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Latitudinal patterns in the abundance of major marine bacterioplankton groups

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ABSTRACT: The present study describes the abundance of major marine bacterioplankton groups and 2 bacterial genera (*Pseudoalteromonas* and *Vibrio*) in surface seawater at 24 stations around the world. Catalyzed reporter deposition–fluorescence *in situ* hybridization showed that *Alphaproteobacteria* (average relative abundance 37%, average absolute abundance 3.7×10^5 cells ml^{-1}) including SAR11 [30% / (3×10^5)], *Gammaproteobacteria* [14% / (1.2×10^5)] and *Bacteroidetes* [12% / (1.3×10^5)] globally dominated the bacterioplankton. The SAR86 clade [4.6% / (4.1×10^4)] and *Actinobacteria* [4.5% / (4×10^4)] were detected ubiquitously, whereas *Archaea* were scarce [0.6% / (4.2×10^3)]. The *Roseobacter* clade [averaging 3.8% / (3.5×10^4)], *Pseudoalteromonas* [2.6% / (2.1×10^4)] and *Vibrio* [1.5% / (1.3×10^4)] showed cosmopolitan occurrence. Principal component analysis revealed a latitudinal pattern in bacterial abundances by clustering samples according to lower and higher latitudes. This was related to significantly different relative abundances of *Bacteroidetes* (peaking at higher latitudes) and of unclassified *Bacteria* and *Vibrio* (both peaking at lower latitudes) between warmer and colder oceans. Relative abundances of *Alphaproteobacteria* (peaking at subtropical) and *Gammaproteobacteria* (polar stations) varied between major oceanic biomes, as did absolute abundances of *Roseobacter* (peaking at temperate and polar stations). For almost all groups, absolute abundances were positively correlated with nutrient concentrations in warmer oceans and negatively correlated with oxygen saturation in colder oceans. On a global scale, *Roseobacter* and SAR86 were correlated with chlorophyll *a*. Linkages of environmental parameters with relative abundances were more complex, with e.g. *Bacteroidetes* being associated with chlorophyll *a*. The finding of differing communities in warmer and colder oceans underlined the presence of biogeographical patterns among marine bacteria and the influence of environmental parameters on bacterial distribution.

KEY WORDS: Marine bacterioplankton · Global quantification · Latitudinal pattern · Biogeography · CARD-FISH · PCA

INTRODUCTION

The diversity, activity and ecology of marine microbes — the main form of biomass in the oceans — have become key research subjects over the previous years, greatly expanding our knowledge of the structure and function of marine microbiota (Giovannoni & Stingl 2005). Given the role of marine bacteria in global nutrient turnover, biogeochemical processes and climate events (Arrigo 2005), the study of microbial distribution and biogeography has received increasing attention (Martiny et al. 2006). Still, there is only a basic understanding of marine bacterial community structure on a global scale, such as to whether 'everything is everywhere, but the environment selects' (Baas-Becking 1934) or if geographically separated regions harbour distinct communities. This discussion also addresses the relation of environmental factors to spatial and temporal patterns among bacteria (Dolan 2005, Martiny et al. 2006, Van der Gucht et al. 2007).

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Characterization of marine bacterial communities on larger geographical scales has been done by shotgun sequencing (Rusch et al. 2007), polymerase chain reaction (PCR)-based techniques (Baldwin et al. 2005, Pommier et al. 2007, Taniguchi & Hamasaki 2008) and catalyzed reporter deposition–fluorescence *in situ* hybridization (CARD-FISH) (Schattenhofer et al. 2009). These studies have indicated that the composition of bacterioplankton differs between oceanic regions, probably related to oceanographic factors such as water temperature (Baldwin et al. 2005, Fuhrman et al. 2008), nutrient availability (Abell & Bowman 2005), or water masses (Teira et al. 2006, Galand et al. 2010). The analysis of a global sample set showed marked variation in bacterial community structure on the 16S rRNA sequence level, with a high degree of endemism and few cosmopolitan sequences (Pommier et al. 2007). A latitudinal gradient in species richness, comparable to observations in the animal and plant kingdoms, has been shown in this context (Pommier et al. 2007, Fuhrman et al. 2008). Terminal–restriction fragment length polymorphism (T-RFLP) demonstrated distinct microbial clusters relating to Arctic, Antarctic, temperate and tropical regions, with mid-latitudinal and equatorial communities being more similar in composition to each other than to cold water communities (Baldwin et al. 2005). Quantitative analyses showed that across an Atlantic Ocean transect, SAR11 was more abundant in the northern Atlantic Ocean than in the southern Atlantic gyre, the biomass of *Prochlorococcus* peaked in the tropical Atlantic Ocean, and *Bacteroidetes* and *Gammaproteobacteria* bloomed in nutrient-rich temperate waters (Schattenhofer et al. 2009). Furthermore, prokaryotic assemblage structure was shown to exhibit strong variability along estuarine gradients (Kirchman et al. 2005), coast–ocean transitions (Baltar et al. 2007) and ocean fronts (Pinhassi et al. 2003).

The present study adds to the understanding of marine bacterial biogeography by analyzing bacterioplankton community structure and environmental parameters along the route of the worldwide Galathea 3 expedition. The Earth's circumnavigation included both a global survey of culturable bacteria with antibacterial activity (Gram et al. 2010) and a cultivation-independent investigation of bacterioplankton by CARD-FISH. This enabled the direct quantification of domains (*Bacteria* and *Archaea*), higher phylogenetic groups (*Alpha-* and *Gammaproteobacteria*, *Bacteroidetes*, *Actinobacteria*), important bacterial clades (SAR11, SAR86, *Roseobacter*) and 2 individual genera (*Pseudoalteromonas* and *Vibrio*). *Roseobacter*, *Pseudoalteromonas* and *Vibrio* were selected, since >90% of the antagonistic strains isolated during the culture-based survey (Gram et al. 2010) were affiliated with one of the 3 groups. The purpose of the present study was to investigate potential patterns in their *in situ* distribution. While species cluster distribution of the *Roseobacter* clade has been studied (Selje et al. 2004), the biogeography of *Pseudoalteromonas* (Skovhus et al. 2007) and *Vibrio* (Thompson et al. 2006) in pelagic marine ecosystems is poorly documented.

We analyzed CARD-FISH and environmental data by principal component analysis (PCA), a statistical tool to identify patterns, associations between factors and underlying causative links within a complex dataset (Martens & Martens 2001). PCA has been used for bacterial community analyses (Sekiguchi et al. 2002, Teira et al. 2008) and served here to investigate global patterns in the bacterioplankton community structure and their relation to environmental parameters. This contributes to the understanding of marine bacterial biogeography and the factors that influence microbial distribution on a global scale.

MATERIALS AND METHODS

Sampling procedures. At 24 stations along the route of Galathea 3 (www.galathea3.dk/uk), surface seawater was sampled using Niskin bottles on an SBE32 rosette (Seabird) connected with a conductivity-temperature-depth (CTD) profiler (MacArtney). Sampling sites covered different oceanic regions, including coastal and pelagic waters (Fig. 1, Table S1 in the supplement at www.int-res.com/articles/suppl/a061p179_supp.pdf). Using a 5 × 100 ml filtration manifold (DHI LAB) 5 samples were prepared per station. Each 50 ml seawater sample was filtered through 5 µm polycarbonate filters (diameter: 25 mm) to remove particle-associated bacteria. Planktonic cells were collected from the 5 µm filtered water on 0.2 µm polycarbonate filters (diameter: 25 mm) and fixed with 2% paraformaldehyde for 1 h in the dark. Filters were washed with 1× phosphate-buffered saline (PBS) and sterile Milli-Q water for 1 min each, air dried and stored at −80°C until further processing. A range of physicochemical environmental parameters were measured by standard methods at each station at which bacterioplankton was sampled. These included (1) oceanographic data (temperature, salinity, density, *in vivo* fluorescence, photosynthetically active radiation); (2) oxygen concentration and saturation; (3) concentrations of inorganic nutrients (total inorganic nitrogen [N] and phosphorus [P], nitrite [NO_2^-], nitrate [NO_3^-], ammonium [NH_4^+], phosphate [PO_4^-], silica [SiO_2]); and (4) the concentration of chlorophyll *a* (Table S1).

Selection of oligonucleotide FISH probes. Bacterioplankton communities were characterized using a range of horseradish peroxidase-labelled FISH probes (Table S2 in the supplement at www.int-res.com/

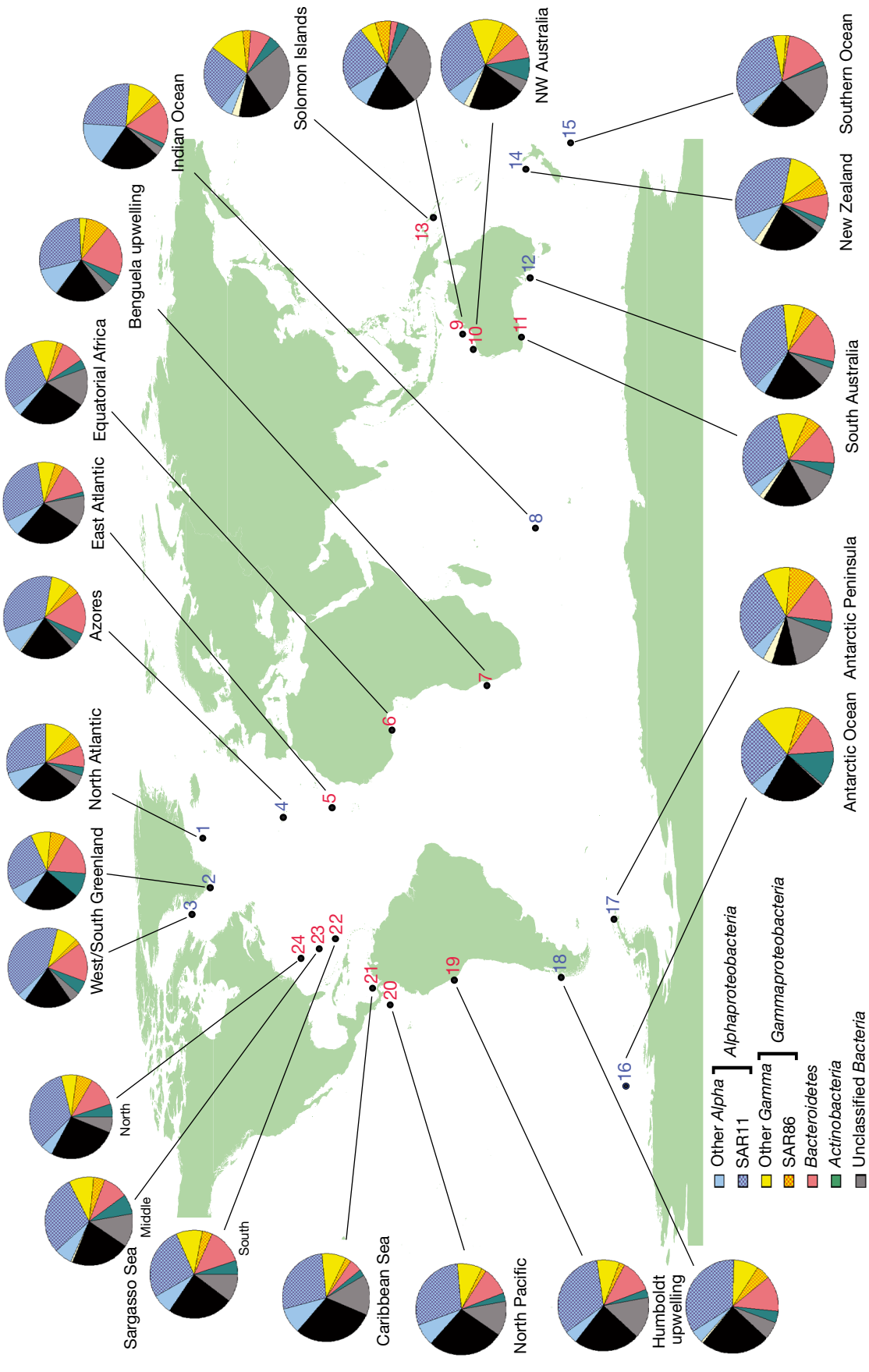

Fig. 1. Relative abundances of higher phylogenetic bacterioplankton groups (in %DAPI) at 24 stations worldwide. Blue numbers designate stations at higher (>35°), red numbers designate stations at lower (0 to 35°) latitudes. Other *Alpha*: cells detected by ALF968, but not by SAR11-441; Other *Gamma*: cells detected by GAM42a, but not by SAR86-1249; Unclassified *Bacteria*: cells detected by EUB338, but not by ALF968, GAM42a, CF319a, or HGC69a; Other (unclassified) cells: DAPI-stained cells not detected by EUB338. All EUB338 fractions refer to the average detectability from lysozyme and combined lysozyme/achromopeptidase permeabilizations

articles/suppl/a061p179_supp.pdf) purchased from biomers. net. All clade- and group-specific probes (SAR11-441, SAR86-1249, ROS536, PSU730, GV) were checked for specificity and coverage of their target groups against the SILVA database, release 96 (Pruesse et al. 2007), using the ARB software package (Ludwig et al. 2004).

CARD-FISH. Cells on filters were permeabilized by different enzyme treatments depending on the subsequent hybridization. For hybridizations targeting *Bacteria*, *Proteobacteria* and *Bacteroidetes*, cells were permeabilized with lysozyme (10 mg ml^{-1} in 1× TE buffer [0.01 M EDTA, 0.1 M Tris-HCl, pH 8.0]) for 60 min at 37°C. For hybridizations targeting *Bacteria* and *Actinobacteria*, cells were permeabilized for 30 min with achromopeptidase (60 U ml^{-1} in 0.01 M NaCl, 0.01 M Tris-HCl, pH 8.0), followed by 30 min with lysozyme (1 mg ml^{-1} in 1× TE buffer) at 37°C (Sekar et al. 2003). For hybridizations targeting *Archaea*, cells were permeabilized with Proteinase K (2 µg ml^{-1} in 1× TE buffer) for 60 min at 37°C (Teira et al. 2004). Filters were stored at –20°C until further processing. CARD-FISH was carried out according to Pernthaler et al. (2004) using FITC-labelled tyramides for signal amplification.

Epifluorescence microscopy. Stained filter sections were inspected on an Axiovert 200M inverse fluorescence microscope (Carl Zeiss) equipped with 63× and 100× objective lenses and Filter Sets 02 (Cat. No. 488002-0000-000) for DAPI and 10 (Cat. No. 488010-0000-000; both Carl Zeiss) for FITC. Per hybridization, from 600 to 1000 DAPI-stained cells were counted in ≥10 microscopic fields that were randomly selected across the filter section. Relative fractions of bacterial groups were corrected by subtraction of negative control counts with probe NON338. To validate reproducibility of hybridizations and accuracy of counts, a selection of samples from widely separated stations was again hybridized with probes targeting higher phylogenetic groups. Deviations in detected relative fractions were ≤3%, which was considered acceptable.

Data analysis. PCA was performed to reduce the complexity of multivariate data (prokaryotic abundances and physicochemical environmental parameters) in order to identify variables accounting for most of the variability in the original data. PCA was performed for each of the following datasets: (1) relative prokaryotic abundances, (2) relative abundances and environmental parameters, (3) absolute abundances and (4) absolute abundances and environmental parameters. Input data were the abundances of *Actinobacteria*; *Bacteroidetes*; SAR11, *Roseobacter*, other *Alphaproteobacteria* (difference between the sum of SAR11 and *Roseobacter* to the total abundance of *Alphaproteobacteria*); SAR86, *Pseudoalteromonas*, *Vibrio*, other *Gammaproteobacteria* (difference between the sum of SAR86, *Pseudoalteromonas* and *Vibrio* to the total abundance of *Gammaproteobacteria*); unclassified *Bacteria* (difference between the sum of *Alphaproteobacteria*, *Gammaproteobacteria*, *Bacteroidetes* and *Actinobacteria* to total bacterial abundance as detected by EUB338-I to -III); and unclassified cells (DAPI-stained cells not detected by probes EUB338-I to -III, EURY806, CREN537/CREN554). In addition, 2-tailed *t*-tests comparing relative and absolute abundances between latitudes and biomes were performed. Abundances were sorted by higher (combining stations from the tropical and subtropical climate zones, 0 to 35°) and lower latitudes (temperate and polar zones, >35°), as well as their association with the 4 major oceanic biomes (Longhurst 1998). These are designated the Polar, Coastal, Westerlies and Trades biomes and categorized by oceanographic characteristics, including seasonal cycles of nutrient availability and illumination. Furthermore, Pearson product moment correlation coefficients, *r*, between prokaryotic abundances of bacterial groups, and between prokaryotic abundances and physicochemical parameters, were calculated (Tables S3 to S5 in the supplement at www.int-res.com/articles/suppl/a061p179_supp.pdf). All reported correlations were statistically significant ($p < 0.05$).

RESULTS

Environmental parameters

Highest concentrations of oxygen (>6.5 ml l^{-1}), total inorganic nitrogen (>35 µM l^{-1}) and phosphorus (>2 µM l^{-1}), nitrate (>20 µM l^{-1}), nitrite (>0.3 µM l^{-1}), ammonium (>0.28 µM l^{-1}) and phosphate (>1 µM l^{-1}) were recorded in temperate and cold waters of the Southern Ocean (Table S1). The concentration of silica peaked in Antarctic waters (up to 76 µM l^{-1}). Elevated nutrient levels were also recorded in the northern Atlantic and in the Benguela (Namibian) and Humboldt (Peruvian) upwelling systems. Temperature ranged from –0.1 (Antarctic Peninsula) to 30.1°C (Solomon Islands), and its negative correlation with nutrients, oxygen, as well as chlorophyll *a* and *in vivo* fluorescence (indicators of phytoplankton biomass), confirmed colder waters as being nutrient richer, more aerated and more productive (*r* between –0.42 and –0.86). The chlorophyll *a* concentration peaked in the pelagic Indian Ocean (1.6 µg l^{-1}) and the Benguela upwelling system (1.2 µg l^{-1}). Solar radiation as a mean of photosynthetically active radiation (PAR) and surface PAR (SPAR) was highest in several subtropical and tropical locations (>630 and >2500 µM photons m^{-2} s^{-2}, respectively).

Abundance of major bacterioplankton groups

Relative fractions of *Bacteria* as detected by probe mix EUB338 ranged from 65% (Stn 21; Caribbean Sea) to 88% (Stn 17; Antarctic Peninsula) of DAPI-stained cells upon cell permeabilization with lysozyme, with variations in absolute numbers between 1×10^5 and 3×10^6 cells ml^{-1} (Table 1). For 15 out of the 24 stations, the detectability increased between 3 and 14% (corresponding to 3.3×10^3 and 5.4×10^5 cells ml^{-1}) upon cell permeabilization with both achromopeptidase and lysozyme. *Archaea* were only detected at 11 out of the 24 stations, most of them in the southern hemisphere, with relative fractions >1% occurring at only 5 locations.

Alphaproteobacteria, *Gammaproteobacteria* and *Bacteroidetes* constituted the major fraction of surface bacterioplankton around the globe (Fig. 1, Table 1). Their combined relative abundance accounted for up to 72% (globally averaged 63%) of DAPI-stained cells, and up to 93% (averaged 81%) of cells detected by EUB338 (average detectability of lysozyme and combined lysozyme/achromopeptidase permeabilization). At 2 out of 5 polar stations (South Greenland and Antarctic Ocean) *Actinobacteria* represented a considerable fraction with 10 and 12%, respectively. Their lowest relative abundances (approximately 1.5%) occurred at pelagic stations in the Atlantic, Indian and Southern Oceans, resulting in an average relative fraction of 4.5%.

Alphaproteobacteria were the most abundant group across all samples, with relative abundances between 29% (Stn 13; Solomon Islands) and 44% (Stn 3; West Greenland) and a global average of 37%. Absolute alphaproteobacterial cell numbers varied between 3.9×10^4 and 1.8×10^6 ml^{-1}, with a global average of 3.7×10^5 ml^{-1}. The SAR11 clade, a subclass of *Alphaproteobacteria*, constituted between 24 and 41% (average 30%) and therefore represented the majority of surface water *Alphaproteobacteria*. The relative abundance of *Gammaproteobacteria* was highest (19 to 20%) at Stns 10, 16 and 17 (NW Australia, Antarctica) and lowest (6%) at Stn 15 (Southern Ocean), globally averaging 14%. The SAR86 clade, a subclass of *Gammaproteobacteria*, constituted between 1% (Stn 15; Southern Ocean) and 9% (Stns 7 and 17; Benguela upwelling and Antarctic Peninsula), with a global average of 4.6%. *Bacteroidetes* outnumbered *Gammaproteobacteria* at several stations, but had a lower average relative abundance (12%) due to their more patchy distribution, which varied between 3% (Stn 9; NW Australia) and 20% (Stn 7; Benguela upwelling). The absolute abundance of *Bacteroidetes*, however, was, on a global average, slightly higher (1.3×10^5 cells ml^{-1}) than that of *Gammaproteobacteria* (1.2×10^5 cells ml^{-1}). This highlighted that absolute cell numbers did not always reflect relative abundances. While, for instance, the relative *Bacteroidetes* abundance at Stns 3 and 4 varied by only 0.7%, actual cell numbers were 16-fold different (6.4×10^5 compared to 3.9×10^4 cells ml^{-1}).

Pseudoalteromonas, *Vibrio* and the *Roseobacter* clade were detected ubiquitously (Table 1). The *Roseobacter* clade (*Alphaproteobacteria*) was most abundant in the Caribbean Sea (Stn 21; 8.2%) and least at equatorial Africa (Stn 6; 1.5%), globally averaging 3.8% corresponding to 3.5×10^4 cells ml^{-1}. *Pseudoalteromonas* (*Gammaproteobacteria*) was most abundant at the Antarctic Peninsula (Stn 17; 6%) and least at South Australia (Stns 11 and 12; 0.5%), globally averaging 2.6% (2.1×10^4 cells ml^{-1}). The abundance of *Vibrio* (*Gammaproteobacteria*) peaked at equatorial Africa (Stn 6; 3.2%), while being lowest in the Azores and Caribbean Sea (Stns 4 and 21; 0.3%), globally averaging 1.5% (1.3×10^4 cells ml^{-1}).

Biogeographical patterns of bacterial distribution

PCA comparing relative bacterial abundances between all 24 stations showed 2 clusters, while Stns 9 (NW Australia), 13 (Solomon Islands) and 17 (Antarctic Peninsula) were positioned separately (Fig. 2). The 2 clusters corresponded to the Earth's colder and warmer climate zones comprising stations from higher (>35°; temperate and polar zone) and lower latitudes (0 to 35°; tropical and subtropical zone), respectively. Four stations (Stns 7, 10, 15 and 24) did not fit the pattern and were positioned in the opposite latitude cluster. Stn 7 is located in the Benguela upwelling system, the colder, nutrient-rich waters of which probably yielded a community structure similar to colder oceans despite the subtropical location. The exclusion of Stn 10 (NW Australia) from the pattern cannot be related to an obvious factor, but was potentially due to unique oceanographic characteristics that also resulted in the entirely separate positioning of its 'sister station' Stn 9. Stns 15 (Southern Ocean) and 24 (northern Sargasso Sea) are located in regions where colder and warmer climates meet, and the opposite positioning probably reflected the fact that those communities were sampled at a transition between colder and warmer waters. PCA with absolute abundances yielded a similar latitudinal grouping of stations, albeit being less distinct as with relative values (data not shown).

PCA demonstrated that the relative abundances of *Bacteroidetes* and unclassified *Bacteria* (cells detected by probe mix EUB338, but not by ALF968, GAM42a, CF319a, or HGC69a) accounted most for the latitudinal pattern. This was consistent with significantly different relative fractions of *Bacteroidetes* (peaking at higher lat-

Table 1. Total bacterial numbers and absolute abundances (cells ml^{-1}) of bacterioplankton groups at 24 stations worldwide from the 4 oceanic biomes (P: Polar; C: Coastal; W: Westerlies; T: Trades) sorted according to higher (>35°) and lower (0 to 35°) latitudes. EUB: *Bacteria* (L: lysozyme permeabilization, L + A: combined lysozyme/achromopeptidase permeabilization); ARCH: *Archaea*; ALF: *Alphaproteobacteria*; ROS: *Roseobacter* clade; GAM: *Gammaproteobacteria*; PSA: *Pseudoalteromonas*; VIB: *Vibrio*; BAC: *Bacteroidetes*; ACT: *Actinobacteria*; Unclassified EUB: cells detected by EUB338 (average detectability from L and L + A permeabilizations), but not by ALF968, GAM42a, CF319a, or HGC69a; Other: unclassified cells, not detected by EUB338 (average detectability from L and L + A permeabilizations). na: not applicable (sum of ALF968, GAM42a, CF319a and HGC69a counts was higher than the EUB338 count); nd: not detected

Stn	Location	Biome	Total count	EUB L	EUB L + A	ARCH	ALF	SAR11	ROS	GAM	SAR86	PSA	VIB	BAC	ACT	Unclassified EUB	Other
Higher latitudes (>35°)																	
1	North Atlantic	P	1.6×10^6	1.1×10^6	1.2×10^6	nd	6×10^5	4.7×10^5	5.7×10^4	2.8×10^5	1×10^5	5.8×10^4	1.6×10^4	1.5×10^5	5.8×10^4	7.8×10^4	4.3×10^5
2	S Greenland	P	7.2×10^5	5×10^5	6×10^5	nd	2.5×10^5	1.9×10^5	1.9×10^4	1.1×10^5	4.7×10^4	1.7×10^4	4.3×10^3	1.3×10^5	7.3×10^4	na	1.7×10^5
3	W Greenland	P	4×10^6	3×10^6	3.5×10^6	nd	1.8×10^6	1.6×10^6	7.7×10^4	4.3×10^5	8.3×10^4	6.1×10^4	3.1×10^4	6.4×10^5	2.2×10^4	1.6×10^5	7.8×10^5
4	Azores	W	2.3×10^5	1.8×10^5	1.8×10^5	1.3×10^3	9.7×10^4	7.7×10^4	4.7×10^3	2.7×10^4	9×10^3	9.3×10^3	7.9×10^2	3.9×10^4	1.1×10^4	5.4×10^3	4.9×10^4
8	Indian Ocean	W	2.5×10^6	1.8×10^6	2.1×10^6	nd	1×10^6	6.3×10^5	1.5×10^5	3.4×10^5	8.8×10^4	3.9×10^4	4.9×10^4	4.2×10^5	4×10^4	8.3×10^4	5.8×10^5
12	South Australia	C	1.5×10^6	1.2×10^6	1.2×10^6	nd	6×10^5	5.4×10^5	3.9×10^4	1.9×10^5	7.6×10^4	6.9×10^3	1.1×10^4	2.7×10^5	3.2×10^4	1.1×10^5	3.1×10^5
14	New Zealand	W	7.3×10^5	5×10^5	6×10^5	1.8×10^4	3.1×10^5	2.4×10^5	5.1×10^4	1.3×10^5	4.3×10^4	2.4×10^4	1.2×10^4	6.8×10^4	1.9×10^4	1.7×10^4	1.6×10^5
15	Southern Ocean	C	7.1×10^5	5.4×10^5	5.7×10^5	2.1×10^3	2.5×10^5	2.1×10^5	2.7×10^4	4.3×10^4	8.7×10^3	6.8×10^3	3.4×10^3	1.1×10^5	1.3×10^4	1.3×10^5	1.7×10^5
16	Antarctic Ocean	P	1.3×10^5	1×10^5	1.1×10^5	nd	3.9×10^4	3.2×10^4	3.2×10^3	2.7×10^4	6.1×10^3	1.7×10^3	1.3×10^3	1.9×10^4	1.6×10^4	1×10^3	2.8×10^4
17	Ant. Peninsula	P	2.5×10^5	2.2×10^5	2.2×10^5	7.9×10^3	8.4×10^4	7.1×10^4	1.2×10^4	4.8×10^4	2.4×10^4	1.5×10^4	6.1×10^3	4×10^4	9.6×10^3	4×10^4	2.2×10^4
18	Humboldt	C	1.6×10^6	1.1×10^6	1.3×10^6	1.3×10^4	6.3×10^5	5.5×10^5	7.2×10^4	2.2×10^5	8.1×10^4	4.6×10^4	1.9×10^4	2×10^5	6.3×10^4	9.9×10^4	3.8×10^5
Lower latitudes (0 to 35°)																	
5	East Atlantic	T	4.8×10^5	3.3×10^5	5.9×10^4	nd	1.7×10^5	1.4×10^5	9.4×10^3	5.1×10^4	1.7×10^4	9.3×10^3	6.1×10^3	6×10^4	7.6×10^3	5.9×10^4	1.3×10^5
6	Equat. Africa	C	1.4×10^5	1×10^5	2.1×10^4	nd	4.6×10^4	4.1×10^4	2.1×10^3	1.7×10^4	2.9×10^3	4.5×10^3	4.5×10^3	1.4×10^4	5×10^3	2.1×10^4	3.8×10^4
7	Benguela	C	1.5×10^6	1.1×10^6	6×10^4	3.1×10^3	5.9×10^5	4.3×10^5	5.3×10^4	1.7×10^5	1.3×10^5	1.4×10^4	8.2×10^3	3×10^5	7.4×10^4	6×10^4	3×10^5
9	NW Australia	C	8.6×10^5	7×10^5	7×10^5	nd	2.8×10^5	2×10^5	2.1×10^4	1×10^5	5.1×10^4	3×10^4	1.6×10^4	2.2×10^4	3.7×10^4	2.7×10^5	1.6×10^5
10	NW Australia	C	9×10^5	6.4×10^5	7.5×10^5	2.1×10^4	3.3×10^5	2.6×10^5	5×10^4	1.7×10^5	6.3×10^4	4.2×10^4	2.1×10^4	8.2×10^4	7.3×10^4	4.2×10^4	1.9×10^5
11	South Australia	C	5.8×10^5	4×10^5	4.7×10^5	9.5×10^3	2×10^5	1.8×10^5	1.6×10^4	9.3×10^4	2.9×10^4	3.3×10^3	6.2×10^3	8.2×10^4	2.6×10^4	6.5×10^4	1×10^5
13	Solomon Islands	T	7.9×10^5	6.7×10^5	6.7×10^5	2.2×10^4	2.3×10^5	2×10^5	3.1×10^4	1.3×10^5	2.6×10^4	2×10^4	1.9×10^4	6.1×10^4	3.7×10^4	2.1×10^5	9.9×10^4
19	Humboldt	C	2×10^6	1.5×10^6	1.6×10^6	nd	7.4×10^5	6.5×10^5	4.4×10^4	2×10^5	3.7×10^4	4.9×10^4	5.3×10^4	2.4×10^5	5.9×10^4	3×10^5	4.7×10^5
20	North Pacific	T	7.2×10^5	4.8×10^5	5.7×10^5	nd	2.7×10^5	2.1×10^5	2.1×10^4	7.4×10^4	1.1×10^4	1.5×10^4	1.4×10^4	7.3×10^4	2.2×10^4	8.9×10^4	2×10^5
21	Caribbean Sea	T	4.2×10^5	2.7×10^5	3.2×10^5	nd	1.6×10^5	1.2×10^5	3.4×10^4	4.6×10^4	8.5×10^3	6.8×10^3	1.1×10^3	2×10^4	1.1×10^4	6.2×10^4	1.3×10^5
22	S Sargasso Sea	T	4.1×10^5	3.2×10^5	3×10^5	nd	1.4×10^5	1.1×10^5	2.4×10^4	5.4×10^4	1.5×10^4	1.8×10^4	5.1×10^3	5.5×10^4	2×10^4	4.2×10^4	9.9×10^4
23	Mid Sargasso Sea	W	2.6×10^5	2.1×10^5	1.9×10^5	2.3×10^3	9.2×10^4	7.6×10^4	1.3×10^4	3.5×10^4	1.1×10^4	8.8×10^3	6.4×10^3	2.4×10^4	1.9×10^4	3.2×10^4	5.6×10^4
24	N Sargasso Sea	W	2×10^5	1.4×10^5	1.6×10^5	2.3×10^2	7.7×10^4	6.7×10^4	9.1×10^3	2.4×10^4	1.3×10^4	5.6×10^3	4.1×10^3	2.3×10^4	9.9×10^3	1.2×10^4	5.3×10^4

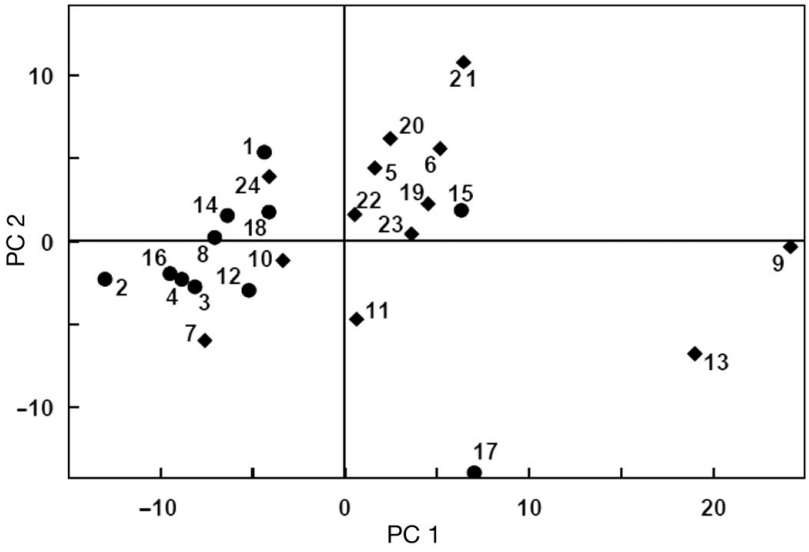

Fig. 2. Principal Component (PC) 2 versus 1 scores comparing relative bacterial abundances between 24 stations worldwide showing 2 clusters comprising samples from higher (●) and lower (◆) latitudes, respectively. The principal components explain 51 and 17%, respectively, of the total variance between stations

Table 2. Pearson product moment correlation coefficients (*r*) between environmental parameters and absolute abundances of bacterioplankton groups. ALF: *Alphaproteobacteria*; ROS: *Roseobacter* clade; GAM: *Gammaproteobacteria*; BAC: *Bacteroidetes*; ACT: *Actinobacteria*; chl-a: chlorophyll *a*; O_2sat: oxygen saturation. Black: global correlations, blue: correlations at higher (>35°) latitudes, red: correlations at lower (0 to 35°) latitudes

	ALF	SAR11	ROS	GAM	SAR86	BAC	ACT
NO_2	0.78	0.71	0.62	0.62	0.82	0.94	0.66
NO_3	0.58				0.79	0.8	0.54
PO_4	0.9	0.84	0.7	0.78	0.83	0.96	0.78
SiO_2	0.61		0.74	0.66	0.97	0.72	0.81
chl-a			0.47		0.38	0.67	
					0.81		
O_2sat	−0.65	−0.68		−0.64	−0.5	−0.62	−0.74
	−0.65	−0.69		−0.65	−0.61	−0.63	−0.76

Table 3. Pearson product moment correlation coefficients (*r*) between environmental parameters and relative abundances of bacterioplankton groups. ALF: *Alphaproteobacteria*; BAC: *Bacteroidetes*; Temp: temperature; Total N: total inorganic nitrogen; chl-a: chlorophyll *a*; O_2c: oxygen concentration. Black: global correlations, blue: correlations at higher (>35°) latitudes, red: correlations at lower (0 to 35°) latitudes

	ALF	SAR86	BAC
Temp	0.72	−0.53	−0.64
	−0.61		−0.75
Total N	−0.74	0.49	0.39
NO_2	−0.84		0.45
	0.55		0.68
NO_3	−0.85	0.38	0.39
	0.59		0.66
PO_4	−0.81	0.4	0.56
chl-a	0.54	0.65	0.47
O_2c	−0.85	0.6	0.59
	0.53		0.79

itudes; p = 0.015) and unclassified *Bacteria* (peaking at lower latitudes; p = 0.034) between colder and warmer oceans. Also *Vibrio* showed latitudinal variation (peaking at lower latitudes; p = 0.039). Comparison between biomes revealed relative abundances of *Alphaproteobacteria* peaking in the Westerlies biome (p = 0.023) and of *Gammaproteobacteria* in the Polar biome (p = 0.028). For *Roseobacter* relative abundances were highest in subtropical and tropical locations (p = 0.027), while absolute abundances peaked in temperate and polar waters (p = 0.041).

Relation of community structure to environmental parameters

Linkages of bacterial distribution with environmental parameters were analyzed by PCA and Pearson product moment correlations. PCA, being a multivariate analysis comparing all parameters, provides insights into more complex correlations and interdependencies. In contrast, Pearson correlations point out direct pairwise associations between abundances and physicochemical parameters (Tables 2 & 3, Tables S4 & S5) and/or between bacterial groups with a comparable response to environmental conditions (Table S3). Both approaches revealed relations of community structure to environmental parameters, with distinct variations depending on whether the analysis was done using relative or absolute bacterial abundances. Absolute abundances of most bacterial groups showed a latitude-dependent pattern, being correlated with nutrient concentrations in warmer, but with oxygen saturation in colder oceans (Tables 2 & S4). PCA highlighted these associations by positioning oxygen saturation and bacterial abundances opposite each other, and nutrients and bacterial abundances at similar positions on the abscissa (Fig. 3a). Absolute cell numbers of *Roseobacter* and SAR86 were globally correlated with chlorophyll *a* (Table 2). The influence of environmental parameters on relative abundances was more complex. While PCA clustered SAR86 with nitrogenous and phosphorous nutrients, *Actinobacteria* with chlorophyll *a*, ammonium and nitrite, and *Roseobacter* with solar radiation, salinity and oxygen saturation (Fig. 3b), only the first was reflected in Pearson correlations. In

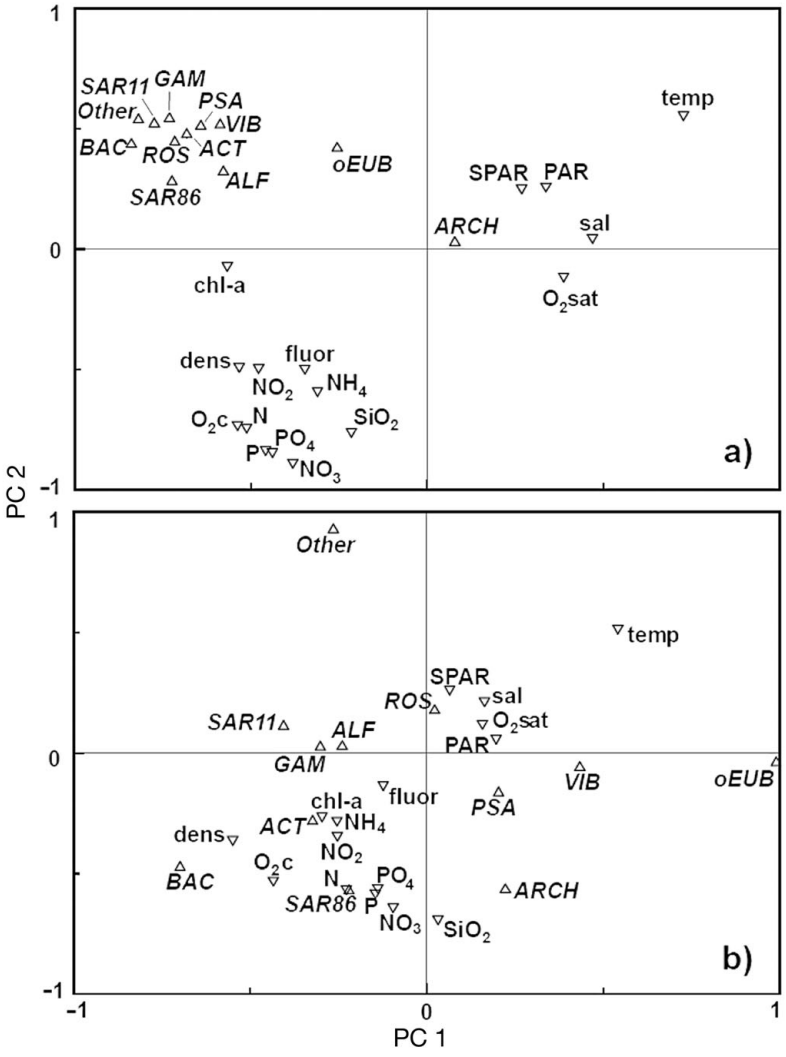

Fig. 3. Principal Component (PC) 2 versus 1 correlation loadings comparing environmental parameters (∇) with (a) absolute and (b) relative bacterial abundances (Δ) between 24 stations worldwide. The principal components explain (a) 30 and 28% and (b) 46 and 17% of the total variance between samples. *ARCH*: *Archaea*; *ALF*: *Alphaproteobacteria*; *ROS*: *Roseobacter* clade; *GAM*: *Gammaproteobacteria*; *PSA*: *Pseudoalteromonas*; *VIB*: *Vibrio*; *BAC*: *Bacteroidetes*; *ACT*: *Actinobacteria*; *oEUB*: unclassified *Bacteria* detected by EUB338, but not by ALF968, GAM42a, CF319a, or HGC69a; *Other*: unclassified cells not detected by EUB338. All EUB338 fractions refer to the average detectability from lysozyme and combined lysozyme/achromopeptidase permeabilizations. temp: temperature; sal: salinity; dens: density; N: total inorganic nitrogen; P: total inorganic phosphorus; chl-a: chlorophyll *a*; fluor: *in vivo* fluorescence; O_2c: oxygen concentration; O_2sat: oxygen saturation; PAR: photosynthetically active radiation; SPAR: surface PAR

contrast, the global associations of *Bacteroidetes* with chlorophyll *a* and different inorganic nutrients were only seen in Pearson correlations (Tables 3 & S5). Several correlations were restricted to either higher or lower latitudes. Furthermore, 4 out of 10 found associations of *Alphaproteobacteria* with environmental parameters differed between colder and warmer waters, having a positive correlation at higher, but a negative correlation at lower latitudes and vice versa (Table 3).

DISCUSSION

The present study adds to recent large-scale surveys of marine bacterial community structure in surface seawater (Baldwin et al. 2005, Pommier et al. 2007, Fuhrman et al. 2008, Biers et al. 2009) by presenting a quantitative *in situ* dimension of marine bacterioplankton around the world. We confirmed the ubiquitous dominance of *Alphaproteobacteria* and the SAR11 clade (Morris et al. 2002, Pommier et al. 2007), medium to high abundance of *Gammaproteobacteria* and *Bacteroidetes* (Giovannoni & Stingl 2005) and low numbers of *Archaea* in oceanic surface waters (DeLong et al. 2006). In addition, this is the first quantitative report of *Actinobacteria*, the SAR86 and *Roseobacter* clades, and the *Pseudoalteromonas* and *Vibrio* genera on a global scale.

In comparison to other CARD-FISH surveys, we reached similar conclusions regarding the relative abundance of higher phylogenetic groups in coastal tropical Atlantic (Baltar et al. 2007) and Antarctic waters (Topping et al. 2006), but found differing fractions of SAR11, *Gammaproteobacteria* and *Bacteroidetes* in the Benguela upwelling system (Schattenhofer et al. 2009). This probably reflected the fact that the samplings were conducted in different seasons (boreal autumn versus spring) and at different coordinates (24° S versus 30° S). The Benguela province harbours several, oceanographically distinct upwelling centres. While the present sampling was done in the most intense upwelling zone, which is additionally influenced by the input of aerosol particulates (representing an environmental barrier), Schattenhofer et al. (2009) sampled in a centre and period of minimal upwelling (Longhurst 1998). Seasonal variation plays an important role in bacterial community dynamics, but cannot be addressed here since samplings were only possible at one time point at each station.

The present study provides further evidence for spatial variation in marine bacterioplankton community structure on a global scale. Finding latitude- and biome-related variations in bacterial distribution highlighted the presence of latitudinal patterns among

marine microbiota (Pommier et al. 2007, Fuhrman et al. 2008) and emphasized that warm water communities are more similar in composition to each other than to cold water communities (Baldwin et al. 2005). Environmental parameters were correlated with both relative and absolute bacterial abundances, indicating a complex interplay of abiotic factors behind the structuring of bacterioplankton communities. The strong influence of nutrient concentrations on bacterial population sizes at lower latitudes probably reflected the characteristic nutrient scarcity in warmer waters. In the richer waters of colder oceans, however, nutrients were likely not limiting; instead, a negative correlation of population sizes with oxygen saturation was found, possibly reflecting the increased oxygen consumption of the larger active bacterial populations.

For *Alphaproteobacteria*, several correlations with environmental parameters differed between latitudes. We assume that these variations reflected the existence of variable dominant populations, or ecotypes (genetically closely related but physiologically distinct populations with unique niches; Cohan 2002) between colder and warmer waters. Widespread bacterial groups commonly share a high diversity of distinct low-level taxa (Kirchman et al. 2005), and ribotypes from all major bacterioplankton groups were shown to be restricted to either higher or lower latitudes (Pommier et al. 2005). Spatially diverging communities were also observed for *Roseobacter* (Selje et al. 2004) and *Prochlorococcus* (Bouman et al. 2006) ecotypes.

The present study highlighted the prevalence of *Gammaproteobacteria* and *Bacteroidetes* in colder waters (Malmstrom et al. 2007, Schattenhofer et al. 2009). Furthermore, the *Bacteroidetes*–chlorophyll *a* correlation substantiated the group as being responsive to phytoplankton blooms (Fandino et al. 2005, Pommier et al. 2007). It should be considered, however, that any apparent correlation can be a side-effect of uncharacterized, superior dependencies (Levin et al. 2001). Furthermore, bacterial biogeography is likely influenced by more parameters than analyzed here, such as hydrography (Teira et al. 2006, Galand et al. 2010) or carbon-flux related variables (Teira et al. 2008).

The *Roseobacter* clade, *Pseudoalteromonas* and *Vibrio* were quantified to complement results from a culture-based survey of antagonistic bacteria performed during the same expedition, and to provide further insight into the marine ecology of these groups. The *Roseobacter* clade is a heterogeneous group involved in global sulphur and greenhouse gas cycling (Moran et al. 2003, Wagner-Döbler & Biebl 2006). While the peak of relative abundances in warmer waters contradicted earlier observations, the finding of significantly higher absolute numbers in colder waters was consistent (Selje et al. 2004). The detection of smaller relative *Roseobacter* fractions than reported elsewhere (Wagner-Döbler & Biebl 2006) potentially reflected the fact that no samplings were performed during phytoplankton blooms, when the clade often dominates the bacterioplankton. Nevertheless, the global correlation of absolute *Roseobacter* cell numbers with chlorophyll *a* underlined the association with algal communities. *Pseudoalteromonas* spp. is often associated with marine eukaryotes (Holmström & Kjelleberg 1999) and produces various antibacterial compounds (Bowman 2007). Despite its prevalence on surfaces, we detected a considerable planktonic population, corresponding to findings by Schattenhofer et al. (2009). *Vibrio* is mainly researched regarding its pathogenicity to humans or aquatic animals (Thompson et al. 2006). The detected fractions of *Vibrio* were consistent with other studies using a hybridization approach (Heidelberg et al. 2002, Schattenhofer et al. 2009). In contrast, the Global Ocean Survey — a metagenomics-based and hence also quantitative analysis — reported an approximately 1% smaller abundance (Biers et al. 2009).

In conclusion, the present study provides a global quantitative survey of the major bacterioplankton groups, important clades and 2 bacterial genera in surface seawater around the world. The latitudinal patterns in community structure, together with the clustering and correlations of bacteria with physicochemical parameters, underlined the existence of biogeographical variation among marine bacteria and the relation of abiotic factors to these patterns. The latitude-dependent variations in both relative and absolute bacterial abundances indicated that bacterial biogeography may follow principles similar to those seen for higher eukaryotes.

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