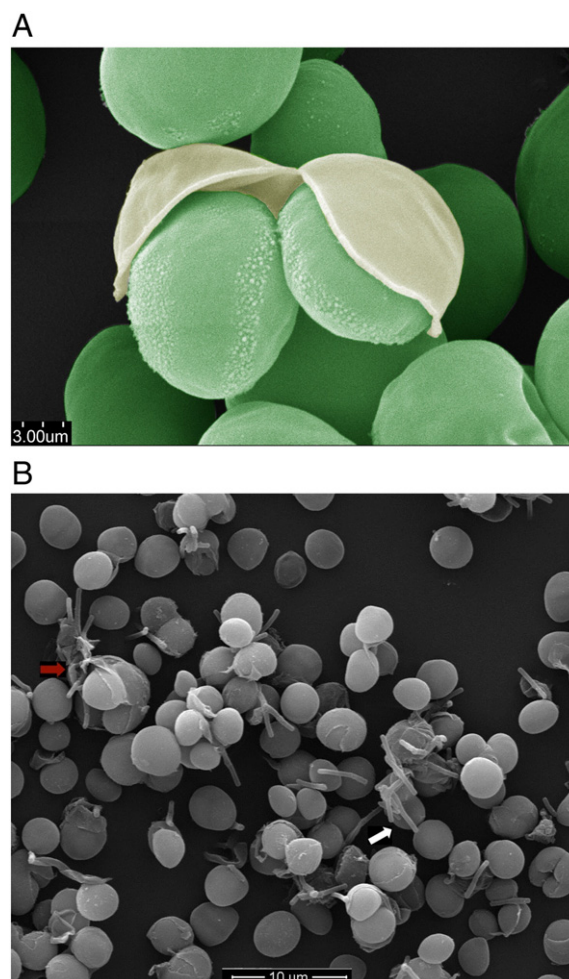
### 3.2. Habitats

It is widely known that algae, bacteria and cyanobacteria live in almost every niche of this Earth – from Antarctic ice to hot springs (Castenholz, 1976; Sakai et al., 1995; Thomas and Dieckmann, 2002), from high altitudes to deep ocean sediments (Ask et al., 2009; Jørgensen et al., 1992; Schippers et al., 2005), from plant roots to leaves and branches (Cocking, 2003; Hoffmann, 1989; Madhaiyan et al., 2006; Neustupa and Škaloud, 2008; Pitman, 1982; Rovira, 1965) – and conceivably beyond. However, this section will deal with two levels of

habitats – an intimate interaction of algae and bacteria in the ‘phycosphere’ and a collective interaction of algae and bacteria with organisms in some defining habitats. Algae and bacteria together play a wide range of roles with other organisms in every ecosystem (Grossart et al., 2006) and it would be beyond the scope of this review to deal with all major ecosystems. Hence, this section will define some interesting and well-known habitats in terrestrial, aquatic and extreme ecosystems.

#### 3.2.1. Phycosphere – an intimate microenvironment

The term ‘Phycosphere’ used for the first time in 1972 (Bell and Mitchell, 1972), defined as “a zone that may exist extending outward from an algal cell or colony for an undefined distance, in which the bacterial growth is stimulated by the extracellular products of the alga” is used sparingly since. Studies from our laboratory (Cho et al., 2015b; Kim et al., 2014a; Lee et al., 2013; Ramanan et al., 2015) and elsewhere (Sapp et al., 2007) suggest that phycosphere is one of the most ignored and distinctive habitat for bacteria. Scanning Electron Microscopy (SEM) images show axenic *C. vulgaris* (Fig. 3A) and xenic *C. vulgaris* with bacteria on the cell wall and beneath the cell sheath (Fig. 3B). The phycosphere is equivalent to an oasis for heterotrophic bacteria, where high concentrations of fixed organic carbon is excreted for consumption, compared with the vast oligotrophic surroundings in ocean and freshwater. This demands a question of why precious fixed organic carbon is wasted by microalgae through excretion. Most



**Fig. 3.** The algal phycosphere and its components. Recoloured SEM images of axenic *C. vulgaris* (A) show the presence of cell sheath in dividing cells, whereas xenic *C. vulgaris* houses bacteria on the cell wall (white arrow) and beneath the cell sheath (red arrow) (B).

plausible explanation is provided by studies which proved increased excretion as consequence of increased exposure to light, especially in the planktonic region as inorganic carbon is non-limiting and serves as a sink to prevent photoinhibition (Cherrier et al., 2014; Le Boulanger et al., 1998). Other studies have also proved that algae abandon Redfield ratio under nitrogen depletion and increase organic carbon secretion, especially as RuBisCo's oxygenase activity fixed glycolate (Granum et al., 2002). Overall, precious fixed carbon is released for a reason by algae, but eventually benefitting bacteria. Recent studies have demonstrated that such benefits are not bestowed upon all invaders. Only bacteria which possess unique abilities are able to survive in this microscopic yet organic rich region.

Studies indicate that specific functional types of bacteria are associated with most algae, which exploit this unique habitat, in some cases also helping algal growth, in a classic case of mutualism (Kim et al., 2014a; Ramanan et al., 2015). These functions include ability to degrade complex polysaccharides, to stave off competition, and provide beneficial attributes to algae. And this requires enormous metabolic activity linked to a complex signaling network to maintain the relationship, backed by fluid genetic machinery. A detailed description of this mechanism is outlined in following sections. Since this close association involves sharing metabolic potential of each organism, in most cases, bacteria and algae define the survival characteristics of each other in that environment through specific interactions, viz., mutualism, commensalism or parasitism, as discussed earlier (Doucette, 1995; Wang et al., 2010). Therefore, a region which hosts such a vital relationship which influences nutrient cycling needs higher attention than a scant mention in few research studies.

### 3.2.2. Lichens

A classic example of algal symbiosis is considered to be lichens. Lichens and their importance have been extensively discussed (Lutzoni and Miadlikowska, 2009; Lutzoni et al., 2001). Studies suggest that lichen can be the determinants of ecosystem health by providing specific signatures on the habitat they live in (McCune, 2000; Stengel et al., 2004). However, a relationship which occurs in lichens has not warranted attention for reasons unknown (Hodkinson and Lutzoni, 2009). Only lately, the role of bacteria in lichens was recognized and has added a new dimension to its studies (Hodkinson and Lutzoni, 2009; Hodkinson et al., 2012). Bacterial diversity in lichens is predominantly Rhizobiales but also encompass members of Acidobacteriaceae, Acetobacteraceae and Brucellaceae. As discussed elsewhere, Rhizobiales are also predominant in the algal phycosphere, help enhance algal growth and hence might have a major role to play in lichen physiology, in symbiosis with algal partner. Recently, microbiome studies on lung lichen, *Lobaria pulmonaria*, show that the lichen hosts algal photobiont (*Dictyochloropsis reticulata*) and cyanobacterium *Nostoc*. Comparative omics analyses of *L. pulmonaria* elucidated that bacteria present in the lichen aid algae by supplying Vitamin B<sub>12</sub>, nutrients, growth hormones and conferring resistance to pathogens (Grube et al., 2015). Moreover, the lung lichen sampled from three different locations share a core fraction of microbiome, indicating that these symbiotic functions are not isolated (Aschenbrenner et al., 2014).

Bacterial symbionts in foliose lichen *Peltigera membranacea* are known to be involved in phosphate solubilization, possibly resulting in algal growth promotion (Sigurbjörnsdóttir et al., 2015). Finally, bacterial community structure is also influenced by the nature of the photobiont, thus proving that algae and bacteria share a symbiotic relationship affecting each other's physiology and existence, therefore collectively affecting lichen survival. Thus, collective effect of algae and bacteria in lichen survival is unquestioned which indicates the ecological significance of these interactions, as lichens are known to be one of the oldest symbiotic relationships (Hodkinson et al., 2012; Lutzoni et al., 2001).

### 3.2.3. Corals

Corals are one of the most dynamic and aesthetic marine ecosystems. Corals resemble epiphytic lichens in many ways. Firstly, corals have a microbial community comprising algae, fungi, bacteria and archaea, similar to lichens. Secondly, coral is very sensitive to environmental changes and hence act as an indicator of ecosystem health (Gascuel et al., 2005; Hoegh-Guldberg et al., 2007; Hughes, 2002; Sheppard and Loughland, 2002). Thirdly, algae have the pivotal role in lichens and corals, supplying photosynthetically derived carbon to sustain both ecosystems. Endosymbiosis between corals and algae is well-known, in fact algae incorporates the coral reefs with its vivid beauty (Brown et al., 1999; Douglas, 2003; Hughes et al., 2003). Algae in coral, popularly called as zooxanthellae, are unicellular dinoflagellates, mostly belonging to *Symbiodinium* genus. Corals help algae to fix carbon by acidifying the microenvironment and consume the photosynthetically derived carbon (Barott et al., 2015). Algal endosymbiosis also seems to play a major role in stress resistance to environmental changes among coral reef community (Wooldridge, 2009). Overall, it is believed that there are several modes of interactions between algae and coral (McCook et al., 2001), and hence highlight the role of algae in this ecosystem. Morphologically, dinoflagellates are housed inside the gastrodermis of coral animal cells, which together is known as symbiosome. The bacteria are located on the surface of the host cell (mucus layer), gastrodermis and calcium carbonate skeleton, but dominated by distinct populations (Rosenberg et al., 2007). Many studies on analysis of bacterial diversity in different corals from different geographic regions revealed that most dominant bacteria belonged to gammaproteobacteria followed by alphaproteobacteria, cyanobacteria, firmicutes and bacteroidetes (Bayer et al., 2013; Littman et al., 2009; Pantos et al., 2015). The overall bacterial diversity is quite similar to that of phycosphere bacterial communities in freshwater algae (Ramanan et al., 2015). Meanwhile, analysis of bacterial communities in corals under varying stages of bleaching demonstrated a subtle change at genus level, with *Vibrio* and *Acidovorax* dominating in the pre-bleached and bleached corals, respectively. The emergence of specific clades of *Vibrio* is an indicator of coral bleaching which results in possible breakdown in the symbiotic relationship between algae and the host (Bourne et al., 2007, 2009; Tout et al., 2015). Many studies also prove that algae and bacteria act in unison to maintain host health as any disturbance in either community leads to coral mortality (Barott et al., 2011, 2012; Reshef et al., 2006; Rosenberg et al., 2007).

The mechanism of symbiosis between algae and bacteria in coral was proved by one of the earlier studies which elucidated that algae supply oxygen at very high concentration, often super-saturating (200% saturation), aiding host and prokaryote growth in addition to preventing infectious organisms (Revsbech, 1995). The algae in the symbiosome help bacteria in the coral tissues, while cyanobacteria in the carbon skeleton aid their symbiotic bacterial partner (Rosenberg et al., 2007). Bacteria on the other hand may provide nutrients including nitrogen possibly to host and algae, as well as protecting them from pathogens by producing antibiotics and by competition, thereby safeguarding symbiosome function and eventually preventing coral bleaching (Lema et al., 2012; Pantos et al., 2015). Summarizing the algal–bacterial interaction in coral with recent evidence, it is concluded that algal exudates in coral are proven to be directly beneficial to bacteria; the bacteria are not yet proven to be directly beneficial to algae alone, rather to the host and algae taken together. Therefore, algal–bacterial interaction in coral is both special and complex. Although it can be safely concluded that type and health of algal–bacterial community would determine the survival of one of the most magnificent ecosystems in the world, more research is needed on definitive roles of each of these partners.

### 3.2.4. Extreme environments

Algae, cyanobacteria and bacteria exhibit a strong resistance for a wide range of extreme habitats as mentioned before. An interesting study showcased the survivability of algae, bacteria and cyanobacteria in outer space environment and under UV radiation for a long time

(548 days) (Cockell et al., 2011). The study demonstrated that phototrophs survive in natural biofilms formed on the rocks when exposed to low-Earth orbit without known carbon and energy source, adding a new dimension to studies on growth of algae and bacteria in extreme environment. In the Antarctic sea-ice, it was proved that algae and bacteria coexist to fight high salinity, lower available free-water, extremely low temperature, low light and inorganic carbon conditions, and even high UV-radiation. Both bacteria and algae cope with such extreme conditions by secreting high levels of EPS, including organic carbon as seen earlier. Special ice-active substances like glycoproteins, which change the physicochemical surroundings of the immediate environment, are also secreted. Another possible mode of survival would be to alter each other's metabolism to suit the partner needs, especially during winter trapping in ice sheets (Thomas and Dieckmann, 2002). In such extreme environments, mutualistic arrangement is the only viable survival strategy. Such arrangement is also seen in a vastly dissimilar habitat, the coastal range of Atacama Desert, the driest and oldest desert on Earth. Here, microalgae and cyanobacteria formed biofilms on spider-webs with coastal water evaporation being the sole source of nutrients (Azua-Bustos et al., 2012). Another study showed that algae and cyanobacteria adapted to the extreme environment in Atacama Desert by switching to endolithic habitats within gypsum deposits in organized succession. The lower cyanobacterial layer was in close association with sepiolite inclusions with little supply of water and an upper algal layer acted as buffer to heat and evapotranspiration. Carotenoids and scytonemin were produced by upper algal and lower cyanobacterial layers respectively to prevent photoinhibition and oxidative damage. The study also found heterotrophic bacterial communities such as proteobacteria and actinobacteria associated with the endolithic communities comprising dominant cyanobacterial lineages, *Chroococcales* and *Synechococcales*, and unclassified algae. In such an arrangement, the role of cyanobacteria might have been to supply nitrogen, and minerals through mineralization, while the algal-bacterial community would have buffered the photoinhibition and evapotranspiration by EPS production and recycling. Taken together, algal-bacterial interaction to produce EPS, packed and organized community structure within the endolithics, and production of anti-oxidants would have helped the community to sustain in such extreme habitat (Wierzbos et al., 2015). Genome of extremophilic red alga, *Galdieria sulphuraria*, which lives in hot, metal-rich, toxic and acidic environments, revealed that horizontal gene transfer from bacteria facilitated its survival over millions of years (Schönknecht et al., 2013). This pathbreaking study highlights both association and eventual evolutionary inheritance from bacteria to algae with long-term implications for understanding algal-bacterial interactions in extreme environments. These studies also give insights on the possibility of convergent evolution which might have paved way for land plants (Azua-Bustos et al., 2012; Wierzbos et al., 2015). Thus these extreme habitats warrant attention as natural mesocosms, providing evidence on organismal evolution and modes of survival.

### 3.2.5. Marine phytoplankton

One of the most ubiquitous interactions in the marine ecosystem is the *Roseobacter*-algae interaction. Members of the *Roseobacter* lineage play a major role in biogeochemical cycling, especially carbon and sulfur, by oxidizing greenhouse gas carbon monoxide and producing dimethylsulfide, both of which enormously influence global climate (Geng and Belas, 2010). The most interesting aspect from the pretext of this review is that they utilize algal osmolytes to produce these compounds. *Roseobacter denitrificans* is the first member of this lineage to be sequenced and they generate energy using anoxygenic photosynthesis process, and in the presence of oxygen (Wagner-Döbler and Biebl, 2006). Not only does this organism possess ancient photosynthetic machinery, but is also known to be associated with algae ubiquitously, possibly throwing light on the age of such associations. Studies on the troponoids produced by marine *Roseobacter* lineage, coined

Roseobactin, show that these bacteria have a robust quorum-sensing based gene-regulation system which responds to environmental cues and dictates their relationship with algae (Geng and Belas, 2010). The mechanism of this ubiquitous interaction is discussed in detail in the following section.

### 3.3. Mechanism of interactions

The interaction between marine algae, *Emiliania huxleyi*, a single-celled phytoplankton ubiquitously distributed from tropic to sub-Arctic waters, possessing highly ornamental calcite shields called colloliths, and its associated bacterium of *Roseobacter* lineage is the most widely studied. Mechanism of their interaction is among the most complete and well-understood. The algae are subject to frequent upheaval and decline in population, succeeding every algal bloom. When algal population decline, members of the population release cell wall degradation products, such as lignin and its degradation by-products, such as *p*-coumaric acid. It is established that members of *Roseobacter* lineage change from a mutualistic partner upon *p*-coumaric acid release, called an elicitor, to an opportunistic pathogen by releasing 11 types of troponoids, which eventually kill algae, and switch the *Roseobacter* member, from a sessile lifestyle on the algal cell wall to motile phase (Geng and Belas, 2010; Sule and Belas, 2013; Wagner-Döbler and Biebl, 2006). Moreover, it was demonstrated that in the brief period of high algal growth, *Roseobacter* not only serves as a perfect mutualistic partner by supplying vitamins and phytohormones to algae, but also provides antibacterial safeguards towards non-roseobacters, in cohesion with algae (Sharifah and Eguchi, 2011). Besides, the precursors of troponoids are synthesized from algal derived carbon, which algae releases during their mutualistic relationship. Thus, algae synthesized molecules that serve *Roseobacter* member during mutualism are diverted for toxin synthesis during parasitism (Seyedsayamdost et al., 2011). This interaction is the closest example of classic continuum theory between algae and bacteria, not proven to be driven by environmental factors, but rather surprisingly determined by algal molecules and growth phase.

However, this mechanism is not the only possible strategy prevalent in all interactions. The mechanism of interaction is species specific as the microenvironment of each alga is different. Modes of interactions between algae and bacteria and their interrelation with the environment are depicted in Fig. 4. In the mechanisms proven so far, carbon and macro- and micro-nutrients seem to play a central role. Studies show micro-nutrients like Vitamins (Croft et al., 2005; Kuo and Lin, 2013; Teplitski and Rajamani, 2011), macronutrients like nitrogen and carbon (Bolch et al., 2011; Kazamia et al., 2012b; Kim et al., 2014a; Teplitski and Rajamani, 2011) and phytohormones (Teplitski and Rajamani, 2011) usually exchange between algae and bacteria. A recent study proved that Indole Acetic Acid (IAA) was transferred to algae in exchange for organosulfur compounds by *Sulfitobacter*, another member of *Roseobacter* clade. The study conclusively proved that both algae and bacteria altered their metabolism to suit each other's needs, and this interaction is potentially very prevalent in the marine ecosystem (Amin et al., 2015).

Yet there are pertinent questions related to mechanism of such uptake. Most are based on the signal generation and recognition, transport and uptake processes. Some studies suggest that 'quorum sensing' plays a major part in these interactions, as in the case of the *Roseobacter* (Teplitski and Rajamani, 2011). It is also important to understand if algal genomic inflexibility to survive under certain conditions results in metabolic complementation and cooperative biosynthesis (Hom et al., 2015). Therefore, whether this chemical exchange and communication eventually leads to genome sharing via horizontal gene transfer is another element to this complex interaction. Most complex questions related to uptake, communication and overall mechanism in a diversity of algal-bacterial interaction are being addressed by single-cell



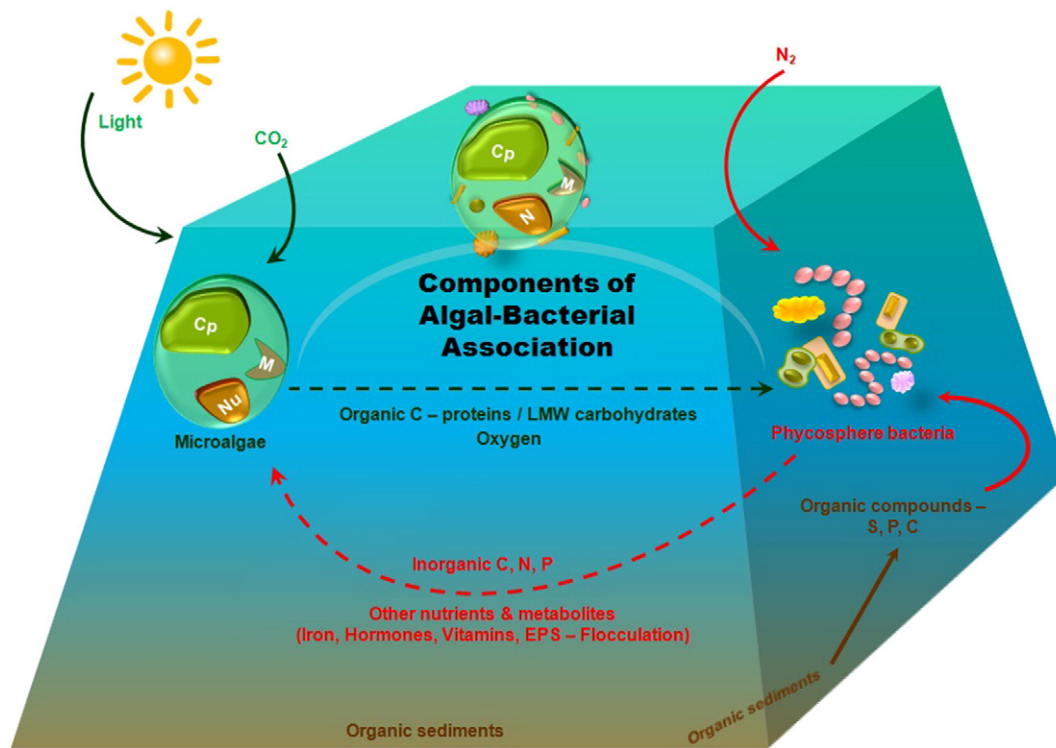


Fig. 4. An illustration of components of algal–bacterial association in aquatic ecosystem and some proven mechanisms. All the mechanisms of exchange have been described in the text.

genomics and other omics approaches and this seems to be the way forward (Cooper and Smith, 2015; Thompson et al., 2012).

### 3.3.1. Omics approach to illuminate interactions

The omics approach to study microbial ecology has transformed our understanding of microbial communities and their environment (Jansson et al., 2012). Although community metagenomics and metatranscriptomics studies were performed in complex microbial communities predominated by algae and bacteria (Moran et al., 2013; Tringe et al., 2005), specific studies on microbiome of algal phycosphere in natural systems and artificial systems like photobioreactors using high-throughput sequencing were only recently constituted (Krohn-Molt et al., 2013; Ramanan et al., 2015). Recent study demonstrated power of using multi-omics data to illuminate the interaction and mechanism thereof in natural assemblages (Amin et al., 2015). Another study showed that the major phylotypes of bacteria from green algae isolated from different habitats are similar, using 454 pyrosequencing (Ramanan et al., 2015). The functional domain of the phylotypes also point to their similarity with PGPB. Unsurprisingly, the study also revealed that basic techniques like Denaturing Gradient Gel Electrophoresis (DGGE) show limited diversity whereas the same samples would have much higher diversity in reality. Several recent studies on the natural assemblages in aquatic ecosystems using next generation sequencing (NGS) technologies have shown unbiased results, as NGS eliminates cloning biases. Moreover, NGS would not only help in sequencing environmental DNA but also RNA as proved by studies on gene expression in oceans (Nowrousian, 2010). The depth and coverage of sequencing platforms could also help in using several genes for elucidating bacterial diversity as the widely used rRNA gene is known to be highly conserved. Besides, studies on specific bacterial community which are lesser-known or in other words not dominant in the association could be sequenced. A review on the role of omics in algal–bacterial interactions suggests the use of combination of methods including traditional approaches such as microbial and biochemical analyses in addition to metabolomics, metagenomics and transcriptomics. The review argues that a metabolomic analyses would be used to decipher range of

compounds exchanged between the partners while metagenomic and transcriptomic approaches would corroborate the existing evidences with insights on cluster interactions, genomic machinery and regulatory pattern (Cooper and Smith, 2015). Taken together, the omics approach and NGS platforms would help answer some basic questions on algal–bacterial association. As microbiome is being explored as operational concept, such analyses using advanced tools inherited from highly studied communities like gut microbiota are being performed. And this knowledge would further unravel algae and dependent microbial communities, their active drivers, functionalities and implications, and the resulting applications.

## 4. Emerging applications

### 4.1. Environmental mitigation

#### 4.1.1. Nutrient removal and wastewater treatment

Algae depend on nitrogen and phosphorus from the environment for growth as they are non-diazotrophic. Macronutrient (N, P, S and C) deprivation of algae for prolonged periods results in severe stress leading to stagnation and eventually death (Ramanan et al., 2013; Schmollinger et al., 2014). On the other hand, nutrient rich wastewaters when discharged in natural surface waters might result in blooms of toxic algae and cyanobacteria (Srivastava et al., 2014). Heterotrophic bacteria require carbon and other nutrients for growth and are widely used for the treatment of wastewater. Naturally, algal–bacterial systems have been extensively used in the treatment of nutrient rich wastewaters since 1950s. One of the earliest descriptions of algal–bacterial interactions in wastewater treatment is presented by Oswald and Gotaas (1957). Early photosynthesis based systems were neither aerated nor mixed, therefore, the treatment efficiency achieved with these systems are a fraction of what could be achieved with ponds or systems developed later (Benemann et al., 1977; Hoffmann, 1998). As early as 1955, it was proposed that in oxidation ponds, algal–bacterial symbiosis results in sewage treatment with exchange of  $O_2$  and  $CO_2$ , and  $NH_4^+$  ions. Thus it was proved technically that most nutrient rich, low

oxygen-demand environments shall be conducive to both algal and bacterial growth (Oswald and Gotaas, 1957). However, this conjunction between algae and bacteria holds enormous environmental potential even today (Kim et al., 2014b).

The advent of high rate algal ponds (HRAP) not only increased the efficiency of the process, but also enhanced the possibility for sewage treatment and biofuel production, with reliable yield (Craggs et al., 2011; Kang et al., 2014; Kim et al., 2014b; Park et al., 2011, 2013). Moreover, it was demonstrated that a desired consortium of algae and bacteria could be maintained in lower scales with better process optimization, monitoring and recycling part of the biomass (Cho et al., 2015a; Park et al., 2013). Our studies have also proved that bacteria help in the flocculation of algae and would be effective for better harvesting of the algal–bacterial biomass, reducing the costs (Kim et al., 2014b; Lee et al., 2013). Apart from nutrients removed from the wastewater, several toxic metal ions are removed by microalgal consumption, achieving the polishing effects of tertiary treatment and leaving the effluent ready to be discharged into surface waters, at optimum operation of HRAP. Several agro-industrial wastewaters can be also treated with such a system (Ferrero et al., 2012; Hernández et al., 2013). van der Ha et al. (2012) demonstrated the use of synergism between methane oxidizing bacteria and microalgae to effectively treat dissolved methane in anaerobically treated wastewaters, which otherwise escape into the atmosphere in other aeration based processes. Considering the efficiency of the treatment, relatively minuscule use of energy, and production of biomass which could be valorized, algal–bacterial sewage treatment process could be a major alternative technology to aeration based technologies like activated sludge treatment (AST) (Kim et al., 2014b). The amount of energy consumed primarily in AST process dependent wastewater treatment plants in Korea alone is ~1000 GWh (Ministry of Environment, 2011). A conservative estimate shows that energy savings of 100 folds could be achieved, if the facilities switch to algal–bacterial process (Kang et al., 2014; Kim et al., 2014b). In addition, costs reduction from decreased usage of chemicals for nutrient removal is possible. However, this potential estimate from these studies needs to be consolidated with life cycle and related economic analyses.

Attached growth systems for sewage and wastewater treatment also depend on the formation of algal–bacterial biofilms. Such technologies are getting widely popular because of the ease of cultivation with relatively lesser self-shading compared to suspended systems, and primarily ease of harvest (Christenson and Sims, 2011; Christenson and Sims, 2012; Hoffmann, 1998; Lee et al., 2014b). The harvesting process includes scrapping of the biomass from the attached systems and drying is relatively easy with the use of solar energy (Lee et al., 2014b). Hence, such systems have lesser capital costs, yet they have not been considered for large scale applications so far. Other engineered systems demonstrated so far include the algal turf scrubber (ATS), in which pulsed wastewaters flow over sloping surfaces with attached, naturally seeded filamentous algae. However, ATS is only recommended as polishing systems for tertiary treatment and lower organic loading rate wastewaters, but used at large scale of 40–80 million liters per day (Adey et al., 2011). However, compared to suspended culture systems, the biofilms in attached systems are complex, as systematic studies on the fundamental processes are less elucidated, and studies on the role of algal–bacterial interactions in such engineered biofilm systems treating wastewater are sparse (Kesaano and Sims, 2014).

#### 4.1.2. Bioremediation

Many studies have dealt with algae–bacteria consortium for metal bioremediation (Boivin et al., 2007) and degradation of organic pollutants (Tang et al., 2010). The effective use of algal–bacterial interactions in degradation of organophosphate insecticides such as monocrotophos, quinalphos and methyl parathion was also demonstrated (Subashchandrabose et al., 2011). Besides, degradation of many other toxic pesticides including DDT, atrazine,  $\alpha$ -endosulfan was reported (Subashchandrabose et al., 2013). Several studies

have shown the involvement of bacteria/cyanobacteria and algae in the treatment of organic pollutants including black oil, acetonitrile, phenol, naphthalene, benzopyrene, dibenzofuran, azo compounds, among others (Mahdavi et al., 2015; Muñoz and Guieysse, 2006; Subashchandrabose et al., 2013). Recent study demonstrated the role of algal–bacterial interactions in the degradation of thiocyanate wastewater, which provides the glimpse of use of this interaction for degradation of toxic substrates (Ryu et al., 2015).

Algae also require several metals for normal growth and metabolism, albeit in small quantities and hence are considered micronutrients. Algae when deprived of these metals, exhibit systematic, specific stress responses, which are well documented (Glaesener et al., 2013; Kropat et al., 2015; Malasarn et al., 2013). On the other hand, higher levels of metal could lead to toxicity in algae, hence algal–bacterial community mutualistically detoxify and assimilate metals from metal rich environments. The process of accumulation of heavy metals would be through various means including physical adsorption, covalent bonding, ion exchange and chemisorption, surface precipitation, redox reactions or crystallization on the cell surface. Moreover, on a lesser scale, metals are quenched by active uptake into the cell interior for metabolism or as a defensive tool to avoid poisoning. Microalgal growth results in the release of metal chelators and increase in pH often also precipitates heavy metals which are taken-up by the associated bacteria. Few excellent reviews on detailed analysis of bioremediation of hazardous pollutants and heavy metals by algal–bacterial consortium are available (Muñoz and Guieysse, 2006; Subashchandrabose et al., 2013).

#### 4.1.3. Bloom control

One of the first research studies on bacterial control of natural algal blooms was again on *Roseobacter* lineage prevalent in algal blooms dominated by *E. huxleyi* and dinoflagellates (González et al., 2000). But from the context of application, it is important to seek solutions for harmful algal blooms (HAB) particularly in fresh waters of human use. For detailed understanding of HAB control by bacteria in marine environment, readers are referred to other studies (Bai et al., 2011; Buchan et al., 2014; Wagner-Döbler and Diehl, 2006). In freshwater ecosystems, several isolated studies have established the use of bacteria for HAB control. An early study on *Rhodococcus*, a Gram-positive bacterium prevalent in a eutropic lake, shows the cyanobactericidal activity of the bacterial filtrate (Lee et al., 2010). Studies on both marine and freshwater HAB revealed the resurgence of bacterial population corresponding to late or post bloom period, indicating that mechanism of action is indifferent. Hence, monitoring of both algal and bacterial populations over time would not only help in understanding the dynamics in freshwater systems but also help in control of the blooms (Srivastava et al., 2014; Srivastava et al., 2013). On the other hand, bacterial growth after the algal bloom could cause grave damage, depriving oxygen leading to fish kills, symbolizing the overall collapse of the ecosystem. Therefore, bacterial role should be thoroughly studied to employ them at the right time and in the right environment. Moreover, the algal bloom is controlled by various positive and negative effectors, which interact in cohesion (Paerl and Otten, 2013). And finally, any treatment of algal or cyanobacterial blooms by heterotrophic, predatory bacteria should be preceded by or in combination with excess nutrient cutoff from the freshwater system.

#### 4.2. Biotechnological potential

##### 4.2.1. Biorefineries – cultivation systems

As discussed in earlier sections, bacteria play a key role in providing phytohormones or macro- and micronutrients to algae which result in various physiological changes within algae most notably enhanced growth rate of algae. However, the role of bacteria in microalgal growth enhancement is often ignored. When the phycosphere bacterial communities, especially PGPB were eliminated, the algal growth rate under phototrophic condition was found to be very slow (Cho et al.,

2015b; Watanabe et al., 2005). Recent studies on co-cultivation of algae with growth enhancing bacteria revealed that bacteria enhance algal growth rate by at least 10% and in specific cases by about 70%. Hence, in mass cultivation of algal cultures, PGPB would be highly useful to enhance growth rates which would result in better productivity. Subsequently, regular monitoring of both algae and bacterial community would be required as it is imperative to have desirable bacterial community associated with microalgae in mass cultivation to achieve higher growth rates (Cho et al., 2015a). Or as mentioned earlier, simple techniques such as recycling of the harvested algal–bacterial community into HRAP might also help ensure the stability of the community. However, it is also held that in algal systems using wastewater as nutrient the influent microbial diversity should also be monitored and controlled to sustain desirable algal–bacterial community (Cho et al., 2015a; Park et al., 2013).

#### 4.2.2. Biorefineries – microalgal harvesting

Another well-known application of algal–bacterial interactions is the role of bacteria in microalgal harvesting (Gardes et al., 2011 and Grossart et al., 2006). Until recently the role of bacteria in microalgal flocculation was speculative, unlike in yeasts (Bester et al., 2012). It is now established that bacteria increase the floc-size of algae thereby enabling settlement, even in lesser flocculation conducive condition. Even though axenic microalgal culture responds to flocculants, without bacteria surrounding its phycosphere, algae cannot form settleable flocs, resulting in non-settleable flocs, which are still in suspension (Lee et al., 2013; Powell and Hill, 2013, 2014). It is also thought that aggregation is made possible in part through charge neutralization by positively charged calcium ions binding to negatively charged teichoic acid residues, especially for Gram-positive bacteria (Powell and Hill, 2014).

Although the role of bacteria is established, the complete mechanism is still not clear; especially the role played by Extracellular Polysaccharide Substances (EPS), and the cell wall and secretory proteins of algae. Bioflocculation was demonstrated more than a decade ago using EPS from *Paenibacillus* sp., yet the compounds or the class of compounds which induce such flocculation and their properties remain elusive (Oh et al., 2001a). A mechanism similar to yeast self-flocculation is also a possibility (Bester et al., 2012). There is also a possibility for a completely reverse mechanism given algal tendencies to shelter itself along the water column depending upon the intensity of light (Neale, 1987). Further research needs to be done to ascertain the function of EPS as bioflocculants, its composition and its interaction with algae. There are also questions over the role of genetic apparatus and quorum sensing in microalgal flocculation. This is important as microalgal harvesting is one of the major biomass production costs (20–30%) in biorefineries (Uduman et al., 2010). In a related development in the algal bioenergy research, algicidal bacteria have been shown to help in the lipid extraction process from microalgae, because of their role in algal cell lysis. This process could be used along with the bio-flocculation technique to enhance lipid productivity (Lenneman et al., 2014).

#### 4.2.3. Advanced biorefineries

Algae are known to produce a variety of compounds, from fuels to cosmetics. The future biorefineries would not only look to capitalize on this enormous potential but also augment this approach to produce more compounds and enhance their respective amounts by using an ecological engineering approach (Cho et al., 2015b). Ecological engineering or synthetic ecology is a broad term used for artificial biomimetic systems which use multi-organism approach for present-day solutions (Cho et al., 2015b; Kazamia et al., 2012a). Any biorefinery system would benefit from the beneficial effects of bacteria for algal growth promotion and harvesting as discussed above. Yet, such interactions have potential to offer beyond what has been demonstrated so far. For instance, in the bioenergy sector, algae–bacteria interactions could be used to good effect, for biodiesel production, electricity generation, biogas, bioethanol and biohydrogen production. Several studies have

demonstrated that electricity producing bacteria, such as *Geobacter*, can coexist with algae to synergistically produce electricity using light microbial solar/fuel cells (He et al., 2009; Nishio et al., 2013; Rosenbaum et al., 2005). Similarly, algal–bacterial wastewater treatment followed by the production of biogas from wet algal–bacterial biomass is also extensively documented (Prajapati et al., 2013). The role of algae and photosynthetic bacteria for biohydrogen production is being studied, but large-scale application has severe limitations (Das and Veziroğlu, 2001; Miura et al., 1992). A study demonstrated the use of symbiotic bacteria to enhance photo-fermentative hydrogen evolution of *Chlamydomonas*, by oxygen elimination and efficient bacterial respiration resulting in activation of algal Fe-hydrogenase (Lakatos et al., 2014). Similarly, two-stage process of coupled biohydrogen and biogas production was demonstrated using a natural mixed population of *Chlamydomonas* sp., *Scenedesmus* sp., and *Rhizobium* sp. Besides, hydrogen production was achieved without resorting to a sulfur-deprivation process and by mere elimination of oxygen by the symbionts, and the resulting biomass was used for the production of biogas (Wirth et al., 2015). Another two-stage production of value added chemicals from biogas was proved to be possible by using microalgae and methane-oxidizing bacteria. In the first stage, CO<sub>2</sub> in the biogas was fixed by *Scenedesmus* sp., producing oxygen, and lipids were produced by the N-depleted culture. In the second stage, the artificial resulting gas mixture of 60% methane and 40% oxygen was treated by a methane oxidizing bacterium to produce intracellular polyhydroxybutyrate (PHB) after repeated nitrogen limitation (van der Ha et al., 2012). This approach was also demonstrated in a single stage by co-cultivation. Such algal–bacterial PHB production process is also studied in laboratory photobioreactors using inoculum from natural environments (Fradinho et al., 2013).

Bio-ethanol production from algal–bacterial co-culture is an enriching advance, which is yet to be fully explored. Some algae can produce up to 38% of starch granules (dry cell weight basis), and various marine bacteria can utilize this starch to produce ethanol, which can be performed as a two-step or one-step process, based on the harmony between the species used (Matsumoto et al., 2003). Another promising approach which unites ecological and genetic engineering approach, is the use of photosynthetically fixed carbon from algae to produce a desired product, such as, succinate by a genetically engineered bacteria, such as *Corynebacterium glutamicum* (Lee et al., 2014a). This approach promises unlimited possibilities for the production of high-value compounds from light energy. In summary, the use of ecological engineering approaches opens a new era for exciting possibilities for algae-based biorefineries for sustainable production of fuels and chemicals (Smith et al., 2010). Finally, such multi-species approach would circumvent the restrictions imposed on using genetically engineered systems on a large scale (Ortiz-Marquez et al., 2013).

#### 4.2.4. Sustainable aquaculture system

Until lately, algae were the only focus of aquaculture feed with scant attention to bacteria. Even within the aquaculture system, control of bacterial diseases was the only rationale, while the role that could be potentially played by beneficial bacteria was largely ignored. A healthy feed would comprise grazers, algae and their associated beneficial bacteria, and it has been used industrially for decades (Spolaore et al., 2006). Several algal species were also used for controlling pathogenic bacteria in aquaculture systems, like *Vibrio harveyi*, by disrupting the quorum sensing communication between the pathogenic bacteria (Natrah et al., 2013). It was also proved that co-ingestion of algae and bacteria results in healthier *Artemia* culture through better nitrogen assimilation (Toi et al., 2014). Many studies have dealt with algal–bacterial treatment of aquaculture wastewater, but the resounding demonstration that these flocs harvested after wastewater treatment would be used as feed again for Pacific white shrimps, *Litopenaeus vannamei*, throws light on the utility of such an integrated, sustainable and recyclable aquaculture system (Natrah et al., 2013; Van Den Hende et al., 2014).



**Table 1**

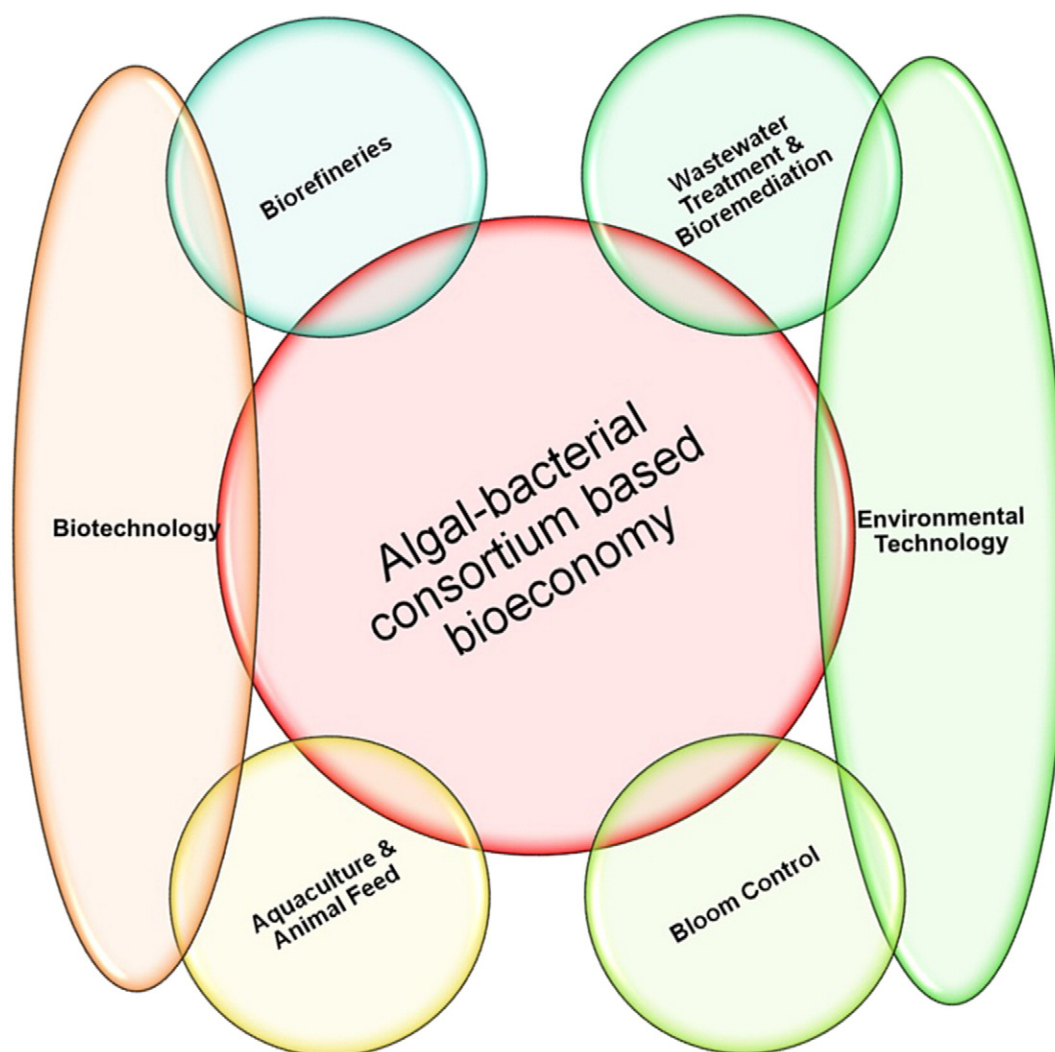
A summary of current understanding of evolutionary and ecological roles to harness biotechnological potential of algal–bacterial interactions.

S. no.	Processes in algal biotechnology	Ecological/evolutionary role	Biotechnological applications	References
1.	Strain selection	Algae harboring PGPB are known to evade pathogens like harmful bacteria and fungi.	Help maintain desirable microbial community and avoid frequent cultivation crashes.	Cho et al. (2015a), Egan et al. (2000) and Wiese et al. (2009)
2.	Cultivation	Bacteria aid algal growth by supplementing various major and minor nutrients in oligotrophic environments. See Fig. 4 for details.	Enhanced growth rate and algal productivity. Reduced dependence on supplied nutrients.	Cho et al. (2015b), Gonzalez and Bashan (2000) and Kouzuma and Watanabe (2015)
3.	Harvesting	Bacteria initiate algal flocculation possibly for two reasons. Firstly, large algal–bacterial flocs help algae evade predators like zooplankton as large flocs are difficult to consume. Secondly, bacteria willingly settle algae resulting in algal death and subsequent bacterial degradation.	Harvesting accounts for 30% of overall costs in algal bio-product industry. Large algal–bacterial flocs settle readily, resulting in reduced use of flocculants and costs, and better yield.	Lee et al. (2013), Montemezzani et al. (2015), Powell and Hill (2013) and Wang et al. (2015)
4.	Extraction	Pathogenic bacteria weaken algal cell wall resulting in disruption and cell death, playing a leading role in decomposition.	A study showed enhanced lipid recovery from bacteria infested algae thereby reducing the cost of organic solvent extraction.	Bai et al. (2011), Halim et al. (2012) and Lenneman et al. (2014)

## 5. Present & future prospects

As previously mentioned, there are more questions than answers in algal–bacterial interactions from its evolution to applications. The present day understanding of ecology and evolution of algal–bacterial interactions has not been exploited in algae based technologies (Shurin et al., 2013). Table 1 summarizes the need for such understanding and

integration in algal biotechnology. Moreover, further studies in ecological engineering would help in the use of algae and bacteria as a production platform for host of industrially important chemicals and fuels in future biorefineries (Brenner et al., 2008; Cho et al., 2015b; Lee et al., 2014a). As prices of traditionally cultivated food products rise with burgeoning population and reduced land area, alternative food products such as algae based diet could gain prominence (Abreu et al., 2014; Tabarsa

**Fig. 5.** Various applications of algal–bacterial interactions for biotechnology and environmental sectors.

et al., 2012; Wijesekara and Kim, 2015). Thus, there is a need to look at algal–bacterial interactions for both high-value products such as nutraceuticals & cosmetics, low value food products for aquaculture and animal feed as well as medium to high value chemicals such as fuels and PHBs. Secondly, algal–bacterial interactions are of potential use in environmental technologies. Algae offer photosynthetically produced oxygen which could be used for algae–bacteria based wastewater treatment (Praveen and Loh, 2015). It has been demonstrated adequately that algae and bacteria combine to remediate toxic chemicals and metals (Subashchandrabose et al., 2011). On the contrary, parasitic bacteria are known to help in the revival of HAB infested freshwater and marine environments (Fig. 5). Therefore, further studies on these interactions would not only help the commercialization stakeholders but also help in understanding some of basic but pertinent questions like involvement in – biogeochemical cycling, endosymbiosis, multicellularity and vital habitats. This makes for an exciting new era with a paradigm shift from single species based approach to community based integration. And this integration closely mimics the natural ecosystem, therefore driving us towards sustainable production and development.

## Acknowledgments

This work was supported by the Advanced Biomass R&D Center (ABC) of Global Frontier Project funded by the (2015M3A6A2065697), grant from Marine Biotechnology Program funded by Korea Government Ministry of Oceans and Fisheries (20150184), and a grant from the host institution through the KRIBB Research Initiative Program ([www.krribb.re.kr](http://www.krribb.re.kr)).

## References

- Abreu, M.H., Pereira, R., Sassi, J.-F., 2014. Marine algae and the global food industry. *Marine Algae: Biodiversity, Taxonomy, Environmental Assessment, and Biotechnology*, p. 300.
- Adey, W.H., Kangas, P.C., Mulbry, W., 2011. Algal turf scrubbing: cleaning surface waters with solar energy while producing a biofuel. *Bioscience* 61, 434–441.
- Afi, L., Metzger, P., Largeau, C., Connan, J., Berkaloff, C., Rousseau, B., 1996. Bacterial degradation of green microalgae: incubation of *Chlorella emersonii* and *Chlorella vulgaris* with *Pseudomonas oleovorans* and *Flavobacterium aquatile*. *Org. Geochem.* 25, 117–130.
- Amin, S.A., Green, D.H., Hart, M.C., Küpper, F.C., Sunda, W.G., Carrano, C.J., 2009. Photolysis of iron-siderophore chelates promotes bacterial–algal mutualism. *Proc. Natl. Acad. Sci.* 106, 17071–17076.
- Amin, S.A., Hmel, L.R., van Tol, H.M., Durham, B.P., Carlson, L.T., Heal, K.R., et al., 2015. Interaction and signalling between a cosmopolitan phytoplankton and associated bacteria. *Nature* 522, 98–101.
- Amin, S.A., Parker, M.S., Armbrust, E.V., 2012. Interactions between diatoms and bacteria. *Microbiol. Mol. Biol. Rev.* 76, 667–684.
- Andersson, S.G.E., Zomorodipour, A., Andersson, J.O., Sicheritz-Ponten, T., Alsmark, U.C.M., Podowski, R.M., et al., 1998. The genome sequence of *Rickettsia prowazekii* and the origin of mitochondria. *Nature* 396, 133–140.
- Arndt, N.T., Nisbet, E.G., 2012. Processes on the young earth and the habitats of early life. *Annu. Rev. Earth Planet. Sci.* 40, 521–549.
- Arora, M., Anil, A.C., Delany, J., Rajarajan, N., Emami, K., Mesbahi, E., 2012. Carbohydrate-degrading bacteria closely associated with *Tetraselmis indica*: influence on algal growth. *Aquat. Biol.* 15 (1), 61–71.
- Aschenbrenner, I.A., Cardinale, M., Berg, G., Grube, M., 2014. Microbial cargo: do bacteria on symbiotic propagules reinforce the microbiome of lichens? *Environ. Microbiol.* 16, 3743–3752.
- Ashen, J.B., Goff, L.J., 2000. Molecular and ecological evidence for species specificity and coevolution in a group of marine algal–bacterial symbioses. *Appl. Environ. Microbiol.* 66, 3024–3030.
- Ask, J., Karlsson, J., Persson, L., Ask, P., Byström, P., Jansson, M., 2009. Whole-lake estimates of carbon flux through algae and bacteria in benthic and pelagic habitats of clear-water lakes. *Ecology* 90, 1923–1932.
- Azam, F., 1998. Microbial control of oceanic carbon flux: the plot thickens. *Science* 280, 694–696.
- Azua-Bustos, A., González-Silva, C., Arenas-Fajardo, C., Vicuña, R., 2012. Extreme environments as potential drivers of convergent evolution by exaptation: the Atacama Desert Coastal Range case. *Front. Microbiol.* 3.
- Bai, S., Huang, L., Su, J., Tian, Y., Zheng, T., 2011. Algicidal effects of a novel marine actinomycete on the toxic dinoflagellate *Alexandrium tamarense*. *Curr. Microbiol.* 62, 1774–1781.
- Barott, K.L., Rodriguez-Brito, B., Janušková, J., Marhaver, K.L., Smith, J.E., Keeling, P., et al., 2011. Microbial diversity associated with four functional groups of benthic reef algae and the reef-building coral *Montastraea annularis*. *Environ. Microbiol.* 13, 1192–1204.
- Barott, K.L., Rodriguez-Mueller, B., Youle, M., Marhaver, K.L., Vermeij, M.J.A., Smith, J.E., et al., 2012. Microbial to reef scale interactions between the reef-building coral *Montastraea annularis* and benthic algae. *Proc. R. Soc. B Biol. Sci.* 279, 1655–1664.
- Barott, K.L., Venn, A.A., Perez, S.O., Tambutti, S., Tresguerres, M., 2015. Coral host cells acidify symbiotic algal microenvironment to promote photosynthesis. *Proc. Natl. Acad. Sci.* 112, 607–612.
- Bashan, Y., Holguin, G., 1998. Proposal for the division of plant growth-promoting rhizobacteria into two classifications: biocontrol-PGPB (plant growth-promoting bacteria) and PGPB. *Soil Biol. Biochem.* 30, 1225–1228.
- Bayer, T., Neave, M.J., Alsheikh-Hussain, A., Aranda, M., Yum, L.K., Mincer, T., et al., 2013. The microbiome of the Red Sea coral *Stylophora pistillata* is dominated by tissue associated endozoomonas bacteria. *Appl. Environ. Microbiol.* 79, 4759–4762.
- Bell, W., Mitchell, R., 1972. Chemotactic and growth responses of marine bacteria to algal extracellular products. *Biol. Bull.* 143, 265–277.
- Benemann, J.R., Weissman, J.C., Koopman, B.L., Oswald, W.J., 1977. Energy production by microbial photosynthesis. *Nature* 268, 19–23.
- Bester, M.C., Jacobson, D., Bauer, F.F., 2012. Many *Saccharomyces cerevisiae* cell wall protein encoding genes are coregulated by *Mss11*, but cellular adhesion phenotypes appear only flo protein dependent. *G3 Genom. Genet.* 2, 131–141.
- Bhat, M.K., 2000. Cellulases and related enzymes in biotechnology. *Biotechnol. Adv.* 18, 355–383.
- Bhattacharya, D., Medlin, L., 1998. Algal phylogeny and the origin of land plants. *Plant Physiol.* 116, 9–15.
- Blankenship, R.E., Hartman, H., 1998. The origin and evolution of oxygenic photosynthesis. *Trends Biochem. Sci.* 23, 94–97.
- Boivin, M.E.Y., Greve, G.D., García-Meza, J.V., Massieux, B., Sprenger, W., Kraak, M.H.S., et al., 2007. Algal–bacterial interactions in metal contaminated floodplain sediments. *Environ. Pollut.* 145, 884–894.
- Bolch, C.J.S., Subramanian, T.A., Green, D.H., 2011. The toxic dinoflagellate *Gymnodinium catenatum* (dinophyceae) requires marine bacteria for growth. *J. Phycol.* 47, 1009–1022.
- Bourne, D.G., Garren, M., Work, T.M., Rosenberg, E., Smith, G.W., Harvell, C.D., 2009. Microbial disease and the coral holobiont. *Trends Microbiol.* 17, 554–562.
- Bourne, D., Iida, Y., Uthicke, S., Smith-Keune, C., 2007. Changes in coral-associated microbial communities during a bleaching event. *ISME J.* 2, 350–363.
- Bratbak, G., Thingstad, T., 1985. Phytoplankton–bacteria interactions: an apparent paradox? Analysis of a model system with both competition and commensalism. *Mar. Ecol. Prog. Ser. Oldendorf* 25, 23–30.
- Brenner, K., You, L., Arnold, F.H., 2008. Engineering microbial consortia: a new frontier in synthetic biology. *Trends Biotechnol.* 26, 483–489.
- Brown, B.E., Dunne, R.P., Ambarari, I., Tissier, M.D.A.L., Satapoomin, U., 1999. Seasonal fluctuations in environmental factors and variations in symbiotic algae and chlorophyll pigments in four Indo-Pacific coral species. *Mar. Ecol. Prog. Ser.* 191, 53–69.
- Bruckner, C.G., Bahulikal, R., Rahalkar, M., Schink, B., Kroth, P.G., 2008. Bacteria associated with benthic diatoms from lake constance: phylogeny and influences on diatom growth and secretion of extracellular polymeric substances. *Appl. Environ. Microbiol.* 74, 7740–7749.
- Buchan, A., LeClerc, G.R., Gulvik, C.A., Gonzalez, J.M., 2014. Master recyclers: features and functions of bacteria associated with phytoplankton blooms. *Nat. Rev. Microbiol.* 12, 686–698.
- Carrillo, P., Medina-Sánchez, J.M., Villar-Argaiz, M., Delgado-Molina, J.A., Bullejos, F.J., 2006. Complex interactions in microbial food webs: stoichiometric and functional approaches. *Limnol. Oceanogr.* 51, 189–204.
- Castenholz, R.W., 1976. The effect of sulfide on the bluegreen algae of hot springs. i. New Zealand and Iceland. *J. Phycol.* 12, 54–68.
- Cherrier, J., Valentine, S., Hamill, B., Jeffrey, W.H., Marra, J.F., 2014. Light-mediated release of dissolved organic carbon by phytoplankton. *J. Mar. Syst.*
- Cho, D.-H., Ramanan, R., Heo, J., Kang, Z., Kim, B.-H., Ahn, C.-Y., et al., 2015a. Organic carbon, influent microbial diversity and temperature strongly influence algal diversity and biomass in raceway ponds treating raw municipal wastewater. *Bioresour. Technol.* 191, 481–487.
- Cho, D.-H., Ramanan, R., Heo, J., Lee, J., Kim, B.-H., Oh, H.-M., et al., 2015b. Enhancing microalgal biomass productivity by engineering a microalgal–bacterial community. *Bioresour. Technol.* 175, 578–585.
- Cho, D.H., Ramanan, R., Kim, B.H., Lee, J., Kim, S., Yoo, C., et al., 2013. Novel approach for the development of axenic microalgal cultures from environmental samples. *J. Phycol.* 49, 802–810.
- Christenson, L., Sims, R., 2011. Production and harvesting of microalgae for wastewater treatment, biofuels, and bioproducts. *Biotechnol. Adv.* 29, 686–702.
- Christenson, L.B., Sims, R.C., 2012. Rotating algal biofilm reactor and spool harvester for wastewater treatment with biofuels by-products. *Biotechnol. Bioeng.* 109, 1674–1684.
- Cockell, C.S., Rettberg, P., Rabbow, E., Olsson-Francis, K., 2011. Exposure of phototrophs to 548 days in low Earth orbit: microbial selection pressures in outer space and on early Earth. *ISME J.* 5, 1671–1682.
- Cocking, E., 2003. Endophytic colonization of plant roots by nitrogen-fixing bacteria. *Plant Soil* 252, 169–175.
- Cole, J.J., 1982. Interactions between bacteria and algae in aquatic ecosystems. *Annu. Rev. Ecol. Syst.* 13, 291–314.
- Cooper, M.B., Smith, A.G., 2015. Exploring mutualistic interactions between microalgae and bacteria in the omics age. *Curr. Opin. Plant Biol.* 26, 147–153.
- Craggs, R.J., Heubeck, S., Lundquist, T.J., Benemann, J.R., 2011. Algal biofuels from wastewater treatment high rate algal ponds. *Water Sci. Technol.* 63, 660–665.
- Croft, M.T., Lawrence, A.D., Raux-Deery, E., Warren, M.J., Smith, A.G., 2005. Algae acquire vitamin B12 through a symbiotic relationship with bacteria. *Nature* 438, 90–93.
- Currie, D.J., Kalf, J., 1984. A comparison of the abilities of freshwater algae and bacteria to acquire and retain phosphorus. *Limnol. Oceanogr.* 29, 298–310.

- Curtis, B.A., Tanifuji, G., Burki, F., Gruber, A., Irimia, M., Maruyama, S., et al., 2012. Algal genomes reveal evolutionary mosaicism and the fate of nucleomorphs. *Nature* 492, 59–65.
- Dahiya, N., Tewari, R., Hoondal, G., 2006. Biotechnological aspects of chitinolytic enzymes: a review. *Appl. Microbiol. Biotechnol.* 71, 773–782.
- Das, D., Veziroglu, T.N., 2001. Hydrogen production by biological processes: a survey of literature. *Int. J. Hydrog. Energy* 26, 13–28.
- Decker, H., Holde, K., 2011. Aerobic Metabolism: benefits from an oxygenated world. *Oxygen and the Evolution of Life*. Springer Berlin Heidelberg, pp. 61–77.
- Doncaster, C.P., Jackson, A., Watson, R.A., 2013. Manipulated into giving: when parasitism drives apparent or incidental altruism. *Proc. R. Soc. B Biol. Sci.* 280.
- Doucette, G.J., 1995. Interactions between bacteria and harmful algae: a review. *Nat. Toxins* 3, 65–74.
- Douglas, A.E., 2003. Coral bleaching—how and why? *Mar. Pollut. Bull.* 46, 385–392.
- Droop, M.R., 2007. Vitamins, phytoplankton and bacteria: symbiosis or scavenging? *J. Plankton Res.* 29, 107–113.
- Egan, S., Thomas, T., Holmström, C., Kjelleberg, S., 2000. Phylogenetic relationship and antifouling activity of bacterial epiphytes from the marine alga *Ulva lactuca*. *Environ. Microbiol.* 2, 343–347.
- Emelyanov, V., 2001. Rickettsiaceae, *Rickettsia*-like endosymbionts, and the origin of mitochondria. *Biosci. Rep.* 21, 1–17.
- Ewald, P.W., 1987. Transmission modes and evolution of the parasitism–mutualism continuum. *Ann. N. Y. Acad. Sci.* 503, 295–306.
- Ferrero, E.M., de Godos, I., Rodríguez, E.M., García-Encina, P.A., Muñoz, R., Bécas, E., 2012. Molecular characterization of bacterial communities in algal–bacterial photobioreactors treating piggyery wastewaters. *Ecol. Eng.* 40, 121–130.
- Field, C.B., Behrenfeld, M.J., Randerson, J.T., Falkowski, P., 1998. Primary production of the biosphere: integrating terrestrial and oceanic components. *Science* 281, 237–240.
- Fradinho, J., Domingos, J., Carvalho, G., Oehmen, A., Reis, M., 2013. Polyhydroxyalkanoates production by a mixed photosynthetic consortium of bacteria and algae. *Bioresour. Technol.* 132, 146–153.
- Gardes, A., Iversen, M.H., Grossart, H.P., Passow, U., Ullrich, M.S., 2011. Diatom-associated bacteria are required for aggregation of *Thalassiosira weissflogii*. *ISME J.* 5, 436–445.
- Gascuel, D., Bozec, Y.-M., Chassot, E., Colomb, A., Laurans, M., 2005. The trophic spectrum: theory and application as an ecosystem indicator. *ICES J. Mar. Sci. J. Conseil* 62, 443–452.
- Geng, H., Belas, R., 2010. Molecular mechanisms underlying roseobacter–phytoplankton symbioses. *Curr. Opin. Biotechnol.* 21, 332–338.
- Glaesener, A.G., Merchant, S.S., Blaby-Haas, C.E., 2013. Iron economy in *Chlamydomonas reinhardtii*. *Front Plant Sci.* 4, 337.
- Goetze, F., Thiel, V., Wiese, J., Labes, A., Imhoff, J.F., 2013. Algae as an important environment for bacteria–phylogenetic relationships among new bacterial species isolated from algae. *Phycologia* 52, 14–24.
- Goff, L.J., Coleman, A.W., 1984. Transfer of nuclei from a parasite to its host. *Proc. Natl. Acad. Sci. U. S. A.* 81, 5420–5424.
- Goff, L.J., Moon, D.A., Nyvall, P., Stache, B., Mangin, K., Zuccarello, G., 1996. The evolution of parasitism in the red algae: molecular comparisons of adelphoparasites and their hosts. *J. Phycol.* 32, 297–312.
- Gonzalez, L.E., Bashan, Y., 2000. Increased growth of the microalga *Chlorella vulgaris* when coimmobilized and cocultured in alginate beads with the plant-growth-promoting bacterium *Azospirillum brasilense*. *Appl. Environ. Microbiol.* 66, 1527–1531.
- González, J.M., Simó, R., Massana, R., Covert, J.S., Casamayor, E.O., Pedrós-Alió, C., et al., 2000. Bacterial community structure associated with a dimethylsulfoniopropionate-producing north atlantic algal bloom. *Appl. Environ. Microbiol.* 66, 4237–4246.
- Granum, E., KIRKWOOD, S., Mykkestad, S.M., 2002. Cellular and extracellular production of carbohydrates and amino acids by the marine diatom *Skeletonema costatum*: diel variations and effects of N depletion. *Mar. Ecol. Prog. Ser.* 242, 83–94.
- Gray, M.W., Burger, G., Lang, B.F., 1999. Mitochondrial evolution. *Science* 283, 1476–1481.
- Gribaldo, S., Brochier-Armanet, C., 2006. The origin and evolution of Archaea: a state of the art. *Philos. Trans. R. Soc. Lond. Ser. B Biol. Sci.* 361, 1007–1022.
- Grossart, H.P., Czub, G., Simon, M., 2006. Algae–bacteria interactions and their effects on aggregation and organic matter flux in the sea. *Environ. Microbiol.* 8, 1074–1084.
- Grover, J.P., 2000. Resource competition and community structure in aquatic micro-organisms: experimental studies of algae and bacteria along a gradient of organic carbon to inorganic phosphorus supply. *J. Plankton Res.* 22, 1591–1610.
- Grube, M., Cernava, T., Soh, J., Fuchs, S., Aschenbrenner, I., Lassek, C., et al., 2015. Exploring functional contexts of symbiotic sustain within lichen-associated bacteria by comparative omics. *ISME J.* 9, 412–424.
- Gurung, T.B., Urabe, J., Nakanishi, M., 1999. Regulation of the relationship between phytoplankton *Scenedesmus acutus* and heterotrophic bacteria by the balance of light and nutrients. *Aquat. Microb. Ecol.* 17, 27–35.
- Halim, R., Danquah, M.K., Webley, P.A., 2012. Extraction of oil from microalgae for biodiesel production: a review. *Biotechnol. Adv.* 30, 709–732.
- Hancock, L., Goff, L., Lane, C., 2010. Red algae lose key mitochondrial genes in response to becoming parasitic. *Genome Biol. Evol.* 2, 897–910.
- He, Z., Kan, J., Mansfeld, F., Angenent, L.T., Nealson, K.H., 2009. Self-sustained phototrophic microbial fuel cells based on the synergistic cooperation between photosynthetic microorganisms and heterotrophic bacteria. *Environ. Sci. Technol.* 43, 1648–1654.
- Helliwell, K.E., Wheeler, G.L., Leptos, K.C., Goldstein, R.E., Smith, A.G., 2011. Insights into the evolution of vitamin B12 auxotrophy from sequenced algal genomes. *Mol. Biol. Evol.* 28, 2921–2933.
- Hernandez, J.-P., de-Bashan, L.E., Rodriguez, D.J., Rodriguez, Y., Bashan, Y., 2009. Growth promotion of the freshwater microalga *Chlorella vulgaris* by the nitrogen-fixing, plant growth-promoting bacterium *Bacillus pumilus* from arid zone soils. *Eur. J. Soil Biol.* 45, 88–93.
- Hernández, D., Riaño, B., Coca, M., García-González, M.C., 2013. Treatment of agro-industrial wastewater using microalgae–bacteria consortium combined with anaerobic digestion of the produced biomass. *Bioresour. Technol.* 135, 598–603.
- Herron, M.D., Michod, R.E., 2008. Evolution of complexity in the volvocine algae: transitions in individuality through Darwin's eye. *Evolution* 62, 436–451.
- Herron, M.D., Hackett, J.D., Aylward, F.O., Michod, R.E., 2009. Triassic origin and early radiation of multicellular volvocine algae. *Proc. Natl. Acad. Sci.* 106, 3254–3258.
- Hirsch, A.M., 2004. Plant–microbe symbioses: a continuum from commensalism to parasitism. *Symbiosis* 37 (1–3).
- Hodkinson, B., Lutzoni, F., 2009. A microbiotic survey of lichen-associated bacteria reveals a new lineage from the Rhizobiales. *Symbiosis* 49, 163–180.
- Hodkinson, B.P., Gittel, N.R., Schadt, C.W., Lutzoni, F., 2012. Photoautotrophic symbiont and geography are major factors affecting highly structured and diverse bacterial communities in the lichen microbiome. *Environ. Microbiol.* 14, 147–161.
- Hoegh-Guldberg, O., Mumby, P.J., Hooten, A.J., Steneck, R.S., Greenfield, P., Gomez, E., et al., 2007. Coral reefs under rapid climate change and ocean acidification. *Science* 318, 1737–1742.
- Hoffmann, L., 1989. Algae of terrestrial habitats. *Bot. Rev.* 55, 77–105.
- Hoffmann, J.P., 1998. Wastewater treatment with suspended and nonsuspended algae. *J. Phycol.* 34, 757–763.
- Holland, H.D., 2006. The oxygenation of the atmosphere and oceans. *Philos. Trans. R. Soc. B Biol. Sci.* 361, 903–915.
- Hollants, J., Leroux, O., Leliaert, F., Decluyre, H., De Clerck, O., Willems, A., 2011. Who is in there? Exploration of endophytic bacteria within the siphonous green seaweed *Bryopsis* (Bryopsidales, Chlorophyta). *PLoS One* 6, e26458.
- Hom, E.F.Y., Aiyar, P., Schaeme, D., Mittag, M., Sasso, S., 2015. A chemical perspective on microalgal–microbial interactions. *Trends Plant Sci.* 20, 689–693.
- Hu, B., Du, J., Zou, R.-Y., Yuan, Y.-J., 2010. An environment-sensitive synthetic microbial ecosystem. *PLoS One* 5, e10619.
- Hughes, G., 2002. Environmental indicators. *Ann. Tour. Res.* 29, 457–477.
- Hughes, T.P., Baird, A.H., Bellwood, D.R., Card, M., Connolly, S.R., Folke, C., et al., 2003. Climate change, human impacts, and the resilience of coral reefs. *Science* 301, 929–933.
- Interlandi, S.J., Kilham, S.S., 2001. Limiting resources and the regulation of diversity in phytoplankton communities. *Ecology* 82, 1270–1282.
- Jansson, J.K., Neufeld, J.D., Moran, M.A., Gilbert, J.A., 2012. Omics for understanding microbial functional dynamics. *Environ. Microbiol.* 14, 1–3.
- Johnson, N.C., Graham, J.H., Smith, F.A., 1997. Functioning of mycorrhizal associations along the mutualism–parasitism continuum. *New Phytol.* 135, 575–585.
- Jørgensen, B.B., Isaksen, M.F., Jannasch, H.W., 1992. Bacterial sulfate reduction above 100 °C in deep-sea hydrothermal vent sediments. *Science* 258, 1756–1757.
- Kang, Z., Kim, B.H., Ramanan, R., Choi, J.E., Yang, J.W., Oh, H.M., et al., 2014. A cost analysis of microalgal biomass and biodiesel production in open raceways treating municipal wastewater and under optimum light wavelength. *J. Microbiol. Biotechnol.*
- Karst, J., Marczak, L., Jones, M.D., Turkington, R., 2008. The mutualism–parasitism continuum in ectomycorrhizas: a quantitative assessment using meta-analysis. *Ecology* 89, 1032–1042.
- Kawafune, K., Hongoh, Y., Hamaji, T., Nozaki, H., 2012. Molecular identification of rickettsial endosymbionts in the non-phagotrophic volvocine green algae. *PLoS One* 7, e31749.
- Kawafune, K., Hongoh, Y., Nozaki, H., 2014. A rickettsial endosymbiont inhabiting the cytoplasm of *Volvox carteri* (Volvocales, Chlorophyceae). *Phycologia* 53, 95–99.
- Kazamia, E., Aldridge, D.C., Smith, A.G., 2012a. Synthetic ecology – a way forward for sustainable algal biofuel production? *J. Biotechnol.* 162, 163–169.
- Kazamia, E., Czesnick, H., Nguyen, T.T., Croft, M.T., Sherwood, E., Sasso, S., et al., 2012b. Mutualistic interactions between vitamin B12-dependent algae and heterotrophic bacteria exhibit regulation. *Environ. Microbiol.* 14, 1466–1476.
- Keeling, P.J., 2009. Chromalveolates and the evolution of plastids by secondary endosymbiosis. *J. Eukaryot. Microbiol.* 56, 1–8.
- Kesaano, M., Sims, R.C., 2014. Algal biofilm based technology for wastewater treatment. *Algal Res.* 5, 231–240.
- Kim, B.H., Kang, Z., Ramanan, R., Choi, J.E., Cho, D.H., Oh, H.M., et al., 2014b. Nutrient removal and biofuel production in high rate algal pond (HRAP) using real municipal wastewater. *J. Microbiol. Biotechnol.* 24, 1123–1132.
- Kim, B.-H., Ramanan, R., Cho, D.-H., Oh, H.-M., Kim, H.-S., 2014a. Role of *Rhizobium*, a plant growth promoting bacterium, in enhancing algal biomass through mutualistic interaction. *Biomass Bioenergy* 69, 95–105.
- Kim, M.-J., Jeong, S.-Y., Lee, S.-J., 2008. Isolation, identification, and algicidal activity of marine bacteria against *Cochlodinium polykrikoides*. *J. Appl. Phycol.* 20, 1069–1078.
- Kirk, D.L., 2001. Germ–soma differentiation in *Volvox*. *Dev. Biol.* 238, 213–223.
- Kirk, D.L., 2005. A twelve-step program for evolving multicellularity and a division of labor. *BioEssays* 27, 299–310.
- Klepac-Ceraj, V., Hayes, C.A., Gilhooly, W.P., Lyons, T.W., Kolter, R., Pearson, A., 2012. Microbial diversity under extreme euxinia: Mahoney Lake, Canada. *Geobiology* 10, 223–235.
- Kloepper, J.W., Leong, J., Teintze, M., Schroth, M.N., 1980. Enhanced plant growth by siderophores produced by plant growth-promoting rhizobacteria. *Nature* 286, 885–886.
- Kopp, R.E., Kirschvink, J.L., Hilburn, I.A., Nash, C.Z., 2005. The paleoproterozoic snowball earth: a climate disaster triggered by the evolution of oxygenic photosynthesis. *Proc. Natl. Acad. Sci. U. S. A.* 102, 11131–11136.
- Kouzuma, A., Watanabe, K., 2015. Exploring the potential of algae/bacteria interactions. *Curr. Opin. Biotechnol.* 33, 125–129.
- Krohn-Molt, I., Wemheuer, B., Alawi, M., Poehlein, A., Güllert, S., Schmeisser, C., et al., 2013. Metagenome survey of a multispecies and alga-associated biofilm revealed



- key elements of bacterial–algal interactions in photobioreactors. *Appl. Environ. Microbiol.* 79, 6196–6206.
- Kropat, J., Gallaher, S.D., Urzica, E.I., Nakamoto, S.S., Strenkert, D., Tottey, S., et al., 2015. Copper economy in *Chlamydomonas*: prioritized allocation and reallocation of copper to respiration vs. photosynthesis. *Proc. Natl. Acad. Sci. U. S. A.* 112, 2644–2651.
- Kudela, R.M., Dugdale, R.C., 2000. Nutrient regulation of phytoplankton productivity in Monterey Bay, California. *Deep-Sea Res. II Top. Stud. Oceanogr.* 47, 1023–1053.
- Kuo, R.C., Lin, S., 2013. Ectobiotic and endobiotic bacteria associated with *Eutreptiella* sp. isolated from Long Island sound. *Protist* 164, 60–74.
- Lakatos, G., Deak, Z., Vass, I., Retfalvi, T., Rozgonyi, S., Rakhely, G., et al., 2014. Bacterial symbionts enhance photo-fermentative hydrogen evolution of *Chlamydomonas* algae. *Green Chem.* 16, 4716–4727.
- Landa, M., Blain, S., Christaki, U., Monchy, S., Obermester, I., 2015. Shifts in bacterial community composition associated with increased carbon cycling in a mosaic of phytoplankton blooms. *ISME J.*
- Leboulanger, C., Martin-Jézéquel, V., Descolas-Gros, C., Sciandra, A., Jupin, H.J., 1998. Photorespiration in continuous culture of *Dunaliella tertiolecta* (Chlorophyta): relationships between serine, glycine, and extracellular glycolate. *J. Phycol.* 34, 651–654.
- Lee, S.H., Oh, H.M., Jo, B.H., Lee, S.A., Shin, S.Y., Kim, H.S., et al., 2014b. Higher biomass productivity of microalgae in an attached growth system using wastewater. *J. Microbiol. Biotechnol.* 24, 1566–1573.
- Lee, J., Sim, S.J., Bott, M., Um, Y., Oh, M.-K., Woo, H.M., 2014a. Succinate production from CO<sub>2</sub>-grown microalgal biomass as carbon source using engineered *Corynebacterium glutamicum* through consolidated bioprocessing. *Sci. Rep.* 4.
- Lee, Y.K., Ahn, C.Y., Kim, H.S., Oh, H.M., 2010. Cyanobactericidal effect of *Rhodococcus* sp. isolated from eutrophic lake on *Microcystis* sp. *Biotechnol. Lett.* 32, 1673–1678.
- Lee, J., Cho, D.-H., Ramanan, R., Kim, B.-H., Oh, H.-M., Kim, H.-S., 2013. Microalgae-associated bacteria play a key role in the flocculation of *Chlorella vulgaris*. *Bioresour. Technol.* 131, 195–201.
- Lema, K.A., Willis, B.L., Bourne, D.G., 2012. Corals form characteristic associations with symbiotic nitrogen-fixing bacteria. *Appl. Environ. Microbiol.* 78, 3136–3144.
- Lenneman, E.M., Wang, P., Barney, B.M., 2014. Potential application of algicidal bacteria for improved lipid recovery with specific algae. *FEMS Microbiol. Lett.* 354 (2), 102–110.
- Leung, T., Poulin, R., 2008. Parasitism, commensalism, and mutualism: exploring the many shades of symbioses. *Vie Milieu* 58 (2), 107.
- Li, S., Nosenko, T., Hackett, J.D., Bhattacharya, D., 2006. Phylogenomic analysis identifies red algal genes of endosymbiotic origin in the chromalveolates. *Mol. Biol. Evol.* 23, 663–674.
- Littman, R.A., Willis, B.L., Pfeffer, C., Bourne, D.G., 2009. Diversities of coral-associated bacteria differ with location, but not species, for three acroporid corals on the Great Barrier Reef. *FEMS Microbiol. Lett.* 68, 152–163.
- Liu, H., Zhou, Y., Xiao, W., Ji, L., Cao, X., Song, C., 2012. Shifting nutrient-mediated interactions between algae and bacteria in a microcosm: evidence from alkaline phosphatase assay. *Microbiol. Res.* 167, 292–298.
- Lovejoy, C., Bowman, J.P., Hallegraeff, G.M., 1998. Algicidal effects of a novel marine *Pseudoalteromonas* isolate (class Proteobacteria, Gamma subdivision) on harmful algal bloom species of the genera *Chattonella*, *Gymnodinium* and *Heterosigma*. *Appl. Environ. Microbiol.* 64, 2806–2813.
- Lutzoni, F., Miadlikowska, J., 2009. Lichens. *Curr. Biol.* 19, R502–R503.
- Lutzoni, F., Pagel, M., Reeb, V., 2001. Major fungal lineages are derived from lichen symbiotic ancestors. *Nature* 411, 937–940.
- Madhaiyan, M., Poonguzhali, S., Sundaram, S.P., Sa, T., 2006. A new insight into foliar applied methanol influencing phyloplane methylotrophic dynamics and growth promotion of cotton (*Gossypium hirsutum* L.) and sugarcane (*Saccharum officinarum* L.). *Environ. Exp. Bot.* 57, 168–176.
- Mahdavi, H., Prasad, V., Liu, Y., Ulrich, A.C., 2015. In situ biodegradation of naphthenic acids in oil sands tailings pond water using indigenous algae–bacteria consortium. *Bioresour. Technol.* 187, 97–105.
- Malasam, D., Kropat, J., Hsieh, S.I., Finazzi, G., Casero, D., Loo, J.A., et al., 2013. Zinc deficiency impacts CO<sub>2</sub> assimilation and disrupts copper homeostasis in *Chlamydomonas reinhardtii*. *J. Biol. Chem.* 288, 10672–10683.
- Martin, W., Baross, J., Kelley, D., Russell, M.J., 2008. Hydrothermal vents and the origin of life. *Nat. Rev. Microbiol.* 6, 805–814.
- Matsumoto, M., Yokouchi, H., Suzuki, N., Ohata, H., Matsunaga, T., 2003. Saccharification of marine microalgae using marine bacteria for ethanol production. In: Davison, B., Lee, J., Finkelstein, M., McMillan, J. (Eds.), *Biotechnology for Fuels and Chemicals*. Humana Press, pp. 247–254.
- Mayali, X., Doucette, G.J., 2002. Microbial community interactions and population dynamics of an algicidal bacterium active against *Karenia brevis* (Dinophyceae). *Harmful Algae* 1, 277–293.
- McCook, L., Jompa, J., Diaz-Pulido, G., 2001. Competition between corals and algae on coral reefs: a review of evidence and mechanisms. *Coral Reefs* 19, 400–417.
- McCune, B., 2000. Lichen communities as indicators of forest health. *Bryologist* 103, 353–356.
- Ministry of Environment, 2011. *Environmental Statistics Yearbook 2011*, p. 24.
- Miura, Y., Saitoh, C., Matsuoka, S., Miyamoto, K., 1992. Stably sustained hydrogen production with high molar yield through a combination of a marine green alga and a photosynthetic bacterium. *Biosci. Biotechnol. Biochem.* 56, 751–754.
- Montemezzani, V., Duggan, I.C., Hogg, I.D., Craggs, R.J., 2015. A review of potential methods for zooplankton control in wastewater treatment high rate algal ponds and algal production raceways. *Algal Res.* 11, 211–226.
- Moran, M.A., Satinsky, B., Gifford, S.M., Luo, H., Rivers, A., Chan, L.K., et al., 2013. Sizing up metatranscriptomics. *ISME J.* 7, 237–243.
- Mulkidjanian, A.Y., Bychkov, A.Y., Dibrova, D.V., Galperin, M.Y., Koonin, E.V., 2012. Origin of first cells at terrestrial, anoxic geothermal fields. *Proc. Natl. Acad. Sci.*
- Muñoz, R., Guieysse, B., 2006. Algal–bacterial processes for the treatment of hazardous contaminants: a review. *Water Res.* 40, 2799–2815.
- Natrah, F.M.I., Bossier, P., Sorgeloos, P., Yusoff, F.M., Defoirdt, T., 2013. Significance of microalgal–bacterial interactions for aquaculture. *Rev. Aquac.* (n/a–n/a).
- Neale, P., 1987. Algal photoinhibition and photosynthesis in the aquatic environment. *Photoinhibition* 9, 39–65.
- Neuhauser, C., Fargione, J.E., 2004. A mutualism–parasitism continuum model and its application to plant–mycorrhizae interactions. *Ecol. Model.* 177, 337–352.
- Neustupa, J., Skaloud, P., 2008. Diversity of subaerial algae and cyanobacteria on tree bark in tropical mountain habitats. *Biologia* 63, 806–812.
- Ni, T., Yue, J., Sun, G., Zou, Y., Wen, J., Huang, J., 2012. Ancient gene transfer from algae to animals: mechanisms and evolutionary significance. *BMC Evol. Biol.* 12, 83.
- Nikolaeva, E.V., Usov, A.I., Sinityn, A.P., Tambiev, A.H., 1999. Degradation of agarophytic red algal cell wall components by new crude enzyme preparations. *J. Appl. Phycol.* 11, 385–389.
- Nisbet, E.G., Sleep, N.H., 2001. The habitat and nature of early life. *Nature* 409, 1083–1091.
- Nishio, K., Hashimoto, K., Watanabe, K., 2013. Light/electricity conversion by defined cocultures of *Chlamydomonas* and *Geobacter*. *J. Biosci. Bioeng.* 115, 412–417.
- Nowrousian, M., 2010. Next-generation sequencing techniques for eukaryotic microorganisms: sequencing-based solutions to biological problems. *Eukaryot. Cell* 9, 1300–1310.
- Nozaki, H., 1990. Ultrastructure of the extracellular matrix of *Gonium* (Volvocales, Chlorophyta). *Phycologia* 29, 1–8.
- Oh, H.-M., Lee, S.J., Kim, J.-H., Kim, H.-S., Yoon, B.-D., 2001b. Seasonal variation and indirect monitoring of microcystin concentrations in Daechung reservoir, Korea. *Appl. Environ. Microbiol.* 67, 1484–1489.
- Oh, H.-M., Lee, S., Park, M.-H., Kim, H.-S., Kim, H.-C., Yoon, J.-H., et al., 2001a. Harvesting of *Chlorella vulgaris* using a bioflocculant from *Paenibacillus* sp. AM49. *Biotechnol. Lett.* 23, 1229–1234.
- Ortiz-Marquez, J.C.F., Do Nascimento, M., Zehr, J.P., Curatti, L., 2013. Genetic engineering of multispecies microbial cell factories as an alternative for bioenergy production. *Trends Biotechnol.* 31, 521–529.
- Oswald, W.J., Gotaas, H.B., 1957. Photosynthesis in sewage treatment. *Trans. Am. Soc. Civ. Eng.* 122, 73–105.
- Paerl, H., Otten, T., 2013. Harmful cyanobacterial blooms: causes, consequences, and controls. *Microb. Ecol.* 65, 995–1010.
- Palmer, J.D., Soltis, D.E., Chase, M.W., 2004. The plant tree of life: an overview and some points of view. *Am. J. Bot.* 91, 1437–1445.
- Pantos, O., Bongaerts, P., Dennis, P.G., Tyson, G.W., Hoegh-Guldberg, O., 2015. Habitat-specific environmental conditions primarily control the microbiomes of the coral *Seriatopora hystrix*. *ISME J.*
- Parfrey, L.W., Lahr, D.J.G., Knoll, A.H., Katz, L.A., 2011. Estimating the timing of early eukaryotic diversification with multigene molecular clocks. *Proc. Natl. Acad. Sci.* 108, 13624–13629.
- Park, J.B.K., Craggs, R.J., Shilton, A.N., 2011. Wastewater treatment high rate algal ponds for biofuel production. *Bioresour. Technol.* 102, 35–42.
- Park, J.B.K., Craggs, R.J., Shilton, A.N., 2013. Enhancing biomass energy yield from pilot-scale high rate algal ponds with recycling. *Water Res.* 47, 4422–4432.
- Perlman, S.J., Hunter, M.S., Zchori-Fein, E., 2006. The emerging diversity of *Rickettsia*. *Proc. R. Soc. B Biol. Sci.* 273, 2097–2106.
- Philippot, L., Raaijmakers, J.M., Lemanceau, P., van der Putten, W.H., 2013. Going back to the roots: the microbial ecology of the rhizosphere. *Nat. Rev. Microbiol.* 11, 789–799.
- Pitman, M.G., 1982. Transport across plant roots. *Q. Rev. Biophys.* 15, 481–554.
- Powell, R.J., Hill, R.T., 2013. Rapid aggregation of biofuel-producing algae by the bacterium *Bacillus* sp. strain RP1137. *Appl. Environ. Microbiol.* 79, 6093–6101.
- Powell, R.J., Hill, R.T., 2014. Mechanism of algal aggregation by *Bacillus* sp. strain RP1137. *Appl. Environ. Microbiol.* 80, 4042–4050.
- Prajapati, S.K., Kaushik, P., Malik, A., Vijay, V.K., 2013. Phycoremediation coupled production of algal biomass, harvesting and anaerobic digestion: possibilities and challenges. *Appl. Environ. Microbiol.* 31, 1408–1425.
- Praveen, P., Loh, K.-C., 2015. Photosynthetic aeration in biological wastewater treatment using immobilized microalgae–bacteria symbiosis. *Appl. Microbiol. Biotechnol.* 1–10.
- Precht, J., Kneip, C., Lockhart, P., Wenderoth, K., Maier, U.-G., 2004. Intracellular spheroid bodies of *Rhopalodia gibba* have nitrogen-fixing apparatus of cyanobacterial origin. *Mol. Biol. Evol.* 21, 1477–1481.
- Ramanan, R., Kang, Z., Kim, B.-H., Cho, D.-H., Jin, L., Oh, H.-M., et al., 2015. Phycosphere bacterial diversity in green algae reveals an apparent similarity across habitats. *Algal Res.* 8, 140–144.
- Ramanan, R., Kim, B.-H., Cho, D.-H., Ko, S.-R., Oh, H.-M., Kim, H.-S., 2013. Lipid droplet synthesis is limited by acetate availability in starchless mutant of *Chlamydomonas reinhardtii*. *FEBS Lett.* 587, 370–377.
- Rasmussen, B., Fletcher, I.R., Brocks, J.J., Kilburn, M.R., 2008. Reassessing the first appearance of eukaryotes and cyanobacteria. *Nature* 455, 1101–1104.
- Reshef, L., Koren, O., Loya, Y., Zilber-Rosenberg, I., Rosenberg, E., 2006. The coral probiotic hypothesis. *Environ. Microbiol.* 8, 2068–2073.
- Revsbech, N.P., 1995. Microenvironment and photosynthesis of zooxanthellae in scleractinian corals studied with microsensors for O<sub>2</sub>, pH and light. *Mar. Ecol. Prog. Ser.* 117, 159–172.
- Rosenbaum, M., Schröder, U., Scholz, F., 2005. Utilizing the green alga *Chlamydomonas reinhardtii* for microbial electricity generation: a living solar cell. *Appl. Microbiol. Biotechnol.* 68, 753–756.
- Rosenberg, E., Koren, O., Reshef, L., Efrony, R., Zilber-Rosenberg, I., 2007. The role of microorganisms in coral health, disease and evolution. *Nat. Rev. Microbiol.* 5, 355–362.
- Rovira, A.D., 1965. Interactions between plant roots and soil microorganisms. *Annu. Rev. Microbiol.* 19, 241–266.

- Ryu, B.-G., Kim, W., Nam, K., Kim, S., Lee, B., Park, M.S., et al., 2015. A comprehensive study on algal–bacterial communities shift during thiocyanate degradation in a microalga-mediated process. *Bioresour. Technol.* 191, 496–504.
- Sachs, J.L., Simms, E.L., 2006. Pathways to mutualism breakdown. *Trends Ecol. Evol.* 21, 585–592.
- Sachs, J.L., Wilcox, T.P., 2006. A shift to parasitism in the jellyfish symbiont *Symbiodinium microadriaticum*. *Proceedings biological sciences/the royal. Society* 273, 425–429.
- Sakai, N., Sakamoto, Y., Kishimoto, N., Chihara, M., Karube, I., 1995. *Chlorella* strains from hot springs tolerant to high temperature and high CO<sub>2</sub>. *Energy Convers. Manag.* 36, 693–696.
- Sapp, M., Schwaderer, A., Wiltshire, K., Hoppe, H.-G., Gerdts, G., Wichels, A., 2007. Species-specific bacterial communities in the phycosphere of microalgae? *Microb. Ecol.* 53, 683–699.
- Sarmiento, H., Gasol, J.M., 2012. Use of phytoplankton-derived dissolved organic carbon by different types of bacterioplankton. *Environ. Microbiol.* 14, 2348–2360.
- Schippers, A., Neretin, L.N., Kallmeyer, J., Ferdelman, T.G., Cragg, B.A., Parkes, R.J., et al., 2005. Prokaryotic cells of the deep sub-seafloor biosphere identified as living bacteria. *Nature* 433, 861–864.
- Schmollinger, S., Mühlhaus, T., Boyle, N.R., Blaby, I.K., Casero, D., Mettler, T., et al., 2014. Nitrogen-sparing mechanisms in *Chlamydomonas* affect the transcriptome, the proteome, and photosynthetic metabolism. *Plant Cell Online* 26, 1410–1435.
- Schönknecht, G., Chen, W.-H., Ternes, C.M., Barbier, G.G., Shrestha, R.P., Stanke, M., et al., 2013. Gene transfer from bacteria and archaea facilitated evolution of an extremophilic eukaryote. *Science* 339, 1207–1210.
- Seyedsayamdoost, M.R., Case, R.J., Kolter, R., Clardy, J., 2011. The Jekyll-and-Hyde chemistry of *Phaeobacter gallaeciensis*. *Nat. Chem.* 3, 331–335.
- Sharifah, E.N., Eguchi, M., 2011. The phytoplankton *Nannochloropsis oculata* enhances the ability of *Roseobacter* clade bacteria to inhibit the growth of fish pathogen *Vibrio anguillarum*. *PLoS One* 6, e26756.
- Sheppard, C., Loughland, R., 2002. Coral mortality and recovery in response to increasing temperature in the southern Arabian Gulf. *Aquat. Ecosyst. Health Manag.* 5, 395–402.
- Sher, D., Thompson, J.W., Kashtan, N., Croal, L., Chisholm, S.W., 2011. Response of *Prochlorococcus* ecotypes to co-culture with diverse marine bacteria. *ISME J.* 5, 1125–1132.
- Sherr, B., Sherr, E., Hopkinson, C., 1988. Trophic interactions within pelagic microbial communities: indications of feedback regulation of carbon flow. *Hydrobiologia* 159, 19–26.
- Shurin, J.B., Abbott, R.L., Deal, M.S., Kwan, G.T., Litchman, E., McBride, R.C., et al., 2013. Industrial strength ecology: trade-offs and opportunities in algal biofuel production. *Ecol. Lett.* 16, 1393–1404.
- Sigurbjörnsdóttir, M.A., Andrésón, Ó.S., Vilhelmsson, O., 2015. Analysis of the *Peltigera membranacea* metagenome indicates that lichen-associated bacteria are involved in phosphate solubilization. *Microbiology* 161, 989–996.
- Sleep, N.H., 2010. The Hadean–Archaean environment. *Cold Spring Harb. Perspect. Biol.* 2.
- Smith, V.H., Sturm, B.S.M., deNoyelles, F.J., Billings, S.A., 2010. The ecology of algal biodiesel production. *Trends Ecol. Evol.* 25, 301–309.
- Spolaore, P., Joannis-Cassan, C., Duran, E., Isambert, A., 2006. Commercial applications of microalgae. *J. Biosci. Bioeng.* 101, 87–96.
- Srivastava, A., Ahn, C.-Y., Asthana, R.K., Lee, H.-G., Oh, H.-M., 2014. Status, alert system, and prediction of cyanobacterial bloom in South Korea. *BioMed Res. Int.*
- Srivastava, A., Singh, S., Ahn, C.-Y., Oh, H.-M., Asthana, R.K., 2013. Monitoring approaches for a toxic cyanobacterial bloom. *Environ. Sci. Technol.* 47, 8999–9013.
- Stengel, D.B., Macken, A., Morrison, L., Morley, N., 2004. Zinc concentrations in marine macroalgae and a lichen from western Ireland in relation to phylogenetic grouping, habitat and morphology. *Mar. Pollut. Bull.* 48, 902–909.
- Subashchandrabose, S.R., Ramakrishnan, B., Megharaj, M., Venkateswari, K., Naidu, R., 2011. Consortia of cyanobacteria/microalgae and bacteria: biotechnological potential. *Biotechnol. Adv.* 29, 896–907.
- Subashchandrabose, S.R., Ramakrishnan, B., Megharaj, M., Venkateswari, K., Naidu, R., 2013. Mixotrophic cyanobacteria and microalgae as distinctive biological agents for organic pollutant degradation. *Environ. Int.* 51, 59–72.
- Sule, P., Belas, R., 2013. A novel inducer of *Roseobacter* motility is also a disruptor of algal symbiosis. *J. Bacteriol.* 195, 637–646.
- Tabarsa, M., Rezaei, M., Ramezanpour, Z., Waaland, J.R., 2012. Chemical compositions of the marine algae *Gracilaria salicornia* (Rhodophyta) and *Ulva lactuca* (Chlorophyta) as a potential food source. *J. Sci. Food Agric.* 92, 2500–2506.
- Tang, X., He, L.Y., Tao, X.Q., Dang, Z., Guo, C.L., Lu, G.N., et al., 2010. Construction of an artificial microalgal–bacterial consortium that efficiently degrades crude oil. *J. Hazard. Mater.* 181, 1158–1162.
- Teplitski, M., Rajamani, S., 2011. Signal and nutrient exchange in the interactions between soil algae and bacteria. In: Witzany, G. (Ed.), *Biocommunication in Soil Microorganisms*. Springer Berlin Heidelberg, pp. 413–426.
- Thomas, D.N., Dieckmann, G.S., 2002. Antarctic sea ice—a habitat for extremophiles. *Science* 295, 641–644.
- Thompson, A.W., Foster, R.A., Krupke, A., Carter, B.J., Musat, N., Vault, D., et al., 2012. Unicellular cyanobacterium symbiotic with a single-celled eukaryotic alga. *Science* 337, 1546–1550.
- Toi, H.T., Boeckx, P., Sorgeloos, P., Bossier, P., Van Stappen, G., 2014. Co-feeding of microalgae and bacteria may result in increased N assimilation in *Artemia* as compared to mono-diets, as demonstrated by a 15N isotope uptake laboratory study. *Aquaculture* 422–423, 109–114.
- Tomitani, A., Knoll, A.H., Cavanaugh, C.M., Ohno, T., 2006. The evolutionary diversification of cyanobacteria: molecular-phylogenetic and paleontological perspectives. *Proc. Natl. Acad. Sci.* 103, 5442–5447.
- Tout, J., Siboni, N., Messer, L.F., Garren, M., Stocker, R., Webster, N.S., et al., 2015. Increased seawater temperature increases the abundance and alters the structure of natural *Vibrio* populations associated with the coral *Pocillopora damicornis*. *Front. Microbiol.* 6.
- Tringe, S.G., von Mering, C., Kobayashi, A., Salamov, A.A., Chen, K., Chang, H.W., et al., 2005. Comparative metagenomics of microbial communities. *Science* 308, 554–557.
- Uduman, N., Qi, Y., Danquah, M.K., Forde, G.M., Hoadley, A., 2010. Dewatering of microalgal cultures: a major bottleneck to algae-based fuels. *J. Renew. Sustain. Energy* 2, 012701–012715.
- Vaishnava, S., Striepen, B., 2006. The cell biology of secondary endosymbiosis—how parasites build, divide and segregate the apicoplast. *Mol. Microbiol.* 61, 1380–1387.
- Valiente-Banuet, A., Verdú, M., 2008. Temporal shifts from facilitation to competition occur between closely related taxa. *J. Ecol.* 96, 489–494.
- Van Den Hende, S., Claessens, L., De Muylder, E., Boon, N., Vervaeeren, H., 2014. Microalgal bacterial flocs originating from aquaculture wastewater treatment as diet ingredient for *Litopenaeus vannamei* (Boone). *Aquac. Res.* (n/a–n/a).
- van der Ha, D., Nachtergaele, L., Kerckhof, F.-M., Rameiyanti, D., Bossier, P., Verstraete, W., et al., 2012. Conversion of biogas to bioproducts by algae and methane oxidizing bacteria. *Environ. Sci. Technol.* 46, 13425–13431.
- van Ommeren, R., Whitham, T., 2002. Changes in interactions between juniper and mistletoe mediated by shared avian frugivores: parasitism to potential mutualism. *Oecologia* 130, 281–288.
- Wagner-Döbler, I., Biebl, H., 2006. Environmental biology of the marine *Roseobacter* lineage. *Annu. Rev. Microbiol.* 60, 255–280.
- Wang, H., Hill, R.T., Zheng, T., Hu, X., Wang, B., 2015. Effects of bacterial communities on biofuel producing microalgae: stimulation, inhibition and harvesting. *Crit. Rev. Biotechnol.* 1–12.
- Wang, X., Li, Z., Su, J., Tian, Y., Ning, X., Hong, H., et al., 2010. Lysis of a red-tide causing alga, *Alexandrium tamarense*, caused by bacteria from its phycosphere. *Biol. Control* 52, 123–130.
- Watanabe, K., Takihana, N., Aoyagi, H., Hanada, S., Watanabe, Y., Ohmura, N., et al., 2005. Symbiotic association in *Chlorella* culture. *FEMS Microbiol. Ecol.* 51, 187–196.
- Wierzbos, J., DiRuggiero, J., Vitek, P., Artieda, O., Souza-Egipsy, V., Skaloud, P., et al., 2015. Adaptation strategies of endolithic chlorophototrophs to survive the hyperarid and extreme solar radiation environment of the Atacama desert. *Front. Microbiol.* 6.
- Wiese, J., Thiel, V., Nagel, K., Staufenberger, T., Imhoff, J., 2009. Diversity of antibiotic-active bacteria associated with the brown alga *Laminaria saccharina* from the Baltic Sea. *Mar. Biotechnol.* 11, 287–300.
- Wijesekara, I., Kim, S.-K., 2015. Application of marine algae derived nutraceuticals in the food industry. *Marine Algae Extracts*. Wiley-VCH Verlag, pp. 627–638.
- Williams, T.A., Foster, P.G., Cox, C.J., Embley, T.M., 2013. An archaeal origin of eukaryotes supports only two primary domains of life. *Nature* 504, 231–236.
- Wilmotte, A., 2004. Molecular evolution and taxonomy of the cyanobacteria. *The Molecular Biology of Cyanobacteria*. Springer, pp. 1–25.
- Wirth, R., Lakatos, G., Maróti, G., Bagi, Z., Minárovics, J., Nagy, K., et al., 2015. Exploitation of algal–bacterial associations in a two-stage biohydrogen and biogas generation process. *Biotechnol. Biofuels* 8, 1–14.
- Wooldridge, S.A., 2009. A new conceptual model for the warm-water breakdown of the coral–algae endosymbiosis. *Mar. Freshw. Res.* 60, 483–496.
- Yoon, H.S., Hackett, J.D., Ciniglia, C., Pinto, G., Bhattacharya, D., 2004. A molecular timeline for the origin of photosynthetic eukaryotes. *Mol. Biol. Evol.* 21, 809–818.
- Zahnle, K., Schaefer, L., Fegley, B., 2010. Earth's earliest atmospheres. *Cold Spring Harb. Perspect. Biol.* 2.
- Zapalski, M.K., 2011. Is absence of proof a proof of absence? Comments on commensalism. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 302, 484–488.