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Abstract: Coastal photosynthetic microbial mats are highly structured microbial communities that populate a variety of shallow environments such as estuaries, sheltered sandy beaches, intertidal flats, salt marshes or hypersaline salterns. In soft sediments, most of these microbial mats are formed of vertically stratified, multicolored and cohesive thin layers, of several functional groups of microorganisms, such as cyanobacteria, colorless sulfur bacteria, purple sulfur bacteria, or sulfate-reducing bacteria, distributed along vertical microgradients of oxygen, sulfide and light. These microbial communities are highly productive, significant contributors to carbon, nitrogen and sulfur cycles and to sediment stability in some shallow-water habitats. Many examples of these communities have been cited in the past, but comparatively few microbial mats have been presented where mass developments of anoxygenic purple bacteria have been observed. Yet, application of molecular approaches has provided fresh insight into the ecology, diversity and evolution of microbial mats. *In situ* measurements using electrochemical and optical microprobes allowed a detailed characterization of the physical and chemical environment whereas reflectance measurements revealed the spatial or temporal heterogeneity of microbial mat surfaces. We hereby report the main discoveries made through the introduction of these powerful techniques and point out the potential insight that might be gained into the study of anoxygenic purple bacterial mats.

Key words: microbial mats, anoxygenic phototrophs, sulfur purple bacteria, diversity, sediment stability, photosynthesis, spectral reflectance

1. Introduction

Microorganisms have the ability to colonize different types of habitats and interact with each other, forming more or less complex communities. Microbial mats that develop in different geographical locations are a remarkable example of these associations. They are found for instance in coral reefs, hypersaline ponds and lakes, salterns, thermal springs, Antarctic lakes, and coastal sediments (Stal and Caumette, 1994). In the latter, they develop at the sediment-water interface in shallow environments such as estuaries, intertidal areas, sandy beaches or hypersaline salt marshes (Herbert, 1985, Stal and Caumette, 1994, Van Gemerden et al., 1989a, Van Gemerden et al., 1989b). Coastal microbial mats are principally inhabited by bacteria (heterotrophic, autotrophic and chemotrophic) as well as eukaryotic microalgae such as benthic diatoms. These consortia are often referred to as microbial mats, laminated microbial communities, microphytobenthos or simply biofilms, in the literature (or any combination) but describe ultimately the association of different microbial cells, embedded in an extracellular polymeric substance (EPS) matrix. These mats can exhibit different morphologies based on the physicochemical environments they experience. Most of the time, the cells are organized according to their physiologies in vertical laminated structure consisting of successive layers.

In the coastal zone, microbial mats are mostly photosynthetic and are composed of several functionally complementary groups of microorganisms whose composition can vary greatly depending on the energy and nutrient source from the top and bottom. Cyanobacteria are often the pioneer organisms and generally dominate the top layer. According to the chemical and light gradients available they can for instance be followed by aerobic or facultative heterotrophic bacteria, chemolithotrophic bacteria (among them colorless sulfur bacteria), anoxygenic phototrophs (purple and green) and sulfate-reducing bacteria, forming several laminated layers distributed within the EPS matrix principally produced by cyanobacteria. Purple bacteria perform anaerobic anoxygenic (without release of oxygen) photosynthesis as, unlike cyanobacteria, they are unable to perform water photolysis due to the lack of the photosystem II. They mostly use, as electron donors, the intermediate products of organic matter degradation from primary producers and some compounds originated from fermentation and anaerobic respiration. In microbial mats, a large diversity in purple bacteria

is generally observed and the genus *Thiocapsa* is often highly represented (Van Gemerden et al., 1989b).

In the last decade, community structure as well as physical-chemical environment of the microbial mats have been reviewed at several occasions (Franks and Stolz, 2009, Paerl and Pinckney, 1996, S tal and Caumette, 1994, Van Gemerden, 1993). The introduction of molecular approaches has indeed provided new insight into the ecology of these mats by allowing the characterization of the community structure (Ranchou-Peyruse et al., 2006, Wieland et al., 2003). Thanks to the development of high resolution microelectrodes, the physical and chemical environment of these mats was characterized at very small spatial scales (µm to mm, Revsbech and Jørgensen, 1983, Visscher et al., 1991). Pigment diversity and *in situ* reflectance measurements revealed the spatial or temporal heterogeneity of microbial mat surfaces (e.g. Brotas and Plante-Cuny, 2003, P aterson et al., 1998). Finally, their role in sediment biostabilisation was revealed (Paterson, 1997). This paper reports the main discoveries made through the introduction of these powerful techniques and points out the gap in current knowledge regarding anoxygenic phototrophic biofilms.

2. Microbial communities in coastal purple phototrophic mats

2.1. Structure of coastal purple phototrophic mats

Photosynthetic microbial mats develop in many different habitats with salinities ranging from freshwater to hypersaline conditions (Overmann and Garcia-Pichel, 2006, Van Gemerden, 1993). Some prominent marine and hypersaline habitats where laminated microbial communities frequently develop in visible masses are represented by coastal sediments of the Great Sippewissett salt marsh (USA) (Nicholson et al., 1987, Rothermich et al., 2000), coastal lagoons in the southern France (Caumette, 1986, Guyoneaud et al., 1996), marine salterns in France (Caumette et al., 1994, G iani et al., 1989) and in Guerrero Negro (Baja California, Mexico, (Canfield and Des Marais, 1993, Ley et al., 2006), sandy flats of the Ebro Delta (Mir et al., 1991, Navarrete et al., 2000), and sheltered beaches on the Orkney islands (Van Gemerden et al., 1989a, Van Gemerden et al., 1989b, W ieland et al., 2003). In such ecosystems, the surface sediment layer covers a transition zone between oxic and anoxic conditions characterized by steep gradients of oxygen and sulfide. These gradients favor the maturation of vertically stratified, multicolored and cohesive layers of several functional

groups of microorganisms. Although the uppermost layer, brown and green in color, may contain benthic diatoms, the dense top material is typically formed by unicellular and filamentous cells of cyanobacteria that are generally the driving force as they provide growth substrates for other organisms. For instance, newly colonized sands mostly comprised *Oscillatoria* sp. and *Spirulina* sp. (Franks and Stolz, 2009). The gliding cyanobacterium *Microcoleus chthonoplastes* often replaces these pioneer species and becomes dominant in mature intertidal mats (Stal et al., 1985, Van Gemerden, 1993). Below the cyanobacteria, a distinct layer of purple sulfur bacteria is often present, sometimes overlying a layer of green sulfur bacteria. Sometimes, a white layer or patches due to sulfide-oxidizing bacteria (including *Beggiatoa* spp.) are visible at the surface of marine sediments that have a sufficiently high production of sulfide from bacterial sulfate reduction (Jorgensen, 1977). They are followed vertically by sulfate-reducing bacteria whose activity leads to the precipitation of iron sulfides visible as black mud. Aerobic heterotrophic organisms are also functionally important as their activity leads to oxygen depletion, and fermentative organisms provide growth substrates for sulfate-reducers. Other, numerically less important groups are nitrifying and denitrifying bacteria and methanogens. Numerous examples have been described in the literature of colored blooms and mass accumulations of phototrophic bacteria in the coastal zones and lagoons (Caumette and Baleux, 1980, Imhoff, 2001, and references herein). Mass developments of purple sulfur bacteria have been observed during warm summer months in the intertidal zone of sandy beaches (Herbert, 1985, Van Gemerden et al., 1989a, Van Gemerden et al., 1989b). Three different laminated microbial mats were described, distinguished by the position of the cyanobacterial layer above or beneath the purple sulfur bacterial layer, or its complete absence and therefore exclusive development of purple sulfur bacteria in the top layer. On the Orkney islands (Herbert, 1985, Van Gemerden et al., 1989a, Van Gemerden et al., 1989b) and in Roscoff Aber Bay (Fig. 1; Hubas, C., Jesus B. M., Jeanthon, C., unpublished data), the latter pattern occurs seasonally when beaches are supplied with a high load of organic matter due to decomposition of macroalgae. These purple sulfur bacteria are therefore almost permanently exposed to oxygen at the sediment surface (e.g. Herbert and Welsh, 1994). Among the purple bacteria, the purple nonsulfur bacteria are also widely distributed in aquatic environments rich in organic matter (Guyoneaud et al., 1996, Hiraishi and Ueda, 1995).

2.2. Cultural and molecular diversity of purple sulfur phototrophic mats

Most ecological studies on the distribution of anoxygenic phototrophs in natural environments have been based on biochemical features such as photopigment composition (see section 3.1) and / or on estimations of bacterial numbers, isolation and characterization of pure cultures (Guyoneaud et al., 1996, Nicholson et al., 1987, Ranchou-Peyruse et al., 2006, Van Gemerden et al., 1989a). The most prominent purple sulfur bacteria, frequently observed and also isolated from marine coastal sediments, have been reviewed by van Gemerden and Mas (1995) and by Imhoff (2001). They were assigned to *Thiocapsa roseopersicina*, *Thiocystis violacea* and *Allochromatium vinosum*. As an example, various organisms have been cultivated from microbial mat communities of the Ebro Delta, one site among the most intensively studied. Vacuolated bacteria, such as *Thiocapsa rosea* and *Lamprobacter modestohalophilus* as well as non vacuolated bacteria such as *Marichromatium gracile*, *T. roseopersicina* or *Ectothiorhodospira* sp. have been isolated (Martinez-Alonso et al., 2005, Villanueva et al., 2010). *T. roseopersicina* , which is easily cultivated, is very common in marine coastal habitats and predominant in most systems where it can reach abundances of 10^6 to 10^7 cells.cm^{-3} (Van Gemerden et al., 1989a).. The adaptation to a wide range of salinities and the high metabolic versatility and flexibility of this organism (tolerance to oxygen and possible aerobic growth in the dark) are important competitive advantages that explain the success of its distribution (de Wit and van Gemerden, 1987 , de Wit and van Gemerden, 1990). *Allochromatium* spp and *Marichromatium* spp are also often observed and may be locally dominant (Imhoff, 2001). From red layers found in mats of hypersaline environments, other members of the family Chromatiaceae such as *Halochromatium salexigens, H. glycolicum* and *Halothiocapsa halophila* have also been isolated (Caumette et al., 1988, 1991, Caumette et al., 1997).

In the last decades, the species composition of microbial mats has mostly been described by dissecting cores into thin horizontal layers and extracting nucleic acids or other cell components for chemical and molecular analysis (Martinez-Alonso et al., 2005, Mouné et al., 2003, Navarrete et al., 2000, Ranchou-Peyruse et al., 2006, Villanueva et al., 2010). With these techniques, a high degree of bacterial diversity was generally found. As an example, the microbial mats within hypersaline lagoons at Guerrero Negro generated more than 1500 16S rRNA sequences representing over 750 species (Ley et al., 2006). Denaturing gradient gel electrophoresis separation of 16S rRNA gene amplification products obtained using specific primer combination for *Chromatiaceae*, the main family of purple sulfur bacteria, showed that

the diversity of members of this family in microbial mats in the Ebro Delta was high and pointed out the presence of novel species not related to any known purple sulfur bacteria (Martinez-Alonso et al., 2005).

The *pufM* gene encodes for the medium (M) subunit of the photosynthetic reaction center of the anoxygenic photosynthetic bacteria of the *Alpha-*, *Beta-*, and *Gammaproteobacteria* and of the *Chloroflexaceae*. Molecular analyses using this functional gene have also been applied in order to specifically study the depth distribution of anoxygenic phototrophs in mat communities (Fourçans et al., 2004, Wieland et al., 2003). Using this method, vertical diel migration of an anoxygenic phototrophic community in responses to oxygen concentrations and pH was detected at a microscale depth level (Fourçans et al., 2006). Only few studies detailed the diversity of anaerobic purple bacteria by the analysis of *pufM* environmental libraries since the pioneering work of Achenbach et al. (2001) and Karr et al. (2003) on Antarctic lake waters and mats. An environmental clone library of the *pufM* gene was obtained from a thin cyanobacterial mat developed at the top of black sediment samples from the Berre lagoon (France) (Ranchou-Peyruse et al., 2006). Surprisingly, most of clones were closely related to aerobic anoxygenic phototrophic bacteria related to the *Roseobacter* clade whereas only two *Roseobacter* strains were isolated. The culture-dependent approach performed in parallel revealed the dominance of anaerobic purple sufur bacteria in these samples. The coexistence of both aerobic and anaerobic anoxygenic phototrophic bacteria has also been demonstrated in sediments from Antarctic and saline lakes (Karr et al., 2003, Thiel et al., 2010).

3. Pigment diversity and reflectance measurements

3.1. Pigment diversity of microbial mats

The microenvironment within a mat is characterized by physical-chemical gradients (e.g. light, pH, nutrients), leading to high variability in the distribution of phototrophic microorganisms, both vertically within the top mm of the sediment (taxonomic stratification) and horizontally (high patchiness). Frequently, there is also significant temporal variability on biofilms that colonize intertidal areas as a result of the large physicochemical variations caused by the tide. The high variability exhibited by biofilms in such small scales cause significant sampling problems, e.g. to fully capture biofilm variability, many samples have to

be taken, often more than it is logistically possible. Also, until recently, most of the available techniques for assessing microorganisms abundance or pigment diversity in biofilms were destructive (e.g. pigment extraction with organic solvents and quantification by HPLC). The destruction of the biofilm removes the existing physical-chemical gradients, changing significantly the environmental conditions of the biofilm under investigation. Thus, there is growing interest in developing remote sensing techniques that allow the non-destructive and non-invasive study of phototrophic microbial biofilms. Such techniques include: spectral reflectance, O_2 micro-electrodes, optodes, Pulse-Amplitude-Modulation (PAM) fluorometry, Fast Repetition Rate Fluorometry (FRRF) fluorometry and Infra Red CO_2 Gas Analyzer (IRGA) benthic chambers (e.g. Kühl, 2005, Kuhl and Polerecky, 2008, Migné et al., 2002, Stephens et al., 2003, Thar et al., 2001, Vopel and Hawes, 2006, Wiggli et al., 1999). All these techniques allow the repetition of measurements in the same biofilm area and some can be used to infer about biofilm biomass or taxonomic composition. In this section we focused on the use of spectral reflectance in the study of photosynthetic microbial mats.

Microbial biofilm taxonomic diversity is reflected in the presence of different pigments. Some of these pigments can be used as "signatures" of the presence of specific groups in the biofilm, e.g. diatom dominated biofilms will show the abundant presence of fucoxanthin and chlorophyll *c*; cyanobacteria dominated biofilms will show a variety of cyanobacterial specific pigments (e.g. mixoxanthophyll, equinenone, etc.); and an anoxygenic bacterial biofilm will mainly show bacteriochlorophylls and carotenoids (Table 1). If for diatom and cyanobacterial biofilms numerous studies exist showing their pigment composition (e.g. Andréfouët et al., 2003, Brotas and Plante-Cuny, 2003, Stephens et al., 2003), only few papers focus on anoxygenic bacterial biofilms (e.g. Masse et al., 2002). Spectral reflectance can be used to identify and quantify the presence of different pigments in the biofilms, but it is first necessary to determine the spectral signatures of these pigments. It is thus useful to have good "ground truth" studies, i.e. spectral measurements taken together with measurements of the pigments present in the biofilm. Currently there are few studies that have attempted to establish the pigment spectral signatures of anoxygenic phototrophic biofilms. Although they are not consensual about which wavelengths should be used to detect bacteriochlorophyll, there are 3 main absorbance peaks attributed to bacteriochlorophyll *a*: around 800 nm, around 850 nm and around 870 nm. The exact wavelengths depend on the type of bacteria present (Table 1).

3.2. Spectral reflectance of microbial phototrophic mats

Spectral reflectance measurements have been used often in the estimation of biofilm microalgal biomass, using chlorophyll *a* as a biomass proxy (e.g. Carrère et al., 2004). Chlorophyll *a* strongly absorbs red light and reflects most of the infrared light. Using this information, a wide variety of chlorophyll *a* based reflectance studies were developed, e.g. Normalized Difference Vegetation Index (NDVI), modified soil-adjusted vegetation index (MSAVI). To our knowledge no similar index exists to estimate anoxygenic phototrophic biofilms; although bacteriochlorophyll *a* is frequently used to infer about the presence of anoxygenic phototrophic bacteria (e.g. Gitelson et al., 1999, Kühl and Jørgensen, 1992, Stal et al., 1984, Steenbergen and Korthals, 1982), it is not common to use the pigment content to quantify anoxygenic phototrophic bacterial biomass. Bacteriochlorophyll *a* dominated biofilms typically show absorption features in the infrared region, whereas chlorophyll *a* dominated biofilms do not (e.g. Stal et al., 1984). In the Roscoff Aber Bay where anoxygenic photosynthetic biofilms seasonally developed at the sediment surface, reflectance spectra recorded from different sediment areas allowed the determination of bacteriochlorophyll absorption features in the infrared region, with absorption maxima at 792 and 850 nm (Fig. 2). A spectral reflectance index is currently being developed by the authors to estimate bacteriochlorophyll content of this biofilm using bacteriochlorophyll absorption features.

Spectral reflectance has also been widely used with benthic phototrophic biofilms to follow diatom vertical migration within the sediment matrix (e.g. Serôdio et al., 2009), to follow photo-regulatory vertical movements (e.g. Perkins et al., 2010), to follow photo-physiological mechanisms (Jesus et al., 2008), and to a lesser extent to identify the presence of different taxonomic groups, e.g. microalgae, cyanobacteria, green and purple bacteria (e.g. Bachar et al., 2008, Prášil et al., 2009, Wiggli et al., 1999). Presently, most of the research done with spectral reflectance on anoxygenic biofilms seems to have been focused on the identification of the presence of different taxonomic groups in the biofilm. With the introduction of hyper-spectral (HS) imaging technology it became possible to map sediment biofilms with high spectral and spatial resolution (e.g. Bachar et al., 2008). HS imaging is a very sensitive and minimally invasive tool that can be used in the investigation of biofilm spatial organization role in mat ecosystem functions, providing the possibility of imaging microbial identity and activity at high spatio-temporal resolution. Presently, the majority of the work involving HS imaging seems to address mainly questions relating spatial distribution of the different taxonomic groups that colonize the sediment, vertically and horizontally (Kuhl and Polerecky,

2008, Polerecky et al., 2009). However, some research has started to emerge using combinations of imaging techniques to infer about the relationships between the different microalgal groups and their environment. For instance, Bachar et al. (2008) used hyperspectral imaging of reflectance spectra (4^{th} derivative of spectral images with 460-913 nm spectral resolution at 30 × 30 μm spatial resolution) and of emission spectra to map the distribution of different pigments (chlorophyll *a*, phycocyanin, bacteriochlorophyll *a* and bacteriochlorophyll *c*). Both spectral methods were sensitive enough to detect biofilm stratification within the sediment, showing the spectral signatures of chlorophyll *a* and zeaxanthin closer to the sediment surface, a mid layer 3-4 mm of bacteriochlorophyll *c* and bacteriochlorophyll *a* at deeper layers (5.5-7 mm). Using HS imagery these authors rejected their original hypothesis that *Chloroflexaceae* would be closely associated with the distribution of oxygenic phototrophs and proposed an alternative hypothesis that *Chloroflexaceae* is maximal in locations where both photosynthate excretion and sulfate reduction occur during a light / dark cycle.

In conclusion, although considerable research on microalgae phototrophic biofilms using spectral reflectance tools already exists, there is a gap in current knowledge regarding the use of these techniques for quantification and study of anoxygenic phototrophs.

4. Role of microbial mats in the functioning of coastal ecosystems

4.1. Role of microbial mats in sediment stability

Although the cohesive strength of one sediment may depend on its physicochemical properties, such as water content, density, mineralogy, plasticity, salinity and pH (Dade et al., 1992), its stability may correlate better with biological parameter than with nonbiological ones (Paterson et al., 2000). Microbial exopolymeric secretions are increasingly recognized as a major stabilising factor (Stal, 2010). Extracellular Polymeric Substances (EPS) are a ubiquitous component of marine ecosystems primarily composed of carbohydrates, proteins and lesser amounts of other components. They have multiple roles in aquatic systems: attachment to substrata, flotation and locomotion, feeding, protection against desiccation / UV / pollution, development of biofilms, communication (Decho, 1990). These molecules, mostly produced by diatoms and bacteria, compose a highly hydrated matrix more or less associated with cells. Tightly-wound capsules are secreted during exponential growth phase and

allegedly serve protective effects to the cell, whereas loose slimes allow microorganisms to attach each other and to sediment (Decho, 1990). The high amounts of EPS present in the sediment glue the grains together, thus enhancing the resistance of sediment to erosion and making it more stable (Paterson et al., 2000, Stal, 2010). If the resistance to erosion generally correlates well with carbohydrate and protein concentrations, variations in EPS quality influence as well sediment stability (Sutherland et al., 1998, van Duyl et al., 2000). Moreover, cyanobacterial filaments trap sediment particles and reinforce cohesion (Stal, 2010). Figure 3 summarised the potential influence of microbial mats on sediment stability. Given the importance of sediment stability in coastal ecosystems (which are typically constrained by strong physical and geochemical gradients), microorganisms are increasingly recognized as ecosystem engineers.

In the future, more studies are required in order to understand how EPS composition and diversity modify sediment properties. Particularly, little is known about stabilisation in mats of anoxygenic phototrophic bacteria. Yet abundance of purple sulphur bacteria may correlate with erosion threshold of sediment, and these bacteria appear to produce far more EPS than diatoms (Grant and Gust, 1987). Thus the erosion of sediment is lower when purple phototrophic mats are present (Van Gemerden et al., 1989a). Recent measurements of sediment adhesion in Roscoff Aber Bay showed that sediment cohesion was enhanced and that sediment was stabilised by purple phototrophic bacteria, particularly under high bacterial abundance (Fig 4). Further investigations are now required to link stabilisation with the quantity or quality of the EPS produced by purple sulphur bacteria.

4.2. Production and respiration of microbial mats organic matter and its fate into the coastal food web

Microbial mats are very productive ecosystems (e.g. about 200 $gC.m^{-2}.y^{-1}$ in the Ebro Delta, Urmeneta et al., 1998). The Winkler titration method (Winkler, 1888), the incorporation of ^{14}C labeled bicarbonate, the fast-responding CO_2 microelectrodes (de Beer et al., 1997) or the measurements of total DIC fluxes (e.g. Wieland et al., 2005) have been used extensively to measure primary production, but most of the estimates in benthic photosynthetic mats were performed to date with oxygen microelectrodes (Oren, 2009), by measuring rates of oxygen depletion at different depths during light–dark shifts (Revsbech and Jørgensen, 1983). This method allows accurate estimation of gross primary production rates across the mat-water

interface from the profiles providing that irradiance, temperature as well as porosity of the substrates are known (Wieland and Kühl, 2000). Oxygen measurements can provide information about both gross primary production and respiration of the microbial mats at millimetre scale. They revealed that microorganisms thrive in such a closeness that they mutually influence each other (Van Gemerden, 1993). Biological processes usually metabolically incompatible are found to occur simultaneously within the mats, which imply a tight coupling between them. The different members of the community are thus mutually dependent so that the entire ecosystem is often considered as self-sustaining (Des Marais, 2003). The development of electrochemical and optical microprobes has attracted many microbiologists during the past decades probably because their resolution is particularly suitable for the study of microbial environments. But, ironically, whilst we have to date a good understanding of the chemical and physical conditions that microorganisms experience at millimeter scales in microbial mats, we still do not know precisely which role microbes play in biogeochemical cycles at larger scales.

In addition, microbial mats can represent a significant source of fixed carbon and nitrogen to the surroundings and they may serve as an important food source to higher trophic levels (Joye and Lee, 2004). Recently, it has been shown that anoxygenic microbial mats may support the diet of inhabiting mud snails (Riera, 2010). In addition, microbial mats of the intertidal area which are dominated by diatoms generally serve as a food source for many invertebrates of the macrofauna and meiofauna (e.g.Hagerthey et al., 2002, Riera and Hubas, 2003), including many commercial species such as penaeid shrimp postlarvae (Al-Maslamani et al., 2009) or the oyster *Crassostrea gigas* (Riera and Richard, 1996). But despite the marked role they play into the coastal food web, the fate of microbial mats organic matter has seldom been addressed. Bacterial production has been proved to be a significant food source to benthic grazers and a sink of organic carbon in the food web of intertidal sediments (van Oevelen et al., 2006) but further studies are still needed particularly concerning anoxygenic microbial mats.

Indeed, mass bloom of anoxygenic phototrophic bacteria can develop at the sediment surface if the organic matter input is strong enough (Herbert and Welsh, 1994) forming purple microbial mats which are characterised by the absence of oxygenic photosynthesis. The accumulation of organic matter at the sediment surface stimulates respiration and, below 2 to 3 mm depth, sediment becomes totally anoxic and characterised by very high sulfate-reducing rates (Bolam et al., 2000, Nedergaad et al., 2002), allowing the exclusive growth of anoxygenic purple bacteria. Primary production and respiration rates measurements are still

scarce on these types of mats. Recently, the high contribution of *Chloroflexus*-like anoxygenic phototrophs (green non-sulphur bacteria) to the gross primary production and community respiration of a microbial mat was found to be strongly dependent upon the light availability in the near infrared region (Polerecky et al., 2007). This highlights the fact that understanding the contribution of anoxygenic phototrophs to total primary production and respiration is more complex than previously thought and that more studies on anoxygenic microbial mats are required.

Microbial mats are a remarkable example of the various forms of respiration that co-exist in aquatic habitats. Anaerobic respiration as well as aerobic respiration and re-oxydation processes have been relatively well studied in these systems. From the surface to the depth, the redox potential decreases, which influence the distribution of the different respiration pathways. Along the sediment depth, the chemical reactions involve different terminal electron acceptors and display apparent free energy yields which decrease with increasing depth (Hoehler, 2004). Carbon fluxes across the mat-water interface are generally deduced from oxygen measurements by applying known respiratory quotients (RQ). However, most of the RQ apply to conventional aerobic respiration and have no useful meaning in case total respiration mainly occurs via anaerobic pathways (Williams and Del Giorgio, 2005). Total DIC fluxes in benthic chamber enclosures or chambers equipped with a CO_2 infra-red gas analysers (Migné et al., 2002) are an efficient way to measure C fluxes across the mat-water or mat-air interface. They have been used extensively on emersed diatom biofilms to estimate their annual carbon budgets (Hubas and Davoult, 2006, Migné et al., 2004, Spilmont et al., 2006) but rarely on other microbial mats to our knowledge.

5. Conclusions and future directions

The current knowledge of ecology, ecophysiology and role of anoxygenic purple microbial mats is far less documented than those dominated by cyanobacteria and / or diatoms. Molecular approaches have provided fresh insight into the diversity of microbial mats but the role of microbial species diversity in sustaining ecosystem processes like primary production has seldom been addressed (but see Forster et al., 2006). As revealed by spectral reflectance measurements, the distribution of phototrophic microorganisms in coastal ecosystems is highly variable. Remote sensing methods are probably an efficient way to perform a real integration of these systems at larger scales. Indeed, coastal habitats are amongst the most

productive ecosystems on earth and the contribution of anoxygenic bacteria to the coastal C and N cycles and their role in sustaining local food webs are probably underestimated.

Techniques such as HS imaging combined with state of the art optical sensors (e.g. optodes, Imaging PAM) will surely help to elucidate the distribution, trophic, geochemical roles of anoxygenic phototrophic biofilms as well as investigate in depth their photobiology in intact samples. In addition, new generations of ion microprobes based on mass spectrometry of secondary ions (SIMS) are now available and particularly appropriate to the study of microbial mats. They allow the analysis of any isotopic composition of a given sample surface and the distribution of labelled molecules (e.g. $H^{13}CO_3^-$) at a sub-cellular scales. It is thus now possible to determine the rate of carbon and nitrogen fixation at the cellular level (Musat et al., 2008) which would give valuable information about the functioning of the microbial mats in the future.

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Figures

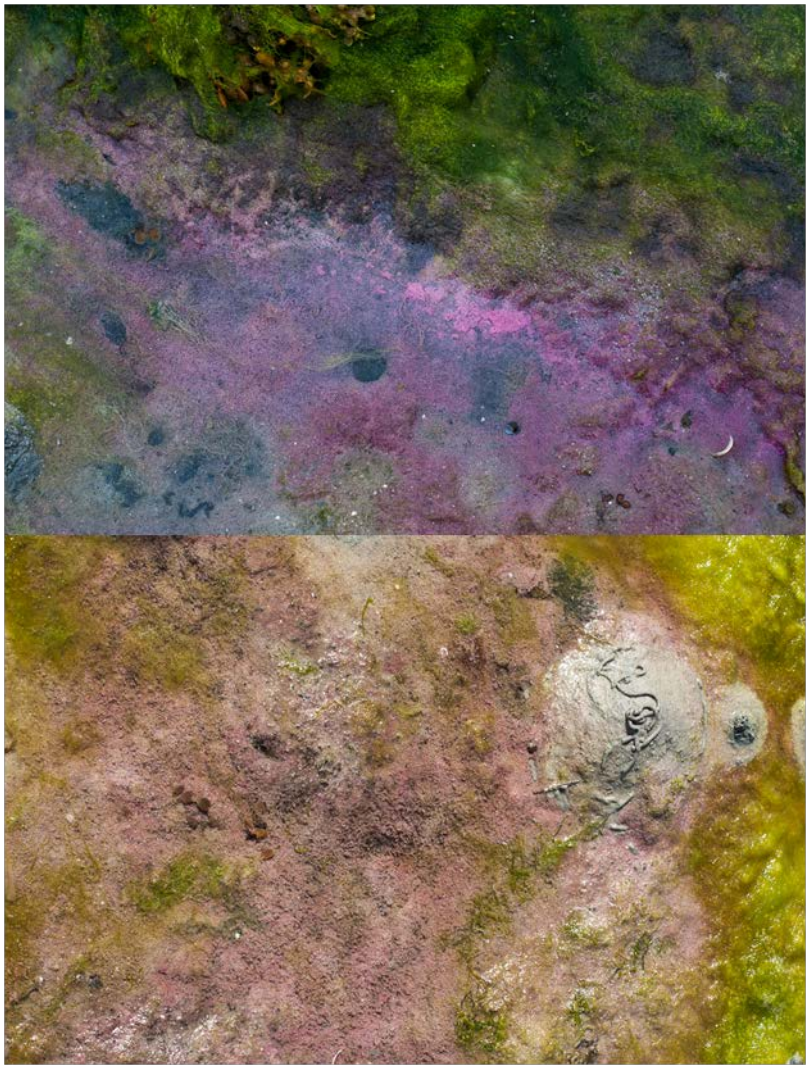

Figure 1: pictures of purple phototrophic mats, underwater (top panel) and emerged (bottom panel), in Roscoff Aber Bay.

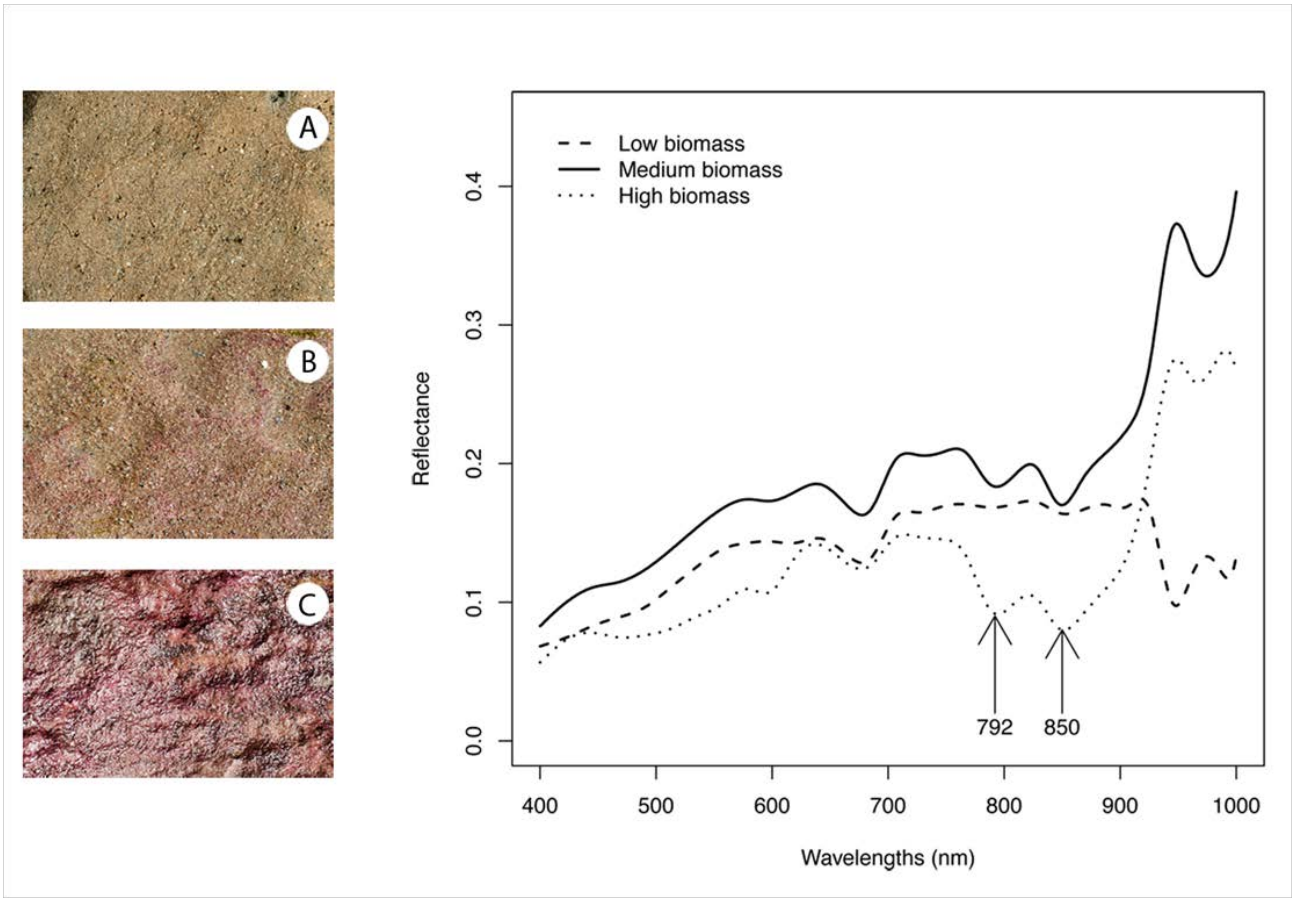

Figure 2: left panel: pictures of sites with low (A), medium (B) and high (C) biomass of purple sulfur bacteria, in Roscoff Aber Bay. Right panel : spectral reflectance of the sediment, in sites with low (dashed line), medium (solid line) and high (dotted line) biomass of these bacteria. The arrows point the bacteriochlorophyll *a* absorption peaks.

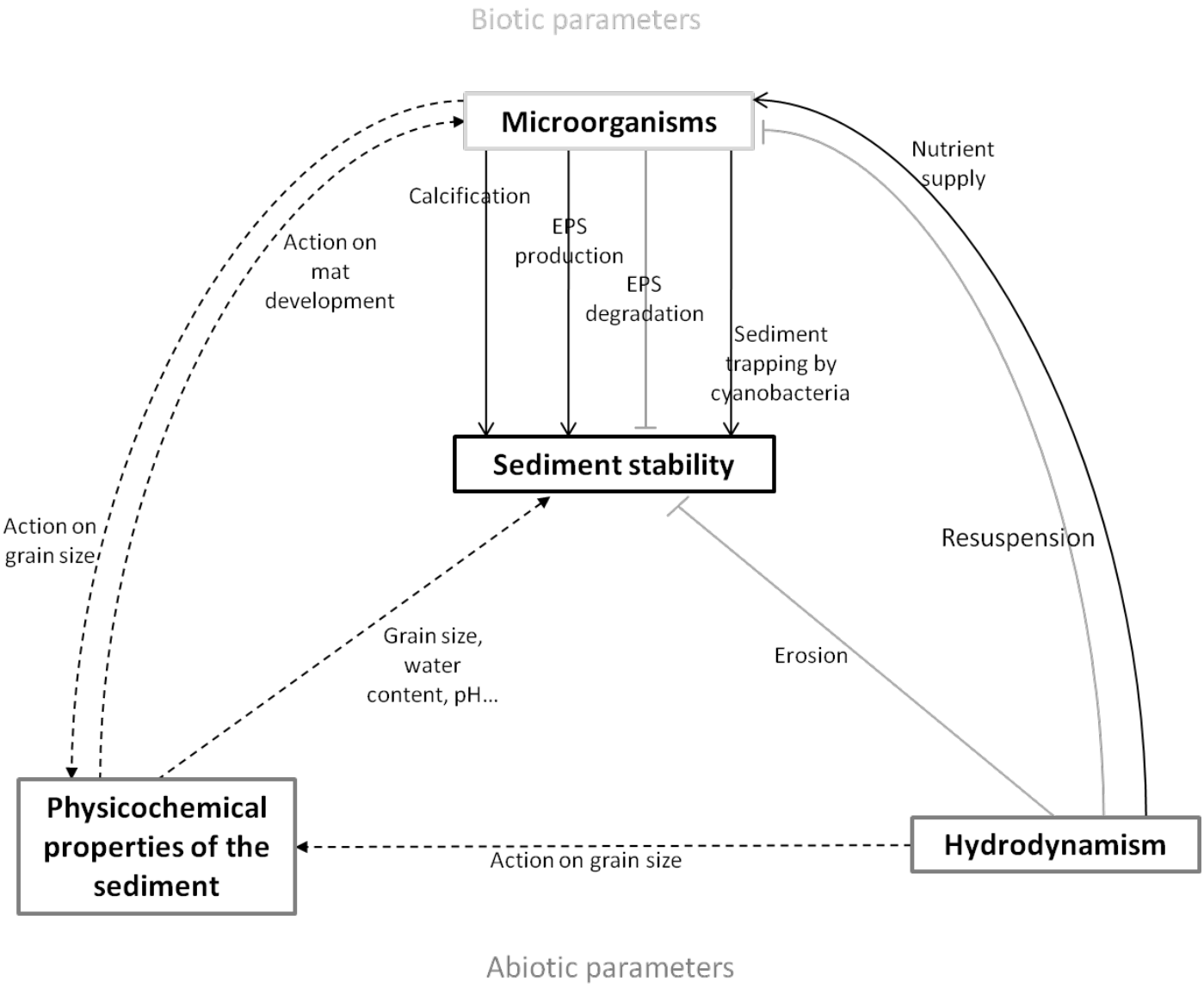

Figure 3: biotic and abiotic parameters influencing sediment stability. Arrow with black solid line: stimulates. Arrow with gray solid line: inhibits. Arrow with dashed line: has an influence on.

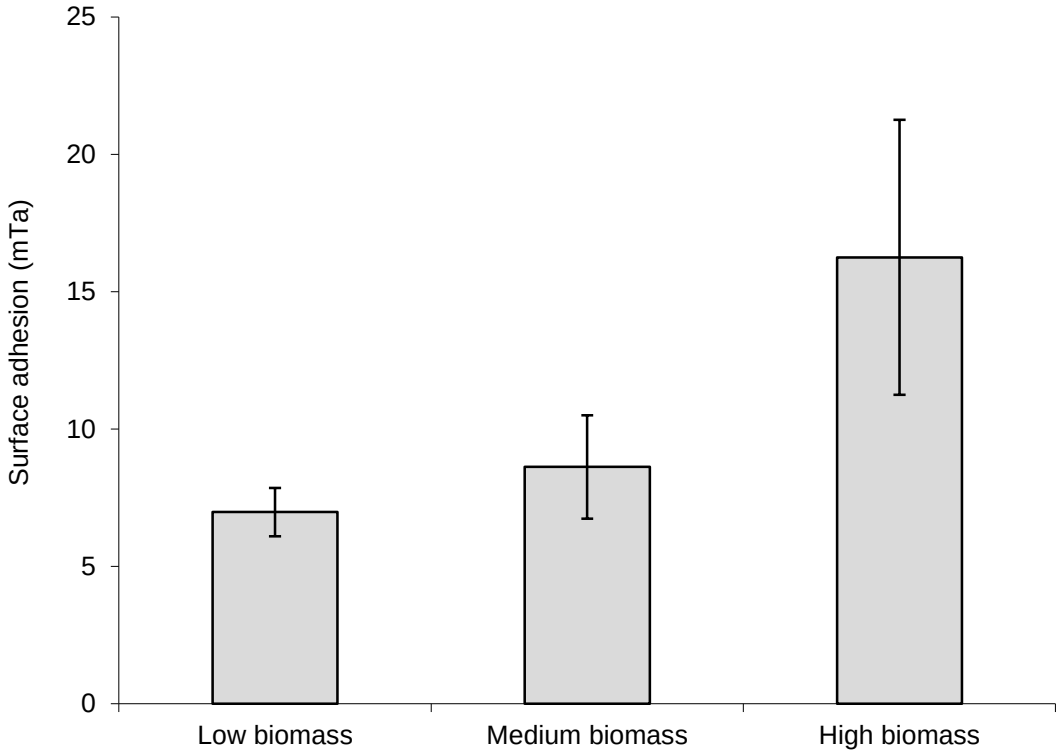

Figure 4: sediment cohesion (mTa; mean ± SD) in sites with low, medium and high biomass of purple sulfur bacteria, in Roscoff Aber Bay (see fig 2). Measurements were performed using a Magnetic Particle Inducer (MagPI), a device recently developed by Larson et al. (2009).

Pigments and in vivo spectral signatures	Type of measurement	Type of microbial community	Reference
BChl*a* (800-810, 860-880), BChl*c* (750), Car (450-550), PC (620)	Reflectance	*Microcoleus chthonoplastes*, Chromatium sp., *Thiocapsa* sp., *Chloroflexus*	Kühl & Jørgensen (1992)
BChl*d* & BChl*e* (720), BChl*a* (835), Chl*a* (680), PE (560, 570), PC (625, 630)	Absorbance	*Chromatium*, *Thiopedia*, *Chloronema*	Steenbergen & Korthals (1982)
Bchl*a* (370, 830), Oke (520)	Absorbance	*Thiocapsa roseopersicina*	Massé et al. (2002)
Bchl*a* (805,860, 880), Spi (480,520,550)	Absorbance and reflectance	*Thiocapsa roseopersicina*	Gitelson et al. (1999)
BChl (800, 801, 804, 806, 808, 835, 837, 862, 865, 867, 868, 870, 879)	Absorbance	Review about aerobic anoxygenic phototrophic bacteria	Yurkov & Csotonyi (2009)
BChl*a* (800, 850, 890), PB (620),	Reflectance	----------	Wiggli et al. (1999)
BChl*a* (790-810,865, 830-880), Chl*a* (675), Chl*c* (630-635), PC (620), PB (560-620),	Reflectance	Sediment biofilm, Cyanobacteria, diatoms and purple sulfur bacteria	Kühl et al. (1994)
Chl*a* (675), Chl*c* (623), DD (500), Fuco (550)	Reflectance	Diatom biofilms	Méléder et al. (2003)
BChl*a* (807,845), BChl*c* (745-750), Chl*a* (440, 675), PC (625)	Absorbance	Sediment cyanobacterial mat, purple and green photosynthetic bacteria	Kühl & Fenchel (2000)
Chl*a* (422, 659, 680), Car (422,448, 478), Myxo (508), PB (534, 570, 594, 628)	Reflectance	Sediment biofilm (cyanobacterial mat)	Andréfouet et al. (2003)
Alo (649), Chl*a* (412, 441, 623, 682), Chl*b* (466), Fuco (525, 540-548,) PE (574)	Reflectance	Rocky shore biofilm, diatoms with cyanobacteria	Murphy et al. (2005)
Chl*a* (422, 444, 676), Chl*b* & Chl*c* (468), Fuco & Per (672), PE (572), PC (620), Zea, lut, ß-car & DD (492)	Reflectance,	Sediment biofilm	Stephens et al. (2003)
Bchl*c* (732), Chl*a* (440, 680), Chl*b* (650-655), Chl*d* (710-712), PE (576), PC (626),	Hyperspectral imaging	Bacterial mat under didemnid ascidian	Kühl & Polerecky (2008)

Table 1: *in vivo* pigment spectral "signatures" collected from available references. Numbers between brackets refer to the absorption features of each pigment. Emphasis was given to references where bacteriochlorophyll samples were found. Alo- alloxanthin, BChl- bacteriochlorophyll, ß-car- ß-carotene, BChl*a* – bacteriochlorophyll *a*, BChl*c* –bacteriochlorophyll *c*, BChl*d* –bacteriochlorophyll *d*, BChl*e* –bacteriochlorophyll *e*, Car- carotenoides, Chl*a*- chlorophyll *a*, Chl*b*- chlorophyll *b*, Chl*c*- chlorophyll *c*, Chl*d*- chlorophyll *d*, DD- diadinoxanthin, Fuco- fucoxanthin, Lut- lutein, Myxo- myxoxantophyll, Oke - Okenone, PC- phycocianin, PB- phycobilin pigments, PE- phycoerythrin, Per- peridinin, Spi – Spirilloxanthin, Zea- zeaxanthin