



HAL
open science

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

Gerhard J. Herndl, H el ene Agogu e, Federico Baltar, Thomas Reinthaler, Eva Sintes, Marta M. Varela

► To cite this version:

Gerhard J. Herndl, H el ene Agogu e, Federico Baltar, Thomas Reinthaler, Eva Sintes, et al.. Regulation of aquatic microbial processes: the ‘microbial loop’ of the sunlit surface waters and the dark ocean dissected. *Aquatic Microbial Ecology*, 2008, 53, pp.59-68. 10.3354/ame01225 . hal-01354363

HAL Id: hal-01354363

<https://hal.science/hal-01354363v1>

Submitted on 18 Aug 2016

HAL is a multi-disciplinary open access archive for the deposit and dissemination of scientific research documents, whether they are published or not. The documents may come from teaching and research institutions in France or abroad, or from public or private research centers.

L’archive ouverte pluridisciplinaire **HAL**, est destin ee au d ep ot et  a la diffusion de documents scientifiques de niveau recherche, publi es ou non,  emanant des  tablissements d’enseignement et de recherche fran ais ou  trangers, des laboratoires publics ou priv es.



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

Gerhard J. Herndl^{1,*}, H el ene Agogu e¹, Federico Baltar^{1,2}, Thomas Reinthaler¹,
Eva Sintes¹, Marta M. Varela^{1,3}

¹Department of Biological Oceanography, Royal Netherlands Institute for Sea Research (NIOZ), PO BOX 59,
1790 AB Den Burg, Netherlands

²Present address: Universidad de Las Palmas de Gran Canaria, Facultad Ciencias del Mar, Las Palmas, Spain

³Present address: Laboratorio de Microbiolog a, Facultad de Ciencias, Universidade da Coru a,
R ua Alejandro de la Sota no. 1, 15008 A Coru a, Spain

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

Resale or republication not permitted without written consent of the publisher

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

*Email: herndl@nioz.nl

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 *Planctomycetes* 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.

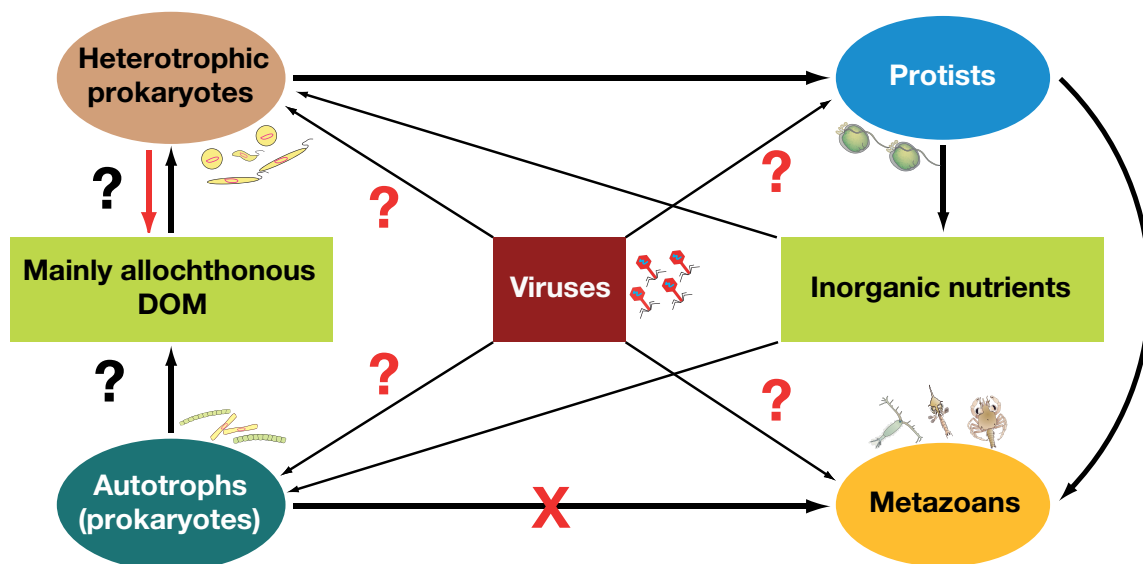


Fig. 1. Scheme of the microbial food web structure and cycling of organic and inorganic matter pool in the meso- and bathypelagic realm. Arrows between the different biotic and abiotic compartments indicate the interactions as we know them from the euphotic layer. Red question marks and crossed arrow 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 (Marañón 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 *Gamma*proteobacteria 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

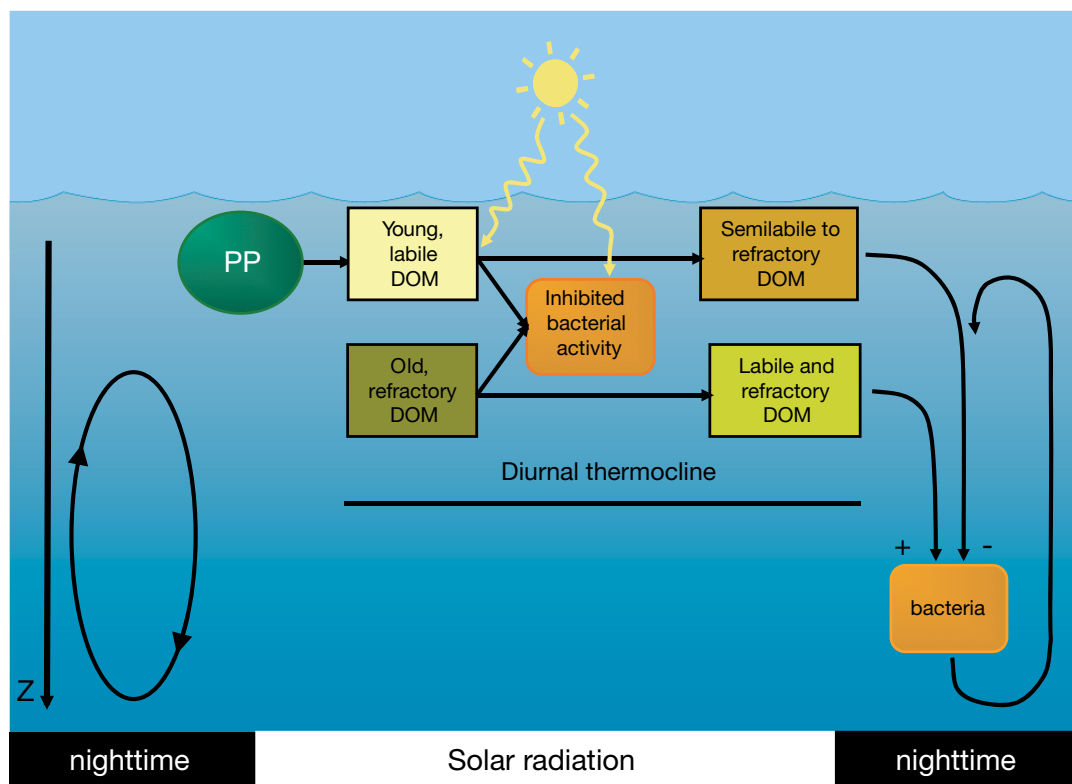


Fig. 2. Interaction of hydrodynamics, photochemistry and the microbial food web in the euphotic layer as influenced by solar radiation. During the day, the surface layers of the water column become stratified due to warming by solar radiation leading to diurnally stratified top layers (Obernosterer et 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, Agogu e 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 (Vezi 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 Crenarchaeota 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 CO₂ as a carbon source and ammonia oxidation as an energy donor (Herndl et al. 2005, K onneke 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 CO₂ fixation. It has been estimated that dark CO₂ 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 CO₂ 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 interactions 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 (Reinthal 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 (Obenosterer 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-depleted 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 (Reinthal 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* monitor-

ing 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.

Acknowledgements. We thank the colleagues in our working group for the continuous scientific discussions on deep ocean microbial life and all the scientific and ship's crew members joining the research cruises on board RV 'Pelagia' in the North Atlantic. Many colleagues shared their opinion on this subject during several workshops. Support for the research cruises (TRANSAT, ARCHIMEDES) was provided by the Earth and Life Science branch of the Netherlands Science Organization (ALW-NWO) to G.J.H. This work was carried out within the frame of the 'Networks of Excellence' MarBef and EurOceans, supported by the 6th Framework Program of the EU.

LITERATURE CITED

- Aas P, Lyons MM, Pledger R, Mitchell DL, Jeffrey WH (1996) Inhibition of bacterial activities by solar radiation in nearshore waters and the Gulf of Mexico. *Aquat Microb Ecol* 11:229–238
- Agogué H, Brink M, Arrieta JM, Herndl GJ (2007) Bacterial and archaeal diversity in the meso- and bathypelagic waters of the eastern north Atlantic basin. *Proc 38th CIESM Congr* 38:338
- Alonso-Sáez L, Gasol JM, Lefort T, Hofer J, Sommaruga R (2006) Effect of natural sunlight on bacterial activity and differential sensitivity of natural bacterioplankton groups in Northwestern Mediterranean coastal waters. *Appl Environ Microbiol* 72:5806–5813
- Amon RMW, Benner R (1994) Rapid cycling of high-molecular-weight dissolved organic matter in the ocean. *Nature* 369:549–552
- Andersson A, Falk S, Samuelsson G, Hagström Å (1989) Nutritional characteristics of a mixotrophic nanoflagellate, *Ochromonas* sp. *Microb Ecol* 17:251–262
- Arenovski AL, Lim EL, Caron DA (1995) Mixotrophic nanoplankton in oligotrophic surface waters of the Sargasso Sea may employ phagotrophy to obtain major nutrients. *J Plankton Res* 17:801–820
- Aristegui J, Barton ED, Montero MF, Garcia-Muñoz M, Escánez J (2003) Organic carbon distribution and water column respiration in the NW Africa-Canaries Coastal Transition Zone. *Aquat Microb Ecol* 33:289–301
- Arrieta JM, Herndl GJ (2002) Changes in bacterial beta-glucosidase diversity during a coastal phytoplankton bloom. *Limnol Oceanogr* 47:594–599
- Arrieta JM, Weinbauer MG, Herndl GJ (2000) Interspecific differences in sensitivity to UV radiation and subsequent recovery in selected isolates of marine bacteria. *Appl Environ Microbiol* 66:1468–1473
- Azam F, Malfatti F (2007) Microbial structuring of marine ecosystems. *Nat Rev Microbiol* 5:782–791
- Azam F, Fenchel T, Field JG, Gray JS, Meyer-Reil LA, Thingstad F (1983) The ecological role of water-column microbes in the sea. *Mar Ecol Prog Ser* 10:257–263

- Baltar F, Sintes E, Aken HMV, Gasol JM, Aristegui J, Herndl GJ (in press) Prokaryotic extracellular enzymatic activity in relation to biomass production and respiration in the meso- and bathypelagic waters of the (sub)tropical Atlantic. *Limnol Oceanogr*
- Béja O, Aravind L, Koonin EV, Suzuki MT and others (2000) Bacterial rhodopsin: evidence for a new type of phototrophy in the sea. *Science* 289:1902–1906
- Benner R (2002) Chemical composition and reactivity. In: Hansell DA, Carlson CA (eds) *Biogeochemistry of marine dissolved organic matter*. Elsevier Science, New York, p 59–90
- Bennett SJ, Sanders RW, Porter KG (1990) Heterotrophic, autotrophic, and mixotrophic nanoflagellates: seasonal abundances and bacterivory in a eutrophic lake. *Limnol Oceanogr* 35:1821–1832
- Bergh Ø, Børsheim KY, Bratbak G, Heldal M (1989) High abundance of viruses found in aquatic environments. *Nature* 340:467–468
- Billen G, Servais P, Becquevort S (1990) Dynamics of bacterioplankton in oligotrophic and eutrophic aquatic environments: bottom-up or top-down control? *Hydrobiologia* 207:37–42
- Bouvier T, del Giorgio PA (2007) Key role of selective viral-induced mortality in determining marine bacterial community composition. *Environ Microbiol* 9:287–297
- Carlson CA, Giovannoni SJ, Hansell DA, Goldberg SJ and others (2002) The effect of nutrient amendments on bacterioplankton growth, DOC utilization, and community structure in the northwestern Sargasso Sea. *Aquat Microb Ecol* 30:19–36
- Carlson CA, Giovannoni SJ, Hansell DA, Goldberg SJ, Parsons R, Vergin K (2004) Interactions among dissolved organic carbon, microbial processes, and community structure in the mesopelagic zone of the northwestern Sargasso Sea. *Limnol Oceanogr* 49:1073–1083
- Church MJ, Ducklow HW, Karl DA (2004) Light dependence of [³H] leucine incorporation in the North Pacific ocean. *Appl Environ Microbiol* 70:4079–4087
- Church MJ, Ducklow HW, Letelier RM, Karl DM (2006) Temporal and vertical dynamics in picoplankton photoheterotrophic production in the subtropical North Pacific Ocean. *Aquat Microb Ecol* 45:41–53
- Conan P, Sondergaard M, Kragh T, Thingstad F and others (2007) Partitioning of organic production in marine plankton communities: the effects of inorganic nutrient ratios and community composition on new dissolved organic matter. *Limnol Oceanogr* 52:753–765
- Dachs J, Calleja ML, Duarte CM, del Vento S, Turpin B, Polidori A, Herndl GJ, Agustí S (2005) High atmosphere-ocean exchange of organic carbon in the NE subtropical Atlantic. *Geophys Res Lett* 32:L21807
- del Giorgio PA, Cole JJ (1998) Bacterial growth yield efficiency in natural aquatic systems. *Annu Rev Ecol Syst* 29:503–541
- del Giorgio PA, Cole JJ (2000) Bacterial energetics and growth efficiency. In: Kirchman DL (ed) *Microbial ecology of the oceans*. Wiley-Liss, New York, p 289–325
- del Giorgio PA, Gasol JM, Vaqué D, Mura P, Agustí S, Duarte CM (1996) Bacterioplankton community structure: protists control net production and the proportion of active bacteria in a coastal marine community. *Limnol Oceanogr* 41:1169–1179
- del Giorgio PA, Cole JJ, Cimberis A (1997) Respiration rates of bacteria exceed phytoplankton in unproductive aquatic systems. *Nature* 385:148–151
- DeLong EF, Preston CM, Mincer T, Rich V and others (2006) Community genomics among stratified microbial assemblages in the ocean's interior. *Science* 311:496–503
- Ducklow HW (1993) Bacterioplankton distribution and production in the northwestern Indian Ocean and Gulf of Oman, September 1986. *Deep-Sea Res* 11:753–771
- Duffy JE, Cardinale BJ, France KE, McIntyre PB, Thébault E, Loreau M (2007) The functional role of biodiversity in ecosystems: incorporating trophic complexity. *Ecol Lett* 10:522–538
- DuRand MD, Olson RJ, Chisholm SW (2001) Phytoplankton population dynamics at the Bermuda Atlantic Time-series station in the Sargasso Sea. *Deep-Sea Res II* 48:1983–2003
- Fenchel T (1982) Ecology of heterotrophic microflagellates. IV. Quantitative occurrence and importance as bacterial consumers. *Mar Ecol Prog Ser* 9:35–42
- Fenchel T (1984) Suspended marine bacteria as a food source. In: Fasham MJR (ed) *Flows of energy and materials in marine ecosystems. Theory and practice*. Pergamon Press, New York and London, p 301–315
- Fenchel T (1986) The ecology of heterotrophic microflagellates. *Adv Microb Ecol* 9:57–97
- Francis CA, Beman JM, Kuypers MMM (2007) New processes and players in the nitrogen cycle: the microbial ecology of anaerobic and archaeal ammonia oxidation. *ISME J* 1: 19–27
- Frank KT, Petrie B, Shackell NL (2007) The ups and downs of trophic control in continental shelf ecosystems. *Trends Ecol Evol* 22:236–242
- Frigaard NU, Martinez A, Mincer TJ, DeLong EF (2006) Proteorhodopsin lateral gene transfer between marine planktonic Bacteria and Archaea. *Nature* 439:847–850
- Fuhrman JA, Azam F (1982) Thymidine incorporation as a measure of heterotrophic bacterioplankton production in marine surface waters: evaluation and field results. *Mar Biol* 66:109–120
- Fuhrman JA, Bell TM (1985) Biological considerations in the measurement of dissolved free amino acids in seawater and implications for chemical and microbiological studies. *Mar Ecol Prog Ser* 25:13–21
- Fuhrman JA, Noble RT (1995) Viruses and protists cause similar bacterial mortality in coastal seawater. *Limnol Oceanogr* 40:1236–1242
- Fuhrman JA, Steele JA (2008) Community structure of marine bacterioplankton: patterns, networks, and relationships to function. *Aquat Microb Ecol* 53:69–81
- Fuhrman JA, Schwalbach MS, Stingl U (2008) Proteorhodopsins: an array of physiological roles? *Nat Rev Microbiol* 6:488–494
- Fukuda R, Sohrin Y, Saotome N, Fukuda H, Nagata T, Koike I (2000) East-west gradient in ectoenzyme activities in the subarctic Pacific: Possible regulation by zinc. *Limnol Oceanogr* 45:930–939
- Gasol JM (1994) A framework for the assessment of top-down vs. bottom-up control of heterotrophic nanoflagellate abundance. *Mar Ecol Prog Ser* 113:291–300
- Giovannoni SJ, Bibbs L, Cho JC, Stapels MD and others (2005) Proteorhodopsin in the ubiquitous marine bacterium SAR11. *Nature* 438:82–85
- Goldman JC, Caron DA, Dennett MR (1987) Regulation of gross growth efficiency and ammonium regeneration in bacteria by substrate C:N ratio. *Limnol Oceanogr* 32: 1239–1252
- Herndl GJ, Brügger A, Hager S, Kaiser E, Obernosterer I, Reitner B, Slezak D (1997) Role of ultraviolet-B radiation on bacterioplankton and the availability of dissolved organic matter. *Plant Ecol* 128:43–51
- Herndl GJ, Reinthaler T, Teira E, van Aken H, Veth C, Pern-

- thaler A, Pernthaler J (2005) Contribution of *Archaea* to total prokaryotic production in the deep Atlantic Ocean. *Appl Environ Microbiol* 71:2303–2309
- Hewson I, Fuhrman JA (2007) Covariation of viral parameters with bacterial assemblage richness and diversity in the water column and sediments. *Deep-Sea Res I* 54:811–830
- Hewson I, Steele JA, Capone DG, Fuhrman JA (2006) Remarkable heterogeneity in meso- and bathypelagic bacterioplankton assemblage composition. *Limnol Oceanogr* 51:1274–1283
- Hoppe HG, Ullrich S (1999) Profiles of ectoenzymes in the Indian Ocean: phenomena of phosphatase activity in the mesopelagic zone. *Aquat Microb Ecol* 19:139–148
- Hoppe HG, Arnosti C, Herndl GJ (2002) Ecological significance of bacterial enzymes in the marine environment. In: Burns RG, Dick RP (eds) *Enzymes in the environment: activity, ecology, and applications*. Marcel Dekker, New York, p 73–108
- Ingalls AE, Shah SR, Hansman RL, Aluwihare LI, Santos GM, Druffel ERM, Pearson A (2006) Quantifying archaeal community autotrophy in the mesopelagic ocean using natural radiocarbon. *Proc Natl Acad Sci USA* 103:6442–6447
- Kaiser K, Benner R (2008) Major bacterial contribution to the ocean reservoir of detrital organic carbon and nitrogen. *Limnol Oceanogr* 53:99–112
- Kaiser E, Herndl GJ (1997) Rapid recovery of marine bacterioplankton activity after inhibition by UV radiation in coastal waters. *Appl Environ Microbiol* 63:4026–4031
- Karentz D, Cleaver JE, Mitchell DL (1991) Cell survival characteristics and molecular responses of Antarctic phytoplankton to ultraviolet-B radiation. *J Phycol* 27:326–341
- Karl DM (2007) Microbial oceanography: paradigms, processes and promise. *Nat Rev Microbiol* 5:759–769
- Karner MB, DeLong EF, Karl DM (2001) Archaeal dominance in the mesopelagic zone of the Pacific Ocean. *Nature* 409:507–510
- Kirchman DL (1994) The uptake of inorganic nutrients by heterotrophic bacteria. *Microb Ecol* 28:255–271
- Kirchman DL, Elifantz H, Dittel AI, Malmstrom RR, Cottrell MT (2007) Standig stocks and activity of *Archaea* and *Bacteria* in the western Arctic Ocean. *Limnol Oceanogr* 52:495–507
- Könneke M, Bernhard AE, de la Torre JR, Walker CB, Waterbury JB, Stahl DA (2005) Isolation of an autotrophic ammonia-oxidizing marine archaeon. *Nature* 437:543–546
- Kuipers B, van Noort GJ, Vosjan JH, Herndl GJ (2000) Diel periodicity of bacterioplankton in the euphotic zone of the subtropical Atlantic Ocean. *Mar Ecol Prog Ser* 201:13–25
- Lauro FM, Bartlett DH (2007) Prokaryotic lifestyles in deep sea habitats. *Extremophiles* 12:15–25
- Lauro FM, Chastain RA, Blankenship LE, Yayanos AA, Bartlett DH (2006) The unique 16S rRNA genes of piezophiles reflect both phylogeny and adaptation. *Appl Environ Microbiol* 73:838–845
- Lenz J, Morales A, Gunkel J (1993) Mesozooplankton standing stock during the North Atlantic spring bloom study in 1989 and its potential grazing pressure on phytoplankton: a comparison between low, medium and high latitudes. *Deep-Sea Res II* 40:559–572
- Lignell R (1990) Excretion of organic carbon by phytoplankton: its relation to algal biomass, primary productivity and bacterial secondary productivity in the Baltic Sea. *Mar Ecol Prog Ser* 68:85–99
- Lopez-Lopez A, Bartual SG, Stal L, Onyshenko O, Rodriguez-Valera F (2005) Genetic analysis of housekeeping genes reveals a deep-sea ecotype of *Alteromonas macleodii* in the Mediterranean Sea. *Environ Microbiol* 7:649–659
- Marañón E (2005) Phytoplankton growth rates in the Atlantic subtropical gyre. *Limnol Oceanogr* 50:299–310
- Martin-Cuadrado AB, Lopez-Garcia R, Alba JC, Moreira D and others (2007) Metagenomics of the deep Mediterranean, a warm bathypelagic habitat. *PLoS One* 2:e914
- Moeseneder MM, Winter C, Arrieta JM, Herndl GJ (2001a) Terminal restriction fragment length polymorphism (T-RFLP) screening of a marine archaeal library to determine the different phylotypes. *J Microbiol Methods* 44:159–172
- Moeseneder MM, Winter C, Herndl GJ (2001b) Horizontal and vertical complexity of attached and free-living bacteria of the eastern Mediterranean Sea, determined by 16S rDNA and 16S rRNA fingerprints. *Limnol Oceanogr* 46:95–107
- Morris RM, Rappé MS, Urbach E, Connon SA, Giovannoni SJ (2004) Prevalence of the *Chloroflexi*-related SAR202 bacterioplankton cluster throughout the mesopelagic zone and deep ocean. *Appl Environ Microbiol* 70:2836–2842
- Mouriño-Carballido B, McGillicuddy DJM Jr (2006) Mesoscale variability in the metabolic balance of the Sargasso Sea. *Limnol Oceanogr* 51:2675–2689
- Nagata T (2000) Production mechanisms of dissolved organic matter. In: Kirchman DL (ed) *Microbial ecology of the oceans*. Wiley-Liss, New York, p 121–152
- Nealson KH, Venter JC (2007) Metagenomics and the global ocean survey: what's in it for us, and why should we care? *ISME J* 1:185–187
- Obernosterer I, Herndl GJ (1995) Phytoplankton extracellular release and bacterial growth: dependence on the inorganic N:P ratio. *Mar Ecol Prog Ser* 116:247–257
- Obernosterer I, Herndl GJ (2000) Differences in the optical and biological reactivity of the humic and non-humic component of marine and terrestrially-derived DOC in two contrasting coastal marine environments. *Limnol Oceanogr* 45:1120–1129
- Obernosterer I, Kraay G, de Ranitz E, Herndl GJ (1999a) Dynamics of low molecular weight carboxylic acids and carbonyl compounds in the Aegean Sea (Eastern Mediterranean) and the turnover of pyruvic acid. *Aquat Microb Ecol* 20:147–156
- Obernosterer I, Reitner B, Herndl GJ (1999b) Contrasting effects of solar radiation on dissolved organic matter and its bioavailability to marine bacterioplankton. *Limnol Oceanogr* 44:1645–1654
- Obernosterer I, Ruardij P, Herndl GJ (2001a) Spatial and diurnal dynamics of dissolved organic matter (DOM) fluorescence and H₂O₂ and the photochemical oxygen demand of surface water DOM across the subtropical Atlantic Ocean. *Limnol Oceanogr* 46:632–643
- Obernosterer I, Sempéré R, Herndl GJ (2001b) Ultraviolet radiation induces a reversal of the bioavailability of DOM to marine bacterioplankton. *Aquat Microb Ecol* 24:61–68
- Pakhomov EA, Perissinotto R (1997) Mesozooplankton community structure and grazing impact in the region of the Subtropical Convergence south of Africa. *J Plankton Res* 19:675–691
- Parada V, Sintés E, van Aken HM, Weinbauer MG, Herndl GJ (2007) Viral abundance, decay, and diversity in the meso- and bathypelagic waters of the North Atlantic. *Appl Environ Microbiol* 73:4429–4438
- Pausz C, Herndl GJ (1999) Role of ultraviolet radiation on phytoplankton extracellular release and its subsequent utilization by marine bacterioplankton. *Aquat Microb Ecol* 18:85–93
- Pausz C, Herndl GJ (2002) Role of nitrogen versus phosphorus availability on the effect of UV radiation on bacterio-

- plankton and their recovery from previous UV stress. *Aquat Microb Ecol* 29:89–95
- Pérez MT, Pausz C, Herndl GJ (2003) Major shift in bacterioplankton utilization of enantiomeric amino acids between surface waters and the ocean's interior. *Limnol Oceanogr* 48:755–763
- Pomeroy LR (1974) The ocean's food web, a changing paradigm. *Bioscience* 24:499–504
- Reinthal T, Herndl GJ (2005) Seasonal dynamics of bacterial growth efficiencies in relation to phytoplankton in the southern North Sea. *Aquat Microb Ecol* 39:7–16
- Reinthal T, van Aken H, Veth C, Williams PJLeb and others (2006) Prokaryotic respiration and production in the meso- and bathypelagic realm of the eastern and western North Atlantic basin. *Limnol Oceanogr* 51:1262–1273
- Sabehi G, Loy A, Jung KH, Partha R and others (2005) New insights into metabolic properties of marine bacteria encoding proteorhodopsin. *PLoS Biol* 3:e273
- Sano E, Carlson S, Wegley L, Rohwer F (2004) Movement of viruses between biomes. *Appl Environ Microbiol* 70:5842–5846
- Schwalbach MS, Brown M, Fuhrman JA (2005) Impact of light on marine bacterioplankton community structure. *Aquat Microb Ecol* 39:235–245
- Sherr BF, Sherr EB, Andrew TL, Fallon RD, Newell SY (1986) Trophic interactions between heterotrophic Protozoa and bacterioplankton in estuarine water analyzed with metabolic inhibitors. *Mar Ecol Prog Ser* 32:169–179
- Sherr EB, Sherr BF (1994) Bacterivory and herbivory: key roles of phagotrophic protists in pelagic food webs. *Microb Ecol* 28:223–235
- Sogin ML, Morrison HG, Huber JA, Welch DM and others (2006) Microbial diversity in the deep sea and the underexplored 'rare biosphere'. *Proc Natl Acad Sci USA* 103:12115–12120
- Stoderegger K, Herndl GJ (1998) Production and release of bacterial capsular material and its subsequent utilization by marine bacterioplankton. *Limnol Oceanogr* 43:877–884
- Stoderegger KE, Herndl GJ (1999) Production of exopolymer particles by marine bacterioplankton under contrasting turbulence conditions. *Mar Ecol Prog Ser* 189:9–16
- Tanaka T, Rassoulzadegan F (2004) Vertical and seasonal variations of bacterial abundance and production in the mesopelagic layer of the NW Mediterranean Sea: bottom-up and top-down controls. *Deep-Sea Res I* 51:531–544
- Teira E, Lebaron P, van Aken H, Herndl GJ (2006) Distribution and activity of Bacteria and Archaea in the deep water masses of the North Atlantic. *Limnol Oceanogr* 51:2131–2144
- Thingstad TF (1987) Utilization of N, P, and organic C by heterotrophic bacteria. I. Outline of a chemostat theory with a consistent concept of 'maintenance' metabolism. *Mar Ecol Prog Ser* 35:99–109
- Thingstad TF (2000) Control of bacterial growth in idealized food webs. In: Kirchman DL (ed) *Microbial ecology of the oceans*. Wiley-Liss, New York, p 229–260
- Tortell PD, Maldonado MT, Price NM (1996) The role of heterotrophic bacteria in iron-limited ocean ecosystems. *Nature* 383:330–332
- Varela MM, van Aken HM, Herndl GJ (2008) Abundance and activity of *Chloroflexi*-type SAR202 bacterioplankton in the meso- and bathypelagic waters of the (sub)tropical Atlantic. *Environ Microbiol* 10:1903–1911
- Vezi A, Campanaro S, D'Angelo M, Simonato F and others (2005) Life at depth: *Photobacterium profundum* genome sequence and expression analysis. *Science* 307:1459–1461
- Weinbauer MG (2004) Ecology of prokaryotic viruses. *FEMS Microbiol Rev* 28:127–181
- Weinbauer M, Brettar I, Höfle MG (2003) Lysogeny and virus-induced mortality of bacterioplankton in surface, deep, and anoxic marine waters. *Limnol Oceanogr* 48:1457–1465
- Whitman WB, Coleman DC, Wiebe WJ (1998) Prokaryotes: the unseen majority. *Proc Natl Acad Sci USA* 95:6578–6583
- Winter C, Moeseneder MM, Herndl GJ (2001) Impact of UV radiation on bacterioplankton community composition. *Appl Environ Microbiol* 67:665–672
- Winter C, Herndl GJ, Weinbauer MG (2004a) Diel cycles in viral infection of bacterioplankton in the North Sea. *Aquat Microb Ecol* 35:207–216
- Winter C, Smit A, Herndl GJ, Weinbauer MG (2004b) Impact of virioplankton on archaeal and bacterial community richness as assessed in seawater batch cultures. *Appl Environ Microbiol* 70:804–813
- Worden AZ, Chisholm SW, Binder BJ (2000) In situ hybridization of *Prochlorococcus* and *Synechococcus* (marine cyanobacteria) spp. with rRNA-targeted peptide nucleic acid probes. *Appl Environ Microbiol* 66:284–289
- Wuchter C, Herfort L, Coolen MJL, Abbas B and others (2006) Archaeal nitrification in the ocean. *Proc Natl Acad Sci USA* 103:12317–12322
- Zubkov M, Tarran GA (2005) Amino acid uptake of *Prochlorococcus* spp. in surface waters across the South Atlantic Subtropical Front. *Aquat Microb Ecol* 40:241–249

Submitted: March 13, 2008; Accepted: July 9, 2008

Proofs received from author(s): July 25, 2008