frontiers in
MICROBIOLOGY

MINI REVIEW ARTICLE
published: 03 June 2014
doi: 10.3389/fmicb.2014.00267

Planctomycetes and macroalgae, a striking association

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Planctomycetes are part of the complex microbial biofilm community of a wide range of macroalgae. Recently, some studies began to unveil the great diversity of Planctomycetes present in this microenvironment and the interactions between the two organisms. Culture dependent and independent methods revealed the existence of a great number of species but, so far, only less than 10 species have been isolated. Planctomycetes comprise the genera *Rhodopirellula*, *Blastopirellula*, and *Planctomyces*, *Phycisphaera* and the uncultured class OM190 and some other taxa have only been found in this association. Several factors favor the colonization of macroalgal surfaces by planctomycetes. Many species possess holdfasts for attachment. The macroalgae secrete various sulfated polysaccharides that are the substrate for the abundant sulfatases produced by planctomycetes. Specificity between planctomycetes and macroalgae seem to exist which may be related to the chemical nature of the polysaccharides produced by each macroalga. Furthermore, the peptidoglycan-free cell wall of planctomycetes allows them to resist the action of several antimicrobial compounds produced by the macroalgae or other bacteria in the biofilm community that are effective against biofouling by other microorganisms. Despite the increase in our knowledge on the successful planctomycetes-macroalgae association, a great effort to fully understand this interaction is needed.

Keywords: planctomycetes, macroalgae, biofilm, association, macroalgae exudates

INTRODUCTION

Planctomycetes are a peculiar group of bacteria within the *Planctomycetes, Verrucomicrobia*, *Chlamydiae* (PVC)—superphylum. They share with archaea or eukaryotes some distinctive characteristics such as peptidoglycan-less cell walls of proteic nature (Lage, 2013), a complex system of endomembranes forming a unique cell plan (Lage et al., 2013; Santarella-Mellwig et al., 2013), the presence of compartments like the anammoxosome (Van Teeseling et al., 2013), budding reproduction in many of their members (Ward et al., 2006) and the lack of the division protein FtsZ (Pilhofer et al., 2008), endocytosis (Lonhienne et al., 2010) and the presence of membrane coat (MC)—like proteins (Santarella-Mellwig et al., 2010). Some of these features place planctomycetes in the center of the discussion of the eukaryotic cell origin (Devos and Reynaud, 2010; Reynaud and Devos, 2011; Fuerst and Sagulenko, 2013).

Metabolically, planctomycetes are mainly aerobic, mesophilic, and neutrophilic organisms. A particular group of planctomycetes, the anaerobic ammonium oxidation (anammox) species, are strict anaerobes. Their diversified metabolism allows them to colonize a wide variety of ecosystems ranging from aquatic (marine, brackish, freshwater, sediments, and marine snow) to terrestrial habitats as well as several extreme environments such as desert soils (Abed et al., 2010; Andrew et al., 2012), hypersaline environments (Baumgartner et al., 2009; Schneider et al., 2013), hot springs (Tekere et al., 2011; Bohorquez et al., 2012), acidophilic habitats (Ivanova and Dedysh, 2012; Lucheta et al., 2013), glacial waters (Liu et al., 2006; Zeng et al., 2013) and Antarctic soils and waters (Newsham et al., 2010; Piquet et al., 2010), hydrocarbon polluted environments (Abed et al., 2011)and other polluted habitats (Reed et al., 2002; Chouari et al., 2003; Caracciolo et al., 2005; Akob et al., 2007; Halter et al., 2011). Furthermore, their association with a great number of diverse eukaryotic organisms has been reported. These include sponges (Webster et al., 2001; Pimentel-Elardo et al., 2003; Zhu et al., 2008; Costa et al., 2013), ascidians (Oliveira et al., 2013), corals (Yakimov et al., 2006; Webster and Bourne, 2007; Duque-Alarcón et al., 2012), prawns (Fuerst et al., 1997), macrophytes (Hempel et al., 2008) and lichens (Grube et al., 2012). They were also found in sphagnum peat bogs (Kulichevskaia et al., 2006), the rock below the lichens (Bjelland et al., 2011) and in the rizosphere of several plants (Jensen et al., 2007; Zhao et al., 2010; Zhang et al., 2013).

Recently, various studies showed that planctomycetes are widespread in the biofilm community of several species of macroalgae and present a high diversity (Bengtsson and Ovreas, 2010; Lachnit et al., 2011; Lage and Bondoso, 2011). Besides a fundamental role in the primary production, beds of macroalgae along ocean coastlines provide the needed structure complexity, habitat and food for a huge and variable community of organisms which range from microscopic forms to larger organisms like fishes. Macroalgae are the dominant habitat-forming organisms on temperate coastlines (Campbell et al., 2014) and offer shelter for many forms of life that can thus avoid predation by higher forms in the food chain. This is particularly evident in the large brown algal kelp forests. At a

microscopic scale, macroalgal surfaces harbor a rich community composed by bacteria, fungi, diatoms, protozoa, spores and larvae of marine invertebrates (Lachnit et al., 2011) that can benefit from the availability of a range of organic carbon sources produced by algae (Armstrong et al., 2001). Bacteria are dominant among primary colonizers (Lachnit et al., 2009). The two major groups are *Bacteroidetes* and *Proteobacteria* followed by *Firmicutes*, *Actinobacteria*, *Verrucomicrobia*, and *Planctomycetes* (Goecke et al., 2013). In this review, we explore several aspects of the interaction between planctomycetes and macroalgae, a topic that recently started to be unveiled.

MACROALGAE THAT HARBOR PLANCTOMYCETES

Planctomycetes are frequent colonizers of macroalgae from the three phyla, Chlorophyta (green algae), Rhodophyta (red algae) and Heterokontophyta (brown algae). Planctomycetes colonization was observed for ulvacean algae like *Cladophora* sp. (Yoon et al., 2014), *Ulva compressa* (Hengst et al., 2010), *Ulva intestinalis* (Hengst et al., 2010; Lachnit et al., 2011; Lage and Bondoso, 2011), *Ulva australis* (Longford et al., 2007; Burke et al., 2011), *Ulva prolifera* (Liu et al., 2010), and *Ulva* sp. (Lage and Bondoso, 2011; Bondoso et al., 2013). This group was also reported to be present in the green macroalgae *Chara aspera* (Hempel et al., 2008) and *Caulerpa taxifolia* (Meusnier et al., 2001). Epiphytic planctomycetes were also found in the red algae *Porphyra umbilicalis* (Miranda et al., 2013), *Laurencia dendroidea* (De Oliveira et al., 2012), *Delisea pulchra* (Longford et al., 2007), and *Gracilaria vermiculophylla* (Lachnit et al., 2011). Isolates were retrieved from *Chondrus crispus*, *Mastocarpus stellatus*, *Gracilaria bursa-pastoris*, *Gelidium pulchellum*, *Grateloupia turuturu*, and *Porphyra dioica* (Lage and Bondoso, 2011). The presence of planctomycetes on *Chondrus crispus*, *Mastocarpus stellatus*, and *Porphyra dioica* was detected by molecular methods (Bondoso et al., 2013). A novel order of planctomycetes containing one species isolated from *Porphyra* sp. was described (Fukunaga et al., 2009). 16S rRNA clone libraries from the brown algae *Fucus vesiculosus* revealed a great diversity of planctomycetes (Lachnit et al., 2011). Planctomycetes were isolated from other brown algae like *Fucus spiralis*, *Sargassum muticum*, *Laminaria* sp. (Lage and Bondoso, 2011), and *Laminaria hyperborea* (Bengtsson and Ovreas, 2010). The presence of planctomycetes has also been confirmed in *Fucus spiralis*, *Sargassum muticum* by Bondoso et al. (2013) and in *Saccharina latissima* and *L. digitata* (Bengtsson, unpublished results). These data suggest that planctomycetes are widespread among macroalgae which can be used for the discovery of novel planctomycetes species.

PLANCTOMYCETES ASSOCIATED WITH MACROALGAE

Although the abundance of planctomycetes is usually observed to be low in marine environments (Rusch et al., 2007) and some macroalgae (Burke et al., 2011; Lachnit et al., 2011; Miranda et al., 2013), Bengtsson and Ovreas (2010) showed, by FISH, that planctomycetes are dominant on *Laminaria hyperborean* where they can account for up to 51–53% of the bacterial biofilm cells.

About 30% of all the studies on macroalgae bacterial communities report the presence of planctomycetes and almost 4% of sequences from these studies belong to the phylum *Planctomycetes* (Hollants et al., 2013). Planctomycete communities on macroalgae can be highly diverse varying from only one to 24 OTUs at a 97% cut-off in the 16S rRNA gene per macroalgae (**Table 1**). With the use of specific primers for planctomycetes, Bengtsson and Ovreas (2010) defined 16 OTUs associated with the kelp *Laminaria hyperborea*, each representing a different species and Bondoso et al. (2013), using PCR-DGGE, identified a total of 21 different OTUs associated with six macroalgae. In a pyrosequencing study, the red macroalga *Porphyra umbilicalis* was found to harbor 24 different OTUs belonging to planctomycetes (Miranda et al., 2013). In total, more than 60 potential different species of planctomycetes are associated with macroalgae and the majority were not isolated in pure culture (**Figure 1**). So far, only 10 species were isolated from macroalgae (Winkelmann and Harder, 2009; Bengtsson and Ovreas, 2010; Lage and Bondoso, 2011) on the basis of the 97% cut-off defined for species delineation (Stackebrandt, 2002) of which four were validly described (Fukunaga et al., 2009; Bondoso et al., 2014; Yoon et al., 2014). The communities of planctomycetes comprise mainly members related to the cultured genera *Blastopirellula*, *Rhodopirellula*, and *Planctomyces* (**Figure 1**) and to the class *Phycisphaerae* which contains the genera *Phycisphaera* and *Algisphaera*. The most abundant taxon reported in culture-independent studies is related to an isolate from *Fucus spiralis*, strain FC18 (Lage and Bondoso, 2011), and can be found in almost all the macroalgae studied but predominantly in the brown macroalgae *Fucus* sp. and *Laminaria hyperborea*. The uncultured class OM190 (SILVA taxonomy), a deeply branching group within the *Planctomycetes*, is also usually reported as being associated to macroalgae (**Figure 1**, **Table 1**).

The planctomycetes associated with red and brown macroalgae seem to have a higher diversity than the ones colonizing green algae (**Figure 1** and **Table 1**). This finding was reported by Lachnit et al. (2011) where only one OTU was associated with *Ulva intestinalis*, but 7 and 6 OTUs were, respectively, associated with *Delisea pulchra* and *Fucus vesiculosus*.

The communities of planctomycetes comprise taxa that were never found before in other habitats, suggesting a specific association with the macroalgae. Thirty nine out of 116 total sequences present in databases were found to be limited to macroalgal surfaces. Moreover, the study performed by Bondoso et al. (2013) also suggested that this association is host-specific and does not change with the geographical location of the macroalgae.

INTERACTIONS BETWEEN MACROALGAE AND PLANCTOMYCETES

The dynamic marine environments where macroalgae live are affected by diverse biotic and abiotic factors which contribute to, and influence the microbial community of their biofilms. Fundamental for this biofilm formation is the complex chemistry of macroalgal surfaces composed of exudates of secondary metabolites and extracellular exopolymeric substances (EPS) (Goecke et al., 2013). The chemistry varies among macroalgal species making each species a unique microenvironment, which induces a unique microbial community. Planctomycetes should be able to adapt easily to these complex environments. They are highly responsive to changes in environmental conditions through complex adaptation machinery. This was observed in

Table 1 | Abundance and phylogenetic affiliation of planctomycetes associated with macroalgae.

Macroalgae	Species/genus	Location	Used method	Planctomycetes				References
				Percentage	Number of genera[a]	Number of species[a]	Phylogenetically related to	
Chlorophyta (Green)	*Caulerpa taxifolia*	Philippines	16S rRNA gene libraries	ND	1	1	*Blastopirellula*	Meusnier et al., 2001
	Chara aspera	Lake Constance	Fluorescence in situ hybridization (FISH)	2-3	ND	ND	ND	Hempel et al., 2008
	Cladophora sp.	Sado Island, Japan	Isolation	ND	1	1	*Phycisphaera*	Yoon et al., 2014
	Ulva australis	Bare Island, Australia	16S rRNA gene libraries	2	2	2	*Blastopirellula, Planctomyces*	Longford et al., 2007
		Shark Point, Clovelly, Australia	16S rRNA gene libraries	3.4	ND	ND	ND	Burke et al., 2011
	Ulva compressa and *intestinalis*	Chañaral Bay, Chile	T-RFLP	1.3	1	1	*Rhodopirellula* and planctomycete FC18	Hengst et al., 2010
	Ulva intestinalis	Kiel fjord, Germany	16S rRNA gene libraries	ND	1	1	Planctomycete FC18	Lachnit et al., 2011
		Porto and Viana do Castelo, Portugal	Isolation	ND	1	1	*Planctomyces*	Lage and Bondoso, 2011
	Ulva profilera	Jiaozhou Bay, China	16S rRNA gene libraries	1	1	1	Planctomycete FC18	Liu et al., 2010
	Ulva sp.	Porto and Viana do Castelo, Portugal	Isolation	ND	2	5	*Rhodopirellula*	Lage and Bondoso, 2011
		Porto and Viana do Castelo, Portugal	DGGE	ND	1	2	Planctomycete FC18	Bondoso et al., 2013
Rhodophyt (Red)	*Chondrus crispus*	Porto and Viana do Castelo, Portugal	Isolation	ND	1	2	*Rhodopirellula*	Lage and Bondoso, 2011
		Porto and Viana do Castelo, Portugal	DGGE	ND	1	2	Planctomycete FC18	Bondoso et al., 2013
	Delisea pulchra	Bare Island, Australia	16S rRNA gene libraries	8	3	7	*Blastopirellula, Planctomyces,* Planctomycete FC18, OM190	Longford et al., 2007
	Gelidium pulchellum	Porto and Viana do Castelo, Portugal	Isolation	ND	1	1	*Rhodopirellula*	Lage and Bondoso, 2011
	Gracilaria bursa-pastoris	Porto and Viana do Castelo, Portugal	Isolation	ND	2	2	*Rhodopirellula*	Lage and Bondoso, 2011
	Gracilaria vermiculophylla	Kiel fjord, Germany	16S rRNA gene libraries	ND	3	6	*Blastopirellula, Rhodopirellula, Planctomyces*	Lachnit et al., 2011

(Continued)

Table 1 | Continued

Macroalgae	Species/genus	Location	Used method	Percentage	Planctomycetes		Phylogenetically related to	References
					Number of genera[a]	Number of species[a]		
	Grateloupia turuturu	Porto and Viana do Castelo, Portugal	Isolation	ND	1	1	*Rhodopirellula*	Lage and Bondoso, 2011
	Laurencia dendroidea	Búzios and Mangaratiba, Brasil	Transcriptome	ND	ND	ND	ND	De Oliveira et al., 2012
	Mastocarpus stellatus	Porto and Viana do Castelo, Portugal	Isolation	ND	1	2	*Rhodopirellula*	Lage and Bondoso, 2011
			DGGE	ND	2	3	*Rhodopirellula,* OM190	Bondoso et al., 2013
	Porphyra dioica	Porto and Viana do Castelo, Portugal	Isolation	ND	2	2	*Rhodopirellula,Planctomyces*	Lage and Bondoso, 2011
		Porto and Viana do Castelo, Portugal	DGGE	ND	2	2	*Rhodopirellula* and planctomycete FC18	Bondoso et al., 2013
	Porphyra umbilicalis	Schoodic Point, USA	Pyrosequencing	0.03–4.06	ND	24	*Planctomyces, Phycisphaera, Rhodopirellula*	Miranda et al., 2013
	Porphyra sp.	Mikura Island, Japan	Isolation	ND	1	1	*Phycisphaera*	Fukunaga et al., 2009
Heterokontophyt (Brown)	*Fucus spiralis*	Porto and Viana do Castelo, Portugal	Isolation	ND	2	6	*Rhodopirellula, FC18*	Lage and Bondoso, 2011
		Porto and Viana do Castelo, Portugal	DGGE	ND	1	1	Planctomycete FC18	Bondoso et al., 2013
	Fucus vesiculosus	Bare Island, Australia	16S rRNA gene libraries	ND	3	6	*Blastopirellula, Planctomyces,* Planctomycete FC18	Lachnit et al., 2011
	Laminaria hyperborea	Bergen, Norway	FISH and 16S rRNA gene libraries	23.7–52.5	4	16	*Blastopirellula, Planctomyces,* Planctomycete FC18, *Rhodopirellula,* OM190	Bengtsson and Ovreas, 2010
		Bergen, Norway	DGGE	46.3	5	8	*Blastopirellula, Planctomyces,* Planctomycete FC18, *Rhodopirellula,* OM190	Bengtsson et al., 2010
		Bergen, Norway	454-pyrosequencing	55.7	ND	ND	*Rhodopirellula,* Planctomycete FC18,	Bengtsson et al., 2012
	Laminaria sp.	Porto and Viana do Castelo, Portugal	Isolation	ND	1	1	*Rhodopirellula*	Lage and Bondoso, 2011
	Sargassum muticum	Porto and Viana do Castelo, Portugal	Isolation	ND	1	2	*Rhodopirellula*	Lage and Bondoso, 2011
		Porto and Viana do Castelo, Portugal	DGGE	ND	3	7	*Planctomyces,* Planctomycete FC18, *Rhodopirellula*	Bondoso et al., 2013

[a] *The sequences reported in the studies above were grouped using cd-hit-est (Huang et al., 2010) based on 97% (species) or 95% (genus) cut-off similarity in the 16S rRNA gene.*

ND, not determined.

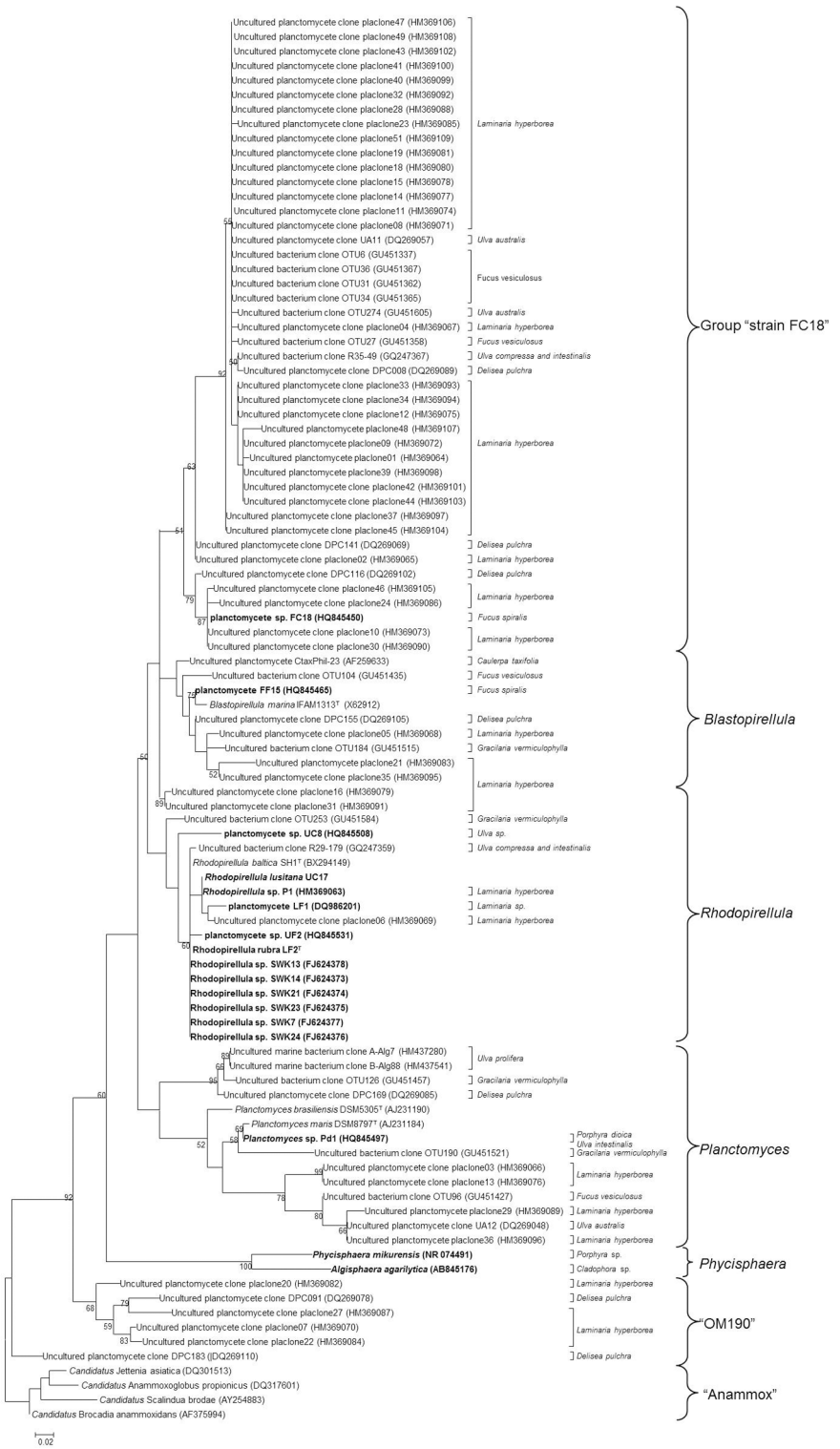

FIGURE 1 | Maximum-Likelihood tree of 16S rRNA gene sequences of planctomycetes associated with macroalgae downloaded from NCBI database. The final set consisted of 116 sequences above 500 bp. Strains in bold represent the isolates from macroalgae described to date. The numbers beside nodes are the percentages for bootstrap analyses; only values above 50% are shown. Scale bar = 0.02 substitutions per 100 nucleotides. The different groups are presented on the right. Anammox 16S rRNA gene sequences were used as outgroup.

Rhodopirellula baltica under stress response to temperature and salinity (Wecker et al., 2009).

Macroalgae produce or release many molecules that can be rich sources of substrates for planctomycetes nutrition. Algal macromolecules include sulfated polysaccharides like carrageenan and agar from red algae, alginate, fucan and laminarinan from brown algae and cellulose and ulvan from green algae. Planctomycetes are well tailored for the utilization of sulfated polysaccharides as revealed by the analysis of the marine *R. baltica* SH1^T genome where the presence of 110 sulphatases was detected (Glockner et al., 2003). Furthermore, Wegner et al. (2013) also found an exceptionally high number of sulphatase genes in the recently sequenced genomes of nine *Rhodopirellula* strains. These authors also verified in *R. baltica* SH1^T sulphatase expression profiles in cells grown on different sulfated polysaccharides. Polysaccharide utilization was also confirmed by the work of Jeske et al. (2013) where *R. baltica* was checked for potential utilization of several polymers. It was able to utilize laminarin, mannitol, pectin, chondroitin sulfate, N-acetylgalactosamine, and D-glucuronic acid. Cellobiose, a product of cellulose degradation, could also be used as carbon source. Weak or moderate degradation was obtained for mannan and its monomer D-mannose, the disaccharide sucrose and D-xylose. The novel species *R. rubra* and *R. lusitana*, both isolated from macroalgae, were shown to utilize the majority of the monomers that constitute the main polysaccharides secreted by macroalgae such as fucose, galactose, xylose, rhamnose, and manitol (Bondoso et al., 2014). Agarolytic activity was also described in a novel representative of the class Phycisphaera, *Algisphaera agarilytica*, isolated from the marine alga *Cladophora* sp. (Yoon et al., 2014). As frequent inhabitants of phytodetrial macroaggregates in marine environments, planctomycetes mineralize organic matter, intervening in important transformations in the global carbon cycle in the sea (DeLong et al., 1993). Very recently, Erbilgin et al. (2014) provided evidence by a metabolic activity screen that Bacterial Microcompartments (BMCs) present in planctomycetes are involved in the degradation of a number of plant and algal cell wall sugars, namely L-fucose and L-rhamnose. This work further supports the great relevance of algal exudates on planctomycetes physiology especially for those associated with macroalgae.

The different substrates produced by each macroalga may explain the specificity of planctomycetes to the algal host. It was found that the same algal species from two localities demonstrated high similarities in the composition of associated planctomycetes (Bondoso et al., 2013). A core of evidence seems to point to the algal host as the main factor controlling the composition and structure of epiphytic bacterial communities (Wahl, 2008; Lachnit et al., 2009, 2011; Hengst et al., 2010). Comparable results were reported for the epibiotic bacterial communities living on corals which seemed to be determined by the nature and composition of host exudates due to strong seasonal effects (Guppy and Bythell, 2006).

Planctomycetes colonize macroalgal surfaces; an attached life style has been well recognized for these bacteria and when in pelagic environments they are mainly associated with particles like marine snow (DeLong et al., 1993). The presence of a holdfast of glycoproteic nature (Lage, 2013; Lage et al., 2013) favors attachment and, thus, the colonization of surfaces (Gade et al., 2005; Lage, 2013; Lage et al., 2013).

Another factor that favors the colonization of macroalgal biofilms by planctomycetes is their ability to resist several antibiotics. These can be produced by the macroalgae or by other competing bacteria in the biofilm. One of the methods to achieve planctomycetes isolation in culture is precisely based on this resistance to antibiotics (Schlesner, 1994; Winkelmann and Harder, 2009; Lage and Bondoso, 2011). Resistance to β-lactam antibiotics that affect peptidoglycan biosynthesis is due to the absence of this molecule in their cell wall.

In a study of the behavior of planctomycetes toward antibiotics, Cayrou et al. (2010) showed that five reference strains of planctomycetes were resistant to β-lactams, to the quinolone nalidixic acid and to the glycopeptide vancomycin. The organisms were, however sensitive to tetracycline and doxycycline. Most were also resistant to chloramphenicol and the aminoglycoside gentamicin as well as rifampicin. A variable resistance to the association sulfomethoxazole/trimethoprim was obtained.

The potential benefits of the planctomycetes to the macroalgae can only be hypothesized. Being heterotrophs, planctomycetes can mineralize organic molecules producing inorganic compounds that meet the nutritional needs of macroalgae. These may also profit from the production of growth factors or antimicrobial molecules by the planctomycetes. It has been shown that morphogenetic factors like thallusin, isolated from an epiphytic marine bacterium, are indispensable to the foliaceous morphology of macroalgae (Matsuo et al., 2005). Unknown factors may be due to planctomycetes. The production of bioactive molecules by planctomycetes was initially searched by genome mining in *R. baltica* (Donadio et al., 2007) and subsequently in 13 genomes (Jeske et al., 2013). Two small nonribosomal peptide synthetases (NRPSs), two monomeric polyketide synthases (PKSs), and a bimodular hybrid NRPS–PKS were found in the genome of *R. baltica* which are probably involved in the synthesis of five different, unknown bioactive products (Donadio et al., 2007). In the 13 genomes analyzed, 102 genes or gene clusters putatively related with the production of secondary metabolites like bacteriocin encoding genes, putative lantibiotic-encoding gene, ectoine synthesis gene cluster, putative phenazine encoding gene cluster were found (Jeske et al., 2013). The potential production of these bioactive molecules may help the macroalgae to control their colonization by undesired bacteria or fungi. Furthermore, we can hypothesize that bioactive molecules should be important for planctomycetes in the process of macroalgal colonization and posterior defense against competitors.

Bacteria can also impact negatively on macroalgae. Members of Bacteroidetes and Gammaproteobacteria can induce several diseases like "shot hole disease" or "hole-rotten disease" (Goecke et al., 2013). Up to now, pathogenicity from planctomycetes on macroalgae was never reported.

CONCLUSIONS

As shown in this review, macroalgae are promising environments for in-depth study of planctomycetes. Macroalgae possess a relatively high number and a diverse community of planctomycetes in their biofilm. Thus, they represent great potential for

the discovery of new taxa that can be isolated from these habitats and their characterization could provide new knowledge on the morphology, physiology and ecology of planctomycetes and on this interaction. New research on the structure, succession and dynamics of the community in this relationship, namely the relation with the macroalgal life cycle, the temporality of planctomycetes diversity and composition and their association with other macroalgae will give new highlights in the ecology of this interaction. Metabolomic approaches will allow obtaining insights into the mechanisms of the nutritional relationship and the role of planctomycetes in biofilm formation and maintenance. The increasing scientific interest in the biology of planctomycetes and biofilms will, most certainly, generate new exciting knowledge that will allow a better comprehension of this association.

ACKNOWLEDGMENTS

This research was supported by the European Regional Development Fund (ERDF) through the COMPETE - Operational Competitiveness Programme and national funds through FCT – Foundation for Science and Technology, under the project PEst-C/MAR/LA0015/2013. The second author was financed by FCT (PhD grant SFRH/BD/35933/2007).

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Conflict of Interest Statement: The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

Received: 28 March 2014; accepted: 15 May 2014; published online: 03 June 2014.
Citation: Lage OM and Bondoso J (2014) Planctomycetes and macroalgae, a striking association. Front. Microbiol. ***5****:267. doi: 10.3389/fmicb.2014.00267*
This article was submitted to Terrestrial Microbiology, a section of the journal Frontiers in Microbiology.