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Regulation of aquatic microbial processes: the 'microbial loop' of the sunlit surface waters and the dark ocean dissected

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ABSTRACT: Our understanding of microbial food web interactions in the ocean is essentially based on research performed in the euphotic layer, where the interactions between phytoplankton and prokaryotic plankton, mainly heterotrophic Bacteria, are well established. In the euphotic layer, particularly in meso- and eutrophic waters, prokaryotic plankton are mainly top-down controlled by bacterivorous flagellates and viruses, affecting metabolically active, fast growing populations more than dormant stages. In the meso- and bathypelagic realm of the ocean, however, prokaryotic plankton are thought to be mainly bottom-up controlled, because the heterotrophic component of the prokaryotic community is limited by the availability of organic carbon. However, deep-water prokaryotes exhibit a number of peculiarities compared to prokaryotes in the euphotic layer, among which are a large genome size and a gene repertoire indicative of a predominately surface-attached mode of life. This indicates that deep-water prokaryotic activity might be primarily associated with particles. Our present knowledge indicates that the microbial communities and their interactions in the deep ocean are likely very different from those known from surface waters. Increasing efforts to shed light on the microbial biota of the ocean's interior will likely lead to the discovery of novel metabolic pathways in prokaryotes and to the resolution of the current discrepancy between the geochemical evidence of remineralization rates of organic matter and actual measurements.

KEY WORDS: Bacteria · Archaea · Biogeography · Bacterial growth · Growth yield · Functional diversity · Virioplankton · Prokaryotes

INTRODUCTION

About a quarter of a century ago, interactions between non-living organic matter and microbial plankton were put into a hypothetical context (Pomeroy 1974), which was later formalized and coined the microbial loop (Azam et al. 1983). Originally, the microbial loop described the path of dissolved organic matter (DOM), taken up by heterotrophic bacteria and converted into living particulate organic matter (POM), which in turn is grazed upon by protists. Via the conversion of DOM into bacterial biomass, organic carbon, which would otherwise not be accessible to metazoa, becomes available for the higher trophic levels. Since its original formulation, the concept has influenced several generations of microbial ecologists, and waves of specific research foci have addressed several aspects of the microbial loop, starting with measuring bacterial production (Fuhrman & Azam 1982) and grazing by protists (Fenchel 1984, Sherr et

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al. 1986), the turnover rates of specific organic compounds (Fuhrman & Bell 1985) to the role of viruses as predators (Bergh et al. 1989). All these major findings were made using a black-box approach, disregarding the different phylogenetic and largely also functional groups within the individual components of the microbial community as depicted in Fig. 1, until the advent of molecular techniques in aquatic microbial ecology in the early 1990s.

The estimated abundance of prokaryotes in the global oceanic water column amounts to about 10^{29} cells (Whitman et al. 1998), distributed equally over the 3 main oceanic depth zones: the sunlit euphotic layer, the mesopelagic layer (200–1000 m depth), and the bathypelagic realm (1000–4000 m depth) (J. Aristegui et al. unpubl. data). Abundance does not necessarily equal importance; however, research over the past 2 decades has unequivocally shown that planktonic microbes are the main drivers of the marine biogeochemical cycles. Heterotrophic prokaryotes channel about half of the primary production into the microbial loop of the euphotic layer (Nagata 2000) and might compete with eukaryotic phytoplankton for inorganic nutrients (Obernosterer & Herndl 1995, Thingstad 2000). Besides heterotrophic prokaryotes, depending on organic carbon for biosynthesis, there is a plethora of autotrophic prokaryotes in the oceanic water column, competing for light and inorganic compounds as energy sources for growth. Well-known photoautotrophs such as the genera *Prochlorococcus* and *Synechococcus* are abundant members of the microbial community in the euphotic zone and responsible for much of the primary production in oligotrophic subtropical gyres (Worden et al. 2000, DuRand et al. 2001).

Only recently, the importance of anaerobic ammonium oxidation by *Planktomycetes* and ammonia oxidizing *Crenarchaeota* have been discovered (Francis et al. 2007). These novel pathways add significantly to our understanding of the ocean's nitrogen cycle, and with more intensive sampling and new technologies, e.g. (meta)genomic approaches (Nealson & Venter 2007), it is likely that we will discover many more peculiar metabolic pathways in prokaryotes. New findings emerging over the next decade will allow us to obtain a refined view on the role of planktonic prokaryotic communities and their interactions with the other groups of the microbial community, the protists and viruses (Fig. 1). Ultimately, we should be able to better link the biogeographic distribution of microbial communities to the cycling of the major elements in the ocean, and hence arrive at a mechanistic understanding of the microbial loop in the different realms of the ocean.

This paper builds on findings over the past 2 to 3 decades and discusses our current perception of the regulation of microbial processes in the oceanic water column. First, the main components of the microbial food web and their interactions in the euphotic layer are summarized. Second, the functional differences between the microbial loop in the upper sunlit ocean and the deep ocean are discussed, and new emerging problems in aquatic microbial ecology are highlighted that have to be addressed to arrive at a mechanistic understanding of microbial oceanographic processes.

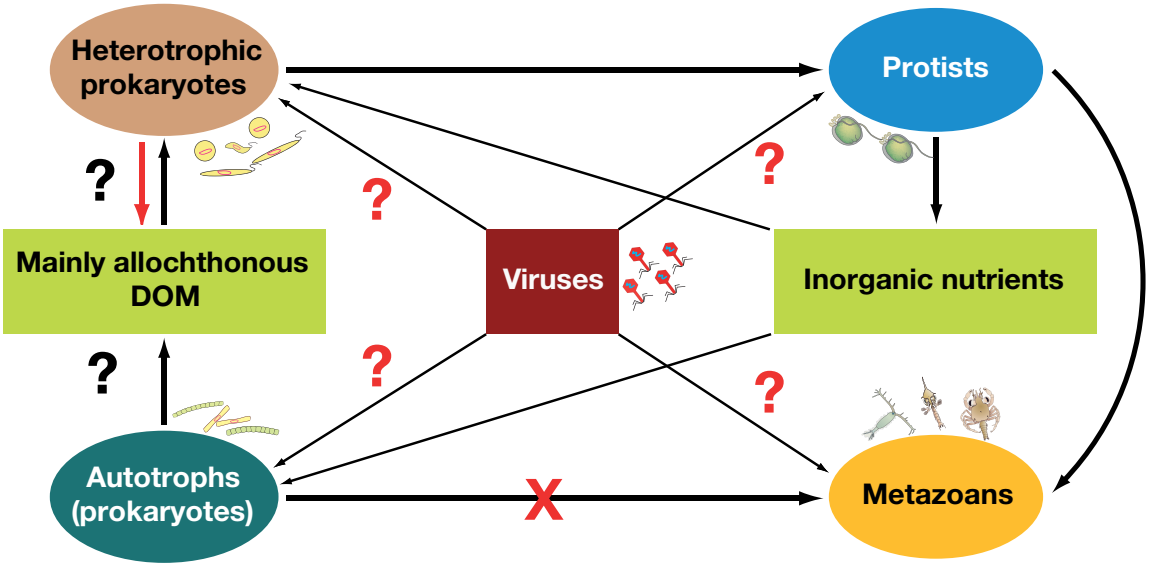

Fig. 1. Scheme of the microbial food web structure and cycling of organic and inorganic matter pool in the meso- and bathypelagic realm. Arrows between the different biotic and abiotic compartments indicate the interactions as we know them from the euphotic layer. Red question marks and crossed arrow indicate major uncertainties on the importance of these interactions and lack of evidence that this flux is significant in the dark ocean, respectively. DOM: dissolved organic matter

MICROBIAL PROCESSES IN SURFACE WATERS

Generally, each trophic level is either controlled by resources (bottom-up) or by predation (top-down). In surface water food webs, these 2 basic controls can change rapidly, even over diel cycles (Kuipers et al. 2000, Winter et al. 2004a). In the sunlit surface ocean, the microbial food web consists of 4 main functional groups of organisms, i.e. photoautotrophic phytoplankton, heterotrophic prokaryotes, heterotrophic protists, and viruses (Fig. 1). The distinction of functional groups is rather artificial, as evidence is accumulating that there is a continuum among phytoplankton taxa from entirely autotrophic to obligatory mixotrophic, and in prokaryotes, chemoautotrophy is abundant as well.

Zubkov & Tarran (2005) found that some phytoplankton do not rely solely on the uptake of inorganic nutrients, but are also capable of directly taking up low molecular weight DOM. Prokaryotes in the surface ocean have long been considered to be predominantly heterotrophic, despite their ability to efficiently compete with phytoplankton for inorganic nitrogen and phosphate (Thingstad 1987, Kirchman 1994). Recent evidence suggests, however, that some heterotrophic bacteria are capable of using solar radiation via proteorhodopsin, a light-driven proton pump providing additional energy (Béja et al. 2000, Giovannoni et al. 2005, Sabehi et al. 2005, Schwalbach et al. 2005, Frigaard et al. 2006, Fuhrman et al. 2008). The extent to which this may supplement heterotrophic metabolism is currently discussed (see Fuhrman & Steele 2008, this Special). Similarly, a large number of protistan plankton, the main predators of prokaryotic plankton along with viruses, is mixotrophic, i.e. capable of performing photosynthesis (Andersson et al. 1989, Bennett et al. 1990, Sherr & Sherr 1994, Arenovski et al. 1995). Hence, the microbial food web in surface waters is characterized by a mix of trophic strategies in all the living compartments of the classic microbial loop, making the trophic interactions substantially more complex than depicted in Fig. 1.

Phytoplankton primary production fuels heterotrophic prokaryotic activity either directly via extracellular release, or indirectly via grazing losses to higher trophic levels (Marañon 2005). Essentially, all trophic levels, not only primary producers, release copious amounts of organic matter (largely in dissolved or colloidal form) into the ambient water, thus providing substrate for heterotrophic prokaryotes (Lignell 1990, Stoderegger & Herndl 1998, Stoderegger & Herndl 1999, Nagata 2000, Conan et al. 2007). The quality of the organic matter and the stoichiometric balance between available carbon, nitrogen and phosphorus determines the efficiency of channeling the DOM into either biomass production or remineralization (Goldman et al. 1987, Obernosterer & Herndl 1995, del Giorgio & Cole 1998, 2000). However, it is likely that micronutrients (such as Fe, Zn, etc.) also exert some control on the growth efficiency (Tortell et al. 1996) and ectoenzymatic activity of bacteria (Fukuda et al. 2000). The prokaryotic carbon demand in the euphotic zone is usually high and about 50 to 80% of primary production (Ducklow 1993, Reinthaler & Herndl 2005, Mouriño-Carballido & McGillicuddy 2006). Thus, much of the newly produced DOM is potentially retained in the surface ocean.

In most parts of the surface ocean, the microbial food web and particularly the prokaryotic community relies mainly on autochthonously produced fresh DOM from phytoplankton primary production. However, in oligotrophic regions, allochthonous organic matter from lateral transfer or dust input from the atmosphere might be an important subsidy of autochthonously produced organic matter (del Giorgio et al. 1997, Aristegui et al. 2003, Dachs et al. 2005).

In the sunlit surface ocean, prokaryotic activity in the top half of the euphotic layer is influenced either directly (Herndl et al. 1997) or indirectly, via changing the DOM availability by solar radiation as depicted in Fig. 2 (Obernosterer et al. 1999a, 2001a,b, Pausz & Herndl 1999, Obernosterer & Herndl 2000). Bacterial groups and strains exhibit remarkable differences in sensitivity to natural levels of solar radiation and in the recovery from solar radiation-induced DNA damage (Arrieta et al. 2000, Alonso-Sáez et al. 2006). While members of the *Gammaproteobacteria* and *Bacteroidetes* groups are largely resistant to solar radiation, *Alphaproteobacteria* appear to be sensitive (Alonso-Sáez et al. 2006). However, these differences have only limited impact on the overall bacterioplankton community composition in surface waters (Winter et al. 2001). Overall, bacterioplankton activity seems to be higher under light conditions than under dark conditions, indicating, on the one hand, photoheterotrophic growth such as shown for *Prochlorococcus* spp. (Church et al. 2006) and, on the other hand, the dependence of heterotrophic prokaryotes on the production of photosynthetic extracellular release by phytoplankton during the light period (Church et al. 2004). As an adaptation to harmful UV-B radiation, surface prokaryotic plankton have the potential to express photolyase as an efficient repair mechanism for induced DNA damage (Aas et al. 1996, Kaiser & Herndl 1997, Arrieta et al. 2000), while phytoplankton produce mycosporine-like amino acids as photoprotective pigments (Karentz et al. 1991) which can be taken up by zooplankton as well.

The extracellular enzymatic activity of prokaryotes plays a key role in the processing of DOM. Prokaryotes preferentially utilize high molecular weight DOM, due to its higher bioreactivity compared to the bulk of low

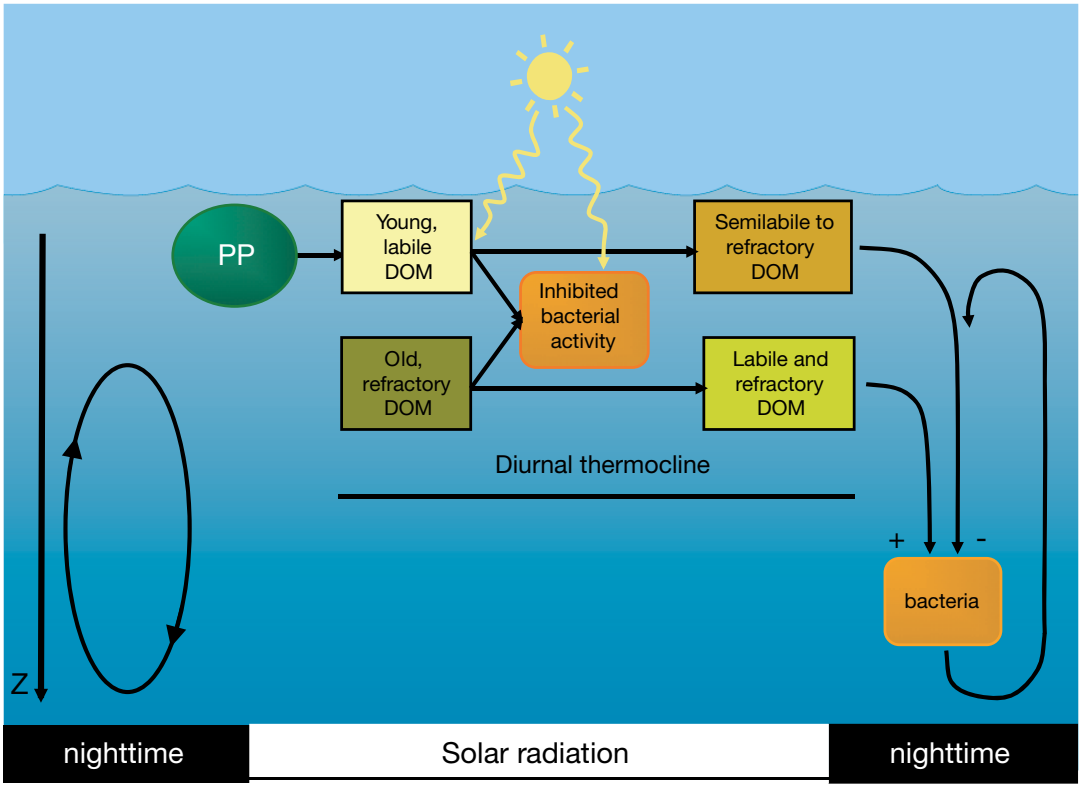

Fig. 2. Interaction of hydrodynamics, photochemistry and the microbial food web in the euphotic layer as influenced by solar radiation. During the day, the surface layers of the water column become stratified due to warming by solar radiation leading to diurnally stratified top layers (Obernosterer et al. 2001a). All organisms in this stratified layer are exposed to a high dose of solar radiation, including harmful ultraviolet radiation, leading to an inhibition of overall microbial activity. The labile component of the dissolved organic matter (DOM) pool becomes more refractory due to photochemical transformation, while originally refractory DOM is at least partly becoming more bioreactive (Obernosterer et al. 1999b). At dusk, when surface waters are cooling off, the top layer of the water column is mixed and photoenzymatic repair of UV-damage is activated by UV-A radiation, resulting in rapid recovery of the microbiota (Arrieta et al. 2000, Winter et al. 2001) and, subsequently, the uptake of photochemically produced labile DOM. The overall impact of solar radiation on microbiota in the upper euphotic layer is therefore a strong diel phasing of the metabolic activity. Z: depth, PP: primary production

molecular weight DOM (Amon & Benner 1994, Benner 2002). This high molecular weight DOM is either directly derived from phytoplankton extracellular release or released during grazing by metazoans. Hoppe et al. (2002) demonstrated that the enzymatic hydrolysis of DOM is tightly linked to the uptake of the resulting oligo- or monomers. However, it is often neglected that, depending on the complexity of the DOM, several similar types of enzymes are expressed by prokaryotes that likely increase the efficiency in cleaving and assimilating DOM (Arrieta & Herndl 2002).

Shifts in the community composition of surface water prokaryotes are commonly attributed to selective grazing losses, either through bacterivorous flagellates or viruses (Fuhrman & Noble 1995). Thus, top-down control is thought to prevail over bottom-up control in the euphotic layer, particularly in meso- and eutrophic coastal systems (Billen et al. 1990, Gasol 1994, Tanaka & Rassoulzadegan 2004, Duffy et al. 2007, Frank et al. 2007). In open ocean surface waters, in contrast, bottom-up control seems to prevail over top-down control (Carlson et al. 2002, 2004), although shifts from bottom-up to top-down control over diel cycles have been reported as well (Kuipers et al. 2000).

Efficient grazing requires sufficiently high contact rates with prokaryotes for both viruses and flagellates. Generally, a threshold of around 10^5 prokaryotes ml^{-1} has been assumed (Fenchel 1986, Weinbauer 2004). However, this threshold value ignores the fact that there is indication that both flagellates and viruses graze primarily selectively. Evidence has been presented that flagellates preferentially graze on highly active bacterial populations, while bacteria with low metabolic activity or in a dormant state experience only low grazing pressure (del Giorgio et al. 1996). Viruses are commonly reported to be highly species- or even strain-specific (Winter et al. 2004b, Hewson &

Fuhrman 2007). This specificity, however, remains to be shown for complex prokaryotic communities, since the members of viral communities are distributed across different biomes (Sano et al. 2004). Predominant viral versus flagellate control of the prokaryotic community can change rapidly, and pronounced diel cycles in bacteriophage production have been reported (Winter et al. 2004a). Regardless of whether viruses or flagellates are the dominant factors controlling prokaryotic abundance, the selective grazing pressure on highly active prokaryotic populations leads to the well-documented situation that the most active prokaryotic populations in a community are commonly not the most abundant ones in marine systems (Bouvier & del Giorgio 2007).

DIFFERENCES OF MICROBIAL PROCESSES IN SURFACE WATERS VERSUS DEEP WATERS

Generally, prokaryotic abundance and biomass production decline exponentially from surface waters to the bathypelagic layers by about 2 and 3 orders of magnitude, respectively (Reinthaler et al. 2006). Traditionally, the deep waters and particularly the bathypelagic realm have been considered to be a homogeneous environment with rather constant DOM concentrations and low temperature. However, recent research suggests that the dark ocean is more heterogeneous than commonly assumed, with relatively high cell-specific activity. Nevertheless, intermediate waters and the bathypelagic ocean harbor a simpler food web than the sunlit surface waters, due to the absence of phytoplankton that serves as the major food source for zooplankton in the surface ocean (Lenz et al. 1993, Pakhomov & Perissinotto 1997). However, this lack of phytoplankton is partly compensated by a major prokaryotic autotrophic component in the mesopelagic waters, recently discovered and described in more detail below.

Deep-water prokaryotic communities exhibit some general features that make them distinctly different from euphotic assemblages. There is a general tendency of increasing nucleic acid content per cell with depth (Reinthaler et al. 2006). This indicates a larger genome size than found in surface water prokaryotes which, in turn, might be indicative of an opportunistic life style (Lauro & Bartlett 2007). Moreover, most of the deep water prokaryotes lack the gene responsible for the expression of photolyase (Lauro et al. 2006). More genes associated with a preferential surface-attached life mode have been detected in deep than in surface waters (DeLong et al. 2006, Lauro et al. 2007).

Despite the decline in prokaryotic abundance with depth by about 2 orders of magnitude, prokaryotic richness decreases only by about 30% from the euphotic to the bathypelagic layer as determined by molecular fingerprinting techniques (Moeseneder et al. 2001b, Hewson et al. 2006, Agogué et al. 2007). There is substantial stratification of the prokaryotic populations, overall showing distinct clusters for different water masses (DeLong et al. 2006). This stratification might reflect differences in the organic matter field with depth (Moeseneder et al. 2001b, DeLong et al. 2006) or, alternatively, adaptations to pressure and temperature, as deep water prokaryotes are frequently phylogenetically most closely affiliated with sea-ice prokaryotes (Vezzi et al. 2005, Lauro et al. 2006). Morris et al. (2004) found that the uncultured *Chloroflexi*-type SAR202 cluster dominated the bacterial community below 500 m depth in the Atlantic, where this cluster contributes up to 40% to the total bacterial abundance (Varela et al. 2008).

While the relative contribution of Bacteria to total prokaryotic abundance decreases with depth, the contribution of Archaea and, more specifically, the Crenarchaea increases with depth (Karner et al. 2001, Moeseneder et al. 2001a, Teira et al. 2006). The role of deep water Crenarchaea is currently being discussed; however, there is evidence that at least some are chemoautotrophs. The only isolate so far, *Nitrosopumilus maritimus*, belonging to the Marine *Crenarcheaota* Group I, as well as genomic and compound-specific stable isotope data and microautoradiography coupled with fluorescent *in situ* hybridization (FISH) analyses indicate that, at least in the mesopelagic zone, a substantial fraction of *Crenarchaeota* uses CO_2 as a carbon source and ammonia oxidation as an energy donor (Herndl et al. 2005, Könneke et al. 2005, Ingalls et al. 2006, Wuchter et al. 2006). In the bathypelagic realm, however, ammonia oxidation is likely not an important energy source considering the low ammonia concentrations commonly found there. Corresponding to that, the bathypelagic crenarchaeal community is predominantly heterotrophic (Teira et al. 2006, Kirchman et al. 2007).

An important albeit poorly recognized aspect in the oxygenated deep waters is the magnitude of CO_2 fixation. It has been estimated that dark CO_2 fixation in the meso- and bathypelagic waters amounts to about 1 mmol C m^{-2} d^{-1} (Herndl et al. 2005). This is a substantial supplement to the surface ocean-derived organic carbon flux into the deep ocean. Moreover, it provides a source of new organic matter production in the dark ocean besides the modified surface water-derived organic matter. Hence, dark CO_2 fixation might be considered to be the dark ocean's 'primary production', although this dark organic matter production might still depend indirectly on sunlit surface water primary production to provide energy sources like

ammonia. The extent to which this source of primary production in the deep ocean drives the meso- and bathypelagic food web remains to be shown.

THE DISSOLVED MATTER FIELD AND PROKARYOTIC METABOLISM

The stratification of heterotrophic prokaryotic populations with depth is most likely a reflection of the shift in the quality and quantity of DOM, rather than of changes in the grazing pressure (see below, 'Biotic interations in the microbial world'). With increasing depth, the bulk DOM is successively depleted in phosphorus (DOP) and nitrogen (DON), leading to an overall increase in the DOC:DON:DOP ratio (Benner 2002). Consequently, the bathypelagic DOM pool is characterized by carbon-rich low molecular weight DOM, supposed to be degradation products from the remineralization of organic matter by the microbial community (Benner 2002). There is recent evidence that about 25% of the detrital carbon pool (dissolved and particulate) and about 50% of the detrital nitrogen pool of the deep-water DOM is of prokaryotic origin (Kaiser & Benner 2008); however, the majority of DOM in the dark ocean has not yet been identified on a molecular level.

The lower reactivity of deep-water DOM and POM, compared to surface water DOM, is reflected in substantially lower prokaryotic growth yields in the deep ocean (Reinthaler et al. 2006), which decrease from ~20% in the surface ocean to 2% in the bathypelagic. Concomitantly with the lower growth yield, deep-water prokaryotes express more extracellular enzymes on a per-cell level than surface water prokaryotes (Baltar et al. in press). Even cell-specific alkaline phosphatase activity is higher in the ocean's interior than in surface waters, even though phosphate is available in high concentrations in deep waters and heterotrophic prokaryotes in this environment are usually considered to be limited by organic carbon availability, rather than phosphate. This high alkaline phosphatase activity has been interpreted as a strategy to acquire carbon moieties of the refractory DOM, rather than phosphate (Hoppe & Ullrich 1999). The higher growth efficiency in surface water prokaryotes, in contrast, is accompanied by a generally lower cell-specific ectoenzymatic activity (Baltar et al. in press).

It seems that prokaryotes in the dark ocean have to use substrate that is generally considered to be energetically less favorable for growth. For example, prokaryotic cells require much more L-amino acids as building blocks for protein synthesis than D-amino acids, while, at the same time, increasing ratios of D-/L-amino acid uptake by bulk prokaryotic plankton with depth have been found (Pérez et al. 2003). Moreover, Teira et al. (2006) found that about twice as many cells of bathypelagic *Crenarchaeota* take up D-amino acids compared to L-amino acids. Consequently, deep-water prokaryotes apparently have to invest relatively more energy to support growth than surface water prokaryotic communities.

Previously, sediment trap data generated the general view of a sharply decreasing POM flux with depth; however, particles over a large size spectrum might be more important in deep waters than hitherto assumed. This is in part supported by the high nucleic acid content of deep-water prokaryotes and by genomic evidence suggesting a preferentially attached life-mode (Lopez-Lopez et al. 2005, DeLong et al. 2006, Martin-Cuadrado et al. 2007). The variability in surface water prokaryotic activity over short-time (diel) scales is largely driven by phytoplankton primary production and extracellular release of DOM (Pausz & Herndl 2002) and by solar radiation, including harmful UV-radiation, influencing mostly the upper half of the euphotic layer (Obernosterer et al. 2001a). Deep-water prokaryotes, however, might be exposed to spatial variability of nutrient concentrations, i.e. refractory DOM and less refractory colloidal and particulate matter sedimenting at different velocities from the euphotic layer into the ocean's interior. Consequently, the resulting heterogeneity, governed by colloidal and truly detrital matter, might lead to a heterogeneous distribution of deep-water microbes. Clearly, there is a need for refined sampling techniques that take the fragile nature of bathypelagic detrital matter and the presumably non-random distribution of deep-water microbes into account. Conventional sampling devices are certainly not suited for this purpose.

BIOTIC INTERACTIONS IN THE MICROBIAL WORLD

In contrast to prokaryotic communities in the euphotic layer, deep-water communities have so far been assumed to be bottom-up controlled. This view, however, is not supported by recent findings. The prokaryote:flagellate ratio only slightly decreases from about 10 in surface waters to around 5 in bathypelagic waters (J. Aristegui et al. unpubl.), while the virus: prokaryote ratio increases from about 10 in the euphotic layer to up to 100 in the bathypelagic North Atlantic (Parada et al. 2007). Although lysogeny (where the prophage is transmitted through cell division of the host) may be the dominant strategy for viruses in the low-abundance host environment of the deep ocean (Weinbauer et al. 2003), the relatively high abundance of viruses in deep waters cannot be reconciled with a random distribution of prokaryotes.

Similarly, it has been hypothesized that a certain threshold is required to maintain bacterivory in flagellates (Fenchel 1982, 1986). Thus, it remains enigmatic how these 2 groups of predators can survive in the ocean's interior, considering that the abundance of prokaryotes in the bathypelagic is 2 orders of magnitude lower than in surface waters. The knowledge of microbial food web interactions we have accumulated over the past decades is based on surface waters, and it is likely that viruses and flagellates either behave fundamentally different in deep waters compared to surface waters, or that bacterivorous grazing and viral infection are largely restricted to colloidal or particulate matter, where prokaryotic abundances are likely to be orders of magnitude higher than in the nutrient-deprived surrounding waters. If the assumption is true that microbes in the ocean's interior are more dependent on particle rain than microbes in the euphotic zone, the resulting non-random distribution of deep-water microbes might facilitate synergistic interactions in the cycling of matter. The potential implication of microzones for microbes has been suggested for some time; however, most measurements still ignore a potential non-random distribution of microbes in the oceanic water column (Azam & Malfatti 2007).

THE CHALLENGE REMAINS IN THE (POST)GENOMIC ERA: MICROBIAL PROCESSES VERSUS GEOCHEMICAL EVIDENCE

Despite the substantial insights we have gained over the past few years on the metabolism and diversity of microbes in the ocean, the gap between geochemical estimates of ocean carbon flow and microbial rate measurements still exists (Reinthaler et al. 2006). Particularly for the deep ocean, we still lack a mechanistic understanding of microbial processes in conjunction with the physico-chemical environment, which makes it impossible to resolve the biogeochemical fluxes in the largest biome of the ocean — but now there is hope. Microbial oceanography is rapidly developing, linking hydrology, biogeochemistry, microbial ecology and genomics together to create a new scientific field (Karl 2007). The available tools range from remote sensing to single cell analyses, from cost-effective sequencing technology such as pyrosequencing (Sogin et al. 2006) to compound-specific stable isotope analyses linked to genomic approaches. Taken together, these tools will allow us to obtain an inventory of all microbial proteins and assign functions to them.

Open ocean observatories like the Hawaii ocean time-series (HOT) and the Bermuda Atlantic time-series (BATS) have revealed long-term trends in the upper layers of the open ocean and the *in situ* monitoring systems that are currently being developed will allow us to obtain near-real time data on the dynamics of the microbial communities in the ocean's interior over the next 2 decades. With these tools, we will be able to shed light onto the deep sea microbial communities and decipher natural variability from anthropogenically induced alterations in the largest oceanic subsystem, the dark ocean.

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