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Biogeochemical controls on the bacterial population in the eastern Atlantic Ocean

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Abstract

Little is known about bacterial dynamics in the oligotrophic ocean, particularly about its cultivable population. We examined the abundance of total and cultivable bacteria in relation to changes in biogeochemical conditions in the eastern Atlantic Ocean with special regard to *Vibrio* spp., a group of bacteria that can cause diseases in human and aquatic organisms. Surface, deep water and plankton samples (<20 µm, 20–55 µm and >55 µm) were collected between 50° N and 24° S. Chlorophyll-*a* was very low (<0.3 µg l^{-1}) in most areas of the nutrient-poor Atlantic, except at a few locations near upwelling regions. In surface water, dissolved organic carbon (DOC) and nitrogen (DON) concentrations were 64–95 µM C and 2–10 µM N accounting for ≥90 % and ≥76 % of total organic C and N, respectively. DOC and DON gradually decreased to ~45 µM C and <5 µM N in the bottom water while dissolved inorganic nutrients (Si, P, N) increased with depth. In the surface layer, culture independent total bacteria, represented by 4′-6-diamidino-2-phenylindole (DAPI) counts, ranged mostly between 10^7 and 10^8 cells l^{-1}, while cultivable bacterial counts (CBC) and *Vibrio* spp. were found at concentrations of 10^4–10^7 and 10^2–10^5 colony forming units (CFU) l^{-1}, respectively. Most bacteria (>99 %) were found in the nanoplankton fraction (<20 µm), however, bacterial abundance did not correlate with suspended particulates (chlorophyll-*a*, particulate organic C and N). Instead, we found a highly significant correlation between bacterial abundance and temperature ($p < 0.001$) and a significant correlation with DOC and DON. Among the cultivable bacteria, the abundance of *Vibrio* was also highly significantly correlated with DOC and DON ($p < 0.0005$ and $p < 0.005$, respectively). In cold waters of the mid-pelagic and abyssal zones, CBC was 50 to 100-times lower than in the surface layer; however, cultivable *Vibrio* spp. could be isolated from the bathypelagic zone and even near the seafloor (average ~10 CFU l^{-1}). In contrast, DAPI counts revealed a homogenous distribution of the non-cultivable bacterial population throughout the oceanic depths. Our study indicates that *Vibrio* and other bacteria may largely depend on dissolved organic matter to survive in nutrient-poor oceanic habitats, without being associated with plankton or particles.

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1 Introduction

Oceans play an important role in maintaining the balance of atmospheric CO_2. Global warming may enhance oceanic stratification and ultimately affect its vertical nutrient flux and other biogeochemical patterns (Sarmiento et al., 1998). Thus there is possibility of considerable changes in oceanic primary production (PP) and its capacity to sequestrate atmospheric CO_2. Apart from the conventional biological pump-driven vertical transport of surface organic carbon into the deep sea, the microbial foodweb remineralizes a large fraction of particulate organic carbon (POC) and ultimately supports PP in the euphotic zone (Azam, 1998). Another part is converted into dissolved organic carbon (DOC) supporting prokaryotic production (Williams, 2000). The interaction between oceanic bacteria and their energy sources in the water column is a key issue for element fluxes in the surface ocean. Therefore, detailed information is required about variations in bacterial abundance caused by changes in ocean's biogeochemistry in surface water and in comparison to the abyss.

Marine DOC (662 Pg C) is one of the largest active reservoir of organic C on Earth (Hansell et al., 2009). DOC concentrations are generally an order of magnitude higher than POC and many microbial processes in the ocean are driven by dissolved organic matter (DOM) fluxes. Bacteria have a high growth efficiency upon freshly produced, "labile" DOC which can be degraded within several hours to days (Reinthaler and Herndl, 2005). The "semi-labile" DOC (about 15–20 % of net PP) can be degraded by bacteria over weeks to seasonal timescales, while "refractory" DOC are resistant to biodegradation and may bear signatures from centuries to millennia (Hansell et al., 2009). Bacterial metabolic activities can convert a portion of labile DOM into a variety of high molecular weight DOC, some of which can be reused by bacteria while others are refractory (Gruber et al., 2006). Progressive utilization of labile and semi-labile DOC through the microbial carbon pump aids in the refractory DOC accumulation (~95 % of total DOC) in the oceans interior (Jiao et al., 2010). In a recent study it was revealed that such transformation processes in the surface ocean are rapid leading to a

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relatively fresh component which molecularly resembles the refractory material (Flerus et al., 2011). Besides DOC, the availability and nature of nitrogenous components of DOM play an important role in the biogeochemical cycle by limiting bacterial growth. The concentration of dissolved inorganic nitrogen (DIN) in oceanic surface water is often very low and thus competitive between phytoplankton and bacterioplankton (Wu et al., 2000). Therefore, recycling of organic nitrogen from particulate (PON) or dissolved (DON) sources may modulate primary production as well as bacterial abundance.

Among the diverse groups of marine and estuarine bacteria, *Vibrio* species have gained increased attention due to their potential of causing diseases in humans such as epidemic cholera by *V. cholerae*. Toxigenic strains of some *Vibrio* spp. can also cause diseases in economically important fishes and shrimps, and coral bleaching and squid luminescence are also attributable to some *Vibrio* spp. (Thomson et al., 2004). As part of their survival strategies in aquatic habitats *Vibrio* spp. can attach or interact with virtually all kinds of aquatic organisms or suspended particulates (Lara et al., 2009, 2011). This kind of association of *Vibrio* and other bacteria is likely facilitated by the release of DOM from plankton or other particulate matters. *Vibrio* spp. are among the few bacteria which can degrade chitinous substrates, which are among the most abundant amino sugars in the ocean (Thompson et al., 2004). Besides, this group of bacteria can also secrete a variety of enzymes to aid the degradation of organic matter, e.g. mucinase, protease, lipase, and laminarinase (Oliver et al., 1986; Alderkamp et al., 2007).

Microbiological investigations on oceanic habitats largely focused on culture independent techniques which are basically qualitative, whereas some studies have applied quantitative fluorescent in situ hybridization (Pernthaler and Amann, 2005). These types of molecular analysis have revealed a frequent occurrence of *Vibrio* spp. in oceanic water, although other subgroups of bacteria, e.g. SAR11, Roseobacter, Alteromonas, and Cytophaga-Flavobacterium-Bacteroides can also be dominant (Eilers et al., 2000; Malmstrom et al., 2005; Weinbauer et al., 2006; Taniguchi and Hamasaki, 2008; Schattenhofer et al., 2009; Weitz et al., 2010). However, culture independent

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techniques cannot represent the active cultivable portion of a species which might be more reactive due to the changes in biogeochemical parameters. Cultivable bacteria are considered as more active with high metabolic activity while the viable but non-cultivable fraction has a reduced metabolism (Roszak and Colwell, 1987; Sun et al., 2008).

Although various studies on *Vibrio* spp. have been performed in coastal habitats (e.g. Heidelberg et al., 2002; Mahmud et al., 2007, 2008) little is known about the regulation of *Vibrio* as well as the overall bacterial population in the ocean in connection with plankton, temperature and biogeochemical conditions. In the present study, we have examined the quantitative abundance of total as well as cultivable bacteria including *Vibrio* spp. at various water depths along a North-South meridional transect through the mostly oligotrophic Atlantic Ocean. Our objectives were to elucidate the importance of particulate and dissolved material for the abundance and distribution of *Vibrio* spp. and total cultivable and non-cultivable bacteria, and to study how organic and inorganic substances influence the occurrence of the bacterial populations. A better understanding of abundance and changes in cultivable as well as total bacterial population will also improve our knowledge of dynamics and transformation processes of carbon and nitrogen in the ocean.

2 Materials and methods

2.1 Study sites and sampling

Water samples were collected on board R/V *Polarstern* during the expedition ANT XVV/1 from Bremerhaven, Germany to Cape Town, South Africa in 2008. The sampling stations covered a variety of geographical areas from ~50° N to ~24° S including marine waters from nearby European shelf, Mediterranean outflow, inter-tropical convergence zone (ITCZ, between 10° N and 2° N), eastern tropical and sub-tropical Atlantic from both the Northern and Southern Hemispheres. During the expedition no heavy rain showers occurred in the ITCZ although intense rainfall is common in this region.

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Surface water (0–10 m depth) samples were obtained by the so-called Teflon "Fish" sampler, an online device deployed alongside the vessel that continuously pumped water on board. Surface samples were collected at 26 stations during 3 to 29 November 2008 (Fig. 1). Besides, surface water (1000 l) were fractionated by filtration through plankton nets (55 µm and 20 µm mesh sizes) at nine locations, each covering 30–50 nautical miles (Fig. 1). Samples representing the <20 µ fraction were collected during each fractionation by combining filtrates. In addition, water samples from various depths (50–200 m; 1500–2500 m and 4000–5500 m) were collected at stations 3, 7, 11, 14, 20, 24 and 26 using a CTD rosette sampler (24 × 12-l bottles) (Fig. 1, Table 1). All samples were transferred into sterile bottles and processed or preserved immediately (within an hour) for microbiological and biogeochemical analyses.

2.2 Oceanographic variables and chlorophyll measurement

In-situ records of oceanographic variables (water temperature, salinity, depth, etc.) were obtained from the online ship devices (see also: Koch and Kattner, 2011). For the chlorophyll-*a* (Chl-*a*) determination, water samples were filtered (GF/F, 47 mm, Whatman) and kept frozen (−70 °C) until extraction with acetone (90 %) and further analyses of pigments by high performance liquid chromatography (HPLC) and fluorometry according to standard methods (Zapata et al., 2000).

2.3 Analyses of nutrients and other biogeochemical parameters

Water samples (3–4 l) were filtered on board (GF/F, Whatman, precombusted at 450 °C, 3 h) and afterwards kept frozen at −20 °C until analysis for POC and PON. Filtrates (50 ml) were poisoned with 150 µl of $HgCl_2$ (35 g l^{-1}) and stored at 4 °C for later nutrient analyses (Kattner, 1999). DIN (nitrate, nitrite, ammonium, all in µM N), silicate (µM Si) and phosphate (µM P) were determined spectrophotometrically according to standard methods for seawater analysis (Kattner and Becker, 1991). DON was determined by wet oxidation with potassium persulfate (Koroleff, 1983). For the DOC determination

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water samples were acidified with phosphoric acid (20 %, v/v) to remove inorganic C. DOC was measured by high temperature (680 °C) catalytic (Al_2O_3 particles containing 0.5 % Pt) oxidation in a TOC analyzer (Dohrmann DC-190, CA, USA) followed by quantification of CO_2 by non-dispersive linearised infrared gas analysis (Skoog et al., 1997). A solution of potassium hydrogen phthalate was used as calibration standard.

To determine POC and PON, the preserved filters were dried at 50 °C for 12 h and kept at room temperature in a desiccator. For POC measurement inorganic C was removed by acidification with HCl (1 N). POC and PON were quantified with an elemental analyzer (Fisons, NA 2100) according to Verado et al. (1990). Standard Reference Material 1515 was used for calibration and at least three replicates of each sample were measured.

Among the trace elements, total Fe was determined using a liquid-liquid extraction method followed by atomic absorption spectrometry as described by Pohl and Hennings (2005).

2.4 Determination of bacterial abundance and cultivable *Vibrio* spp.

Heterotropic cultivable bacterial counts (CBC) were determined on marine agar (Difco, MI, USA). In case of low cultivable counts, samples were concentrated 500-times (4 l to 8 ml) by filtration (0.2 µm filters, Millipore). 10 ml of concentrated plankton sample was homogenized with an Ultra-Turrax (T25, Ika-Werke, Staufen, Germany) prior to bacterial analysis. Selective TCBS (thiosulfate citrate bile salts sucrose) and MacConkey agars (Difco, 3 % NaCl in both) were used for *Vibrio* and presumptive Enterobacteriaceae counts, respectively. In each case of cultivable counts, a 100 µl aliquot of sample was spread plated on media in triplicate. Additional filters, each containing concentrated bacteria from a 2 l sample, were also enriched at 25 °C for 18 h in alkaline peptone water [1 % Bacto-peptone (w/v, Difco), 3 % NaCl (w/v, Difco), pH 8.5] and Trypticase Soy Broth (Difco, 3 % NaCl) for *Vibrio* and Enterobacteriaceae, respectively, followed by plating on selective agars. Cultivable counts (colony forming unit, CFU), were enumerated after three days growth at a temperature gradient, i.e. 20 °C for 12 h

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followed by 25 °C for 12 h, 30 °C for 24 h and 33 °C for 24 h to obtain optimum cultivable cell numbers. Representative colonies from each sample were stocked in T_1N_3 soft agar [1 % Tryptone (w/v, Difco), 3 % NaCl (w/v), 0.8 % Bacto-agar (w/v, Difco)].

Presumptive *Vibrio* isolates were verified by oxidase and gelatinase tests followed by partial sequencing (~800 bp) of 16S rRNA gene using universal primers (forward 9F, 5′-GAGTTTGATCCTGGCTC-3′, and reverse 800R, 5′-CTACCAGGGTATCTAAT-3′). Initial PCR products were purified using the QIAQuick PCR purification kit (QIAGEN GmbH, Hilden, Germany), then cycle sequencing was carried out using the BigDye terminator cycle sequencing kit (Applied Biosystems) in a GeneAmp 9700 thermal cycler (Applied Biosystems) according to the manufacturer's instruction. Afterwards a further purification was done using CleanSEQ (Agencourt Bioscience), and nucleotide sequences were determined in an ABI PRISM 3100 Avant Genetic Analyzer (Applied Biosystems). The sequences were checked for sequence homology to the nearest species by BLAST (http://blast.ncbi.nlm.nih.gov/Blast.cgi). Besides, the isolates were subjected to multiplex PCR analysis for proper screening of some potentially pathogenic and closely-related *Vibrio* strains (Haldar et al., 2010; Neogi et al., 2010).

An aliquot of the water samples (5 ml) was fixed with formaldehyde (4 %), stained with 4′,6-diamidino-2-phenylindole (DAPI) for 30 min according to the manufacturers' manual (Sigma-Aldrich). Then total culture-independent bacterial abundance was determined following a standard protocol (Porter and Feig, 1980) using an epifluorescence microscope (DM2500, Leica Microsystems). During counting of cells the number of large phytoplankton and zooplankton were excluded to assess a more realistic bacterial abundance.

2.5 Statistical analysis

Statistical analyses were carried out using "Xact" (version 7.21d, SciLab) and Statistica (ver. 10.0, StatSoft). Regression fits were applied to explore correlations between

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variables. Log transformed values of bacterial counts were used for statistical analyses. A "p" value of <0.05 was considered as significant.

3 Results

3.1 Nutrients and other biogeochemical parameters in surface water

Surface water temperature was 13.3 °C at ~50° N near the European shelf, gradually increasing up to 29.4 °C at ~5° N, and then decreasing to 19.0 °C at the southernmost station. Salinity ranged from 35.2 to 36.9. Chl-*a* was higher (>0.3 µg l^{-1}) between 50° N and 37° N near the European shelf as well as between 17° S and 24° S, where also higher phosphate values (0.2–0.5 µM P) were observed. In addition, a rise in Chl-*a* was observed between 17° N and 10° N (Table 1). DIN consisted predominantly of nitrate (60–97 %). Nitrate, nitrite and ammonium ranged from <0.03 µM (detection limit) to 3.5 µM, 0.1 µM and 0.3 µM, respectively (data not shown). Higher DIN values were observed at higher latitudes of the transect (above 40° N and 15° S, Table 1). The N/P ratio of DIN was mostly below 3 (0.2 to 3) while the highest value (11.6) was observed at the southern outskirt area of English Channel (~48° N). The concentration of total Fe varied between 0.5 and 6.0 nM, with higher values (>4) in the ITCZ and near 30° N (Table 1).

DOC concentrations (64–95 µM C) were an order of magnitude higher than DON (2–10 µM N). The higher concentrations of both DOC and DON did not significantly correlate with Chl-*a* (Table 1). The C/N ratios of DOM were generally below 20 (Table 1). On average, DOC contributed 93 ± 3 % of TOC (POC + DOC) while DON represented 87 ± 12 % of total dissolved N (DIN + DON) and 85 ± 9 % of total organic N (DON + PON). Dissolved silicate concentrations fluctuated between 0.4 and 1.6 µM with relatively higher values between 10° N and 24° S (Table 1).

Among particulate associated variables, the concentrations of POC and PON were 2.0–11.8 µM C (average 5.2 ± 2.5 µM C) and 0.30–1.69 µM N (average 0.75 ± 0.34 µM

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N), respectively (Table 1). In suspended particulate matter, the proportion (w/w) of organic C and N represented 0.3–4.7 % and 0.03–0.9 %, respectively (data not shown).

3.2 Bacterial abundance in surface water

Culture independent DAPI counts ranged from $\sim 10^6$ cells l^{-1} in the northern temperate zone to $\sim 10^8$ cells l^{-1} in warm tropical waters, while CBC varied between 10^4 and 10^7 CFU l^{-1} (Fig. 2a). Fluctuations in CBC followed a similar trend as DAPI counts, and their abundance was highest at station 13 (14.66° N). In most samples, CBC represented 0.06–5.0 % of the DAPI counts. An exceptionally high CBC (~20 % of the DAPI counts) was observed at 14.66° N and 17.73° S (Fig. 2a). *Vibrio* and presumptive Enterobacteriaceae accounted for 0–1.8 % and 0.01–5.5 % of CBC, respectively. *Vibrio* counts were comparatively higher ($\sim 10^5$ CFU l^{-1}) in samples at 14.66° N and 5.43° N while their abundance varied mostly between 10^2 and 10^4 CFU l^{-1} (Fig. 2b), similar to the abundance of presumptive Enterobacteriaceae counts. However, *Vibrio* numbers were higher than Enterobacteriaceae in 9 out of 26 stations. Near the European shelf (50° N–37° N), where surface water temperature was <18 °C, cultivable *Vibrio* counts were comparatively low ($<10^2$ CFU l^{-1}) except at 42.77° N (Fig. 2b). 16S rRNA gene sequencing of representative *Vibrio* isolates ($n = 215$) followed by multiplex PCR detection revealed that the cultivable population was dominated by *V. campbellii* (36 %) followed by *V. alginolyticus* (25 %), *V. harveyi* (17 %) and *V. corallilyticus* (11 %) while among others *V. natrigens*, *V. pelagius* and *V. splendidus* were present in low number (<2 %). At each sampling location the cultivable *Vibrio* portion was overwhelmingly dominated by only one to three species.

The comparative analysis of bacterial abundance in the fractionated samples revealed that most bacteria were present in the <20 µm fraction (Fig. 3). This general trend was found in all nine different geographic locations (Fig. 1). DAPI counts ranged from 10^7 to 10^8 cells l^{-1} in the <20 µ fraction, while only $\sim 10^4$ cells l^{-1} were present in the 20–55 µm and >55 µm fractions. Similarly, exclusively higher occurrences of CBC including *Vibrio* and Enterobacteriaceae were also observed in the

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<20 µm fraction. Interestingly, in the plankton samples (>20 µm) a large portion of the associated bacteria (10–60 % of DAPI counts) remained in cultivable form. In association with both, larger phytoplankton (20–55 µm fraction) and zooplankton (>55 µm fraction), CBC had a similar abundance while in zooplankton samples, Enterobacteriaceae showed a higher abundance than *Vibrio* (Fig. 3).

3.3 Relationship between bacterial abundance and biogeochemical parameters in surface water

A highly significant positive correlation was observed between temperature and bacterial counts (DAPI: $r = 0.75$, $p < 0.001$; CBC: $r = 0.67$, $p < 0.001$, Fig. 4). A highly significant correlation also existed between water temperature and cultivable *Vibrio* spp. ($r = 0.76$, $p < 0.00005$, Fig. 4c). In contrast, cultivable Enterobacteriaceae only showed a significant correlation ($r = 0.42$, $p < 0.05$) with temperature.

POC and PON were positively correlated with Chl-*a*, ($r = 0.60$ and 0.68, respectively, $p < 0.01$) but did not increase with temperature. At the most northern and southern stations, higher values of Chl-*a* coincided with higher concentrations of DIN (Table 1, Fig. 2a). POC correlated highly significantly with PON ($r = 0.90$, $p < 0.00001$) and had an average C/N ratio of 6.4 (Fig. 4e). Besides, both POC and PON had a highly significant correlation with phosphate ($r = 0.73$ and 0.66, respectively, $p < 0.001$). Intriguingly, DOC was highly significantly correlated with temperature ($r = 0.66$, $p < 0.0005$, Fig. 4d).

Bacterial counts did not show significant relationships with particulate parameters (POC, PON, Chl-*a*). However, DAPI and CBC correlated positively with DOC ($r = 0.63$, $p < 0.001$ and $r = 0.66$, $p < 0.01$, respectively) and DON ($r = 0.71$, $p < 0.001$ and $r = 0.63$, $p < 0.05$, respectively). Higher bacterial abundances in the tropical zone coincided with higher DOM, while an opposite scenario, i.e. lower bacterial counts with lower DOM, was observed nearby the temperate zone (Fig. 2). Among the bacterial variables cultivable *Vibrio* abundance were significantly correlated with DOC ($r = 0.68$, $p < 0.0005$, Fig. 4g) and DON ($r = 0.58$, $p < 0.005$, Fig. 4h). Interestingly, cultivable

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Vibrio abundance had a negative correlation with the C/N ratio of DOM ($r = -0.53$, $p < 0.01$, Fig. 4i).

Although temperature had a strong influence on the *Vibrio* population like on most other bacteria, the *Vibrio* counts at some sampling locations showed unexpected variations. At station 4 (44.04° N) the water temperature was low (<16 °C) but there were high *Vibrio* counts that coincided with higher DON concentrations. Similarly, towards station 22 (11.70° S) the temperature followed a gradually decreasing trend but the *Vibrio* population increased along with increasing DOC (Fig. 2b). These spatial variations in *Vibrio* counts were congruent with the variations in DOC and DON (Fig. 2b). Increases in bacterial abundance also coincided with higher Fe concentration at 30° N and in the ITCZ (Fig. 2). In contrast, surface bacterial counts did not correlate with the dissolved inorganic nutrients, nitrate, nitrite and ammonium.

3.4 Depth variations in bacterial abundance and biogeochemical parameters

Samples from the deep ocean (Table 1, Fig. 1) were categorized into surface (0–10 m), lower euphotic (50–200 m) including samples from fluorescence (Chl-*a*) maximum layers at stations 11, 14, 20 and 24, mid-pelagic (1000–2500 m) and abyssal (4000–5500 m) zones. Temperature gradually decreased to 3.1–5.8 °C and 1.1–2.5 °C at the mid-pelagic and abyssal zone, respectively. At stations in the northern and southern extremes (above 40° N and 15° S) the existence of a thermocline layer in the euphotic zone was not obvious. In contrast, in the tropical regions, particularly between 15° N and 12° S, a prominent thermocline layer with drastic temperature change of 10–15 °C within 150 m depth was observed. Bacterial abundance and biogeochemical parameters followed consistent patterns at all seven stations (Fig. 5).

DAPI counts did not change with depth but CBC gradually decreased (Fig. 5a). However, CBC at surface (average $\sim 10^6$ CFU l^{-1}) was 50 to 100-times higher than in the pelagic zone (average $\sim 10^4$ CFU l^{-1}). Interestingly, a small increase in CBC was observed near the seafloor compared to the mid-pelagic zone. In the fluorescence maximum layer of the euphotic zone, the abundance of CBC including *Vibrio* spp. was lower

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(5–10 times) than surface waters, although DAPI counts were similar. Presumptive Enterobacteriaceae counts also had a vertical decreasing trend but increased again near the seafloor (Fig. 5a). The *Vibrio* abundance was at least 10 times lower in the mid-pelagic and abyssal zones (average ~10 CFU l^{-1}) than in the surface water (Fig. 5a).

Inorganic nutrients gradually increased with depth, and the highest values were always near the seafloor (Fig. 5b and c). The average silicate concentrations in the surface and lower euphotic zones were ~1 µM and 2 µM, respectively and increased to ~20 µM in the mid-pelagic and to ~50 µM near the sea-floor. Phosphate increased from an average of ~0.3 µM at surface to ~1.3 µM in the abyssal zone. Similarly, DIN also increased from an average of ~0.7 µM at surface to ~21 µM near the sea-floor (Fig. 5c). Below the euphotic zone nitrate represented >99 % of DIN. The average N/P ratio increased to ~15.5 in the mid-pelagic and near sea bottom zones. PON decreased sharply from an average of ~1.0 µM N at surface to ~0.2 µM N or less below the euphotic zone (Fig. 5c). POC decreased gradually with depth (e.g. average ~7.0 µM C at surface to ~1.0 µM C in the mid-pelagic zone). Intriguingly, more variable and higher POC values (average ~3.5 µM C) were observed near the sea-floor (Fig. 5d). When comparing spatial data, higher POC values were found near the sea-floor in tropical regions than in regions near the temperate zone. The results from this limited number of samples did not reveal any statistical significance between bacterial abundance with POC or DOC in deep sea. DOC decreased gradually from ~70 µM C at the surface to ~45 µM C near the sea floor (Fig. 5d).

4 Discussion

The present study shows that bacterial dynamics in the eastern Atlantic Ocean are consistently linked to the changes in organic matter and temperature. A considerable fraction of the bacterial population was cultivable not only in surface waters but also in cold waters at great depths. The relative fluctuations of the abundance of cultivable *Vibrio* in relation to some important biogeochemical parameters indicate that this group

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of bacteria may have good capability in contributing to the turnover of organic C and N in the open ocean.

4.1 Role of POM on bacterial dynamics in surface water

In the nutrient-limited oceanic environment, particulate matter in form of aggregates or marine snow can support part of the bacterial population (Azam and Long, 2001). However, our study indicates a passive role of POM in regulating bacterial abundance. Our observation, that there is no correlation with particulate parameters, is congruent with the inference that bacterial C demand exceeds photosynthetic production as POC in the marine habitat (del Giorgio and Duarte, 2002). The average C/N ratio of 6.4 in the surface POM samples suggests phytoplankton and fresh detritus as the primary source of POM (Redfield et al., 1963). Chl-*a* concentration in the majority of stations was very low except in the nutrient-rich northern and southern extremes as well as in the central region (10–18° N) near the eastern coastal province (Table 1). A similar trend of low PP due to the exhaustion of DIN has been reported previously (Hoppe et al., 2002). The dissolved inorganic N/P ratio in surface water samples of the present study is much lower (mostly <4) than the Redfield ratio of 16, suggesting an N poor environment for optimum growth of primary producers.

Larger phytoplankton (>20 µm) or zooplankton (>55 µm) played a minor role in harboring bacteria including *Vibrio* spp. since most (>99 %) bacteria were observed in the <20 µm fraction (Fig. 3). Smaller particulate matters (<20 µm, including pico- and nanoplankton) and/or DOM probably act as main sources of bacterial nutrients. A recent finding shows that most of the *Vibrio* population in the coastal habitat occurs in the <20 µm fraction (Lara et al., 2011). Pigment composition analysis has revealed that picoplankton and nanoplankton are the dominant primary producers in the Atlantic surface water (Taylor et al., 2011). Nevertheless, a positive correlation with bacterial abundance and Chl-*a* was not discernable in our study. This indicates a major role of DOM in nourishing bacterial populations. In the eastern Atlantic Ocean, higher bacterial production can be also coupled with the peaks in Fe in some locations (Fig. 2). As

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shown with a high correlation between the Fe concentrations in aersosol and surface water over the same cruise (Schmitt-Kopplin, unpublished data), atmospheric input of Saharan dust is the most likely reason of high Fe concentration, particularly in ITCZ, which may increase PP (Pohl et al., 2011). Freshly produced POM can also be quickly degraded to DOM by bacteria generating a possible time-lag between POM and bacterial dynamics in surface water (e.g. Fig. 4f).

4.2 Temperature influence on DOC production and bacterial abundance

Higher abundance of bacteria including *Vibrio* spp. was significantly correlated with temperature in the Atlantic Ocean. However, bacteria including *Vibrio* spp. in Atlantic surface waters may significantly utilize DOM, here quantified as DOC or DON, to facilitate their survival without being associated with larger plankton (Figs. 3, 4). Due to higher metabolic rates at higher temperatures bacteria are able to degrade organic substrates more rapidly (Pomeroy and Wiebe, 2001). This may be a good reason for the positive correlation between DOC and temperature. Our analyses of the filter solvent extracts by ultrahigh resolution mass spectrometry (ESI-ICR-FT/MS) followed by interpretations in the KEGG database via our built MassTRIX interface revealed that the number of annotated metabolic compounds increased with bacterial abundance and the sum of intensity of metabolites had a strong positive correlation with temperature and DOC (Schmitt-Kopplin et al., unpublished). Bacteria can also produce semi-labile and refractory DOC during organic matter degradation (Ogawa et al., 2001; Gruber et al., 2006). Therefore, part of the correlation could also be explained by the microbial generation of DOM. The majority (>60 %) of cultivable marine bacteria can express peptidase, lipase and phosphatase with increasing trend in warm seasons (Zaccone et al., 2002). Moreover, vertical stratification of the upper water column of tropical and subtropical oceans favors the high DOC concentration (Hansell et al., 2009). The strong thermocline layers observed in the Atlantic regions between 15° N and 12° S might have also favored DOC accumulation in surface water. Nevertheless, at some Atlantic stations near the equator the DOC concentrations were low and comparable to

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those of the northern or southern extremes having no effective vertical stratification (Table 1). Comparatively low DOC or DON in the highly productive northern and southern extremes (Fig. 2) might be due to a decrease in bacterial degradation capacity at low temperature. Besides, bacteria may require more DOM to grow at low temperatures (10–15 °C) than at high temperatures (>20 °C) (Wiebe et al., 1993). A combination of higher temperature and PP can also boost DOC and DON concentration in tropical regions (e.g. 14.66° N, Table 1). It has been shown that DOM (e.g. glucose) and higher temperature may synergistically act on marine bacterial growth in laboratory microcosm (Kirchman and Rich, 1997).

4.3 Vertical changes in biogeochemical profile and bacterial abundance

The DOC concentrations (mostly 60–80 µM) in the Atlantic surface are comparable to the tropical zones of other oceans. Depth-wise decrease in DOC reaching 45–48 µM at bottom (Fig. 5d) indicated its "semi-refractory" nature. Persistence of semi-labile DOC (e.g. carbohydrates in a complex matrix) in the oldest bottom waters has been confirmed by spectroscopic and chemical analyses (Hansell et al., 2009). When considering overall oceanic DOC, a high proportion (>90 %) is recalcitrant (Jiao et al., 2010). Yet, a highly significant positive correlation of DOC with bacterial abundance in the Atlantic surface suggests the vital role of labile or semi-labile DOC in survival and growth of *Vibrio* spp. and other bacteria. Molecular analyses have confirmed that the majority of the degradation of DOM occurs in the surface water (Flerus et al., 2011). The upward flux of inorganic N may not be sufficient to meet the biological demands in the surface layer, thus primary producers as well as bacteria may largely depend on DON availability and recycling (e.g. Fig. 4h). The decrease in PON and POC from surface towards mesopelagic zone confirms the dissolution of sinking POM to support bacterial metabolism.

The high efficiency of deep sea bacteria in degrading freshly cultured organic matter was evidenced by an in situ experiment at the ocean bottom (Cole et al., 1987). Comparatively low CBC in deep sea than surface water (Fig. 5a) is presumably due to low

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temperature and scarcity of bioavailable organic substrates. Even in the fluorescent maximum zones at 50–200 m depth, characterized by higher POM but lower temperature than surface, there was no significant difference in DAPI counts, and CBC was comparatively much less when compared to the surface (Fig. 5a). CBC represented only a small fraction (mostly <1 to 5 %) of total bacterioplankton (DAPI count), which is consistent with previous studies (Eilers et al., 2000). According to an estimate, the average culture-independent *Vibrio* counts in oceanic surface is $\sim 10^7$ cells l^{-1} or ~1.5 % of total bacterioplankton (Weitz et al., 2010). Cultivable *Vibrio* population in the Atlantic surface was comparatively lower than their generally observed abundance in eutrophic estuarine and near-shore habitats (Mahmud et al., 2007, 2008; Lara et al., 2009). Nonetheless, the present study indicates that *Vibrio* spp. are well adapted in oligotrophic oceanic habitats including mid-pelagic and bottom waters. However, our study is a pioneering effort to quantify cultivable *Vibrio* spp. from various depths of the ocean. The depth profiles of DOC and inorganic nutrients were opposite, which suggest bacterial mineralization of sinking organic matters. Intriguingly, a fairly homogenous distribution of culture independent DAPI counts throughout the oceanic depths (Fig. 5a) indicates that deep sea bacteria predominantly remain in non-cultivable form and may utilize the semi-labile DOM for their survival. It is plausible that a high intensity of settling particle flux along with bioavailable POM or DOM may support bacterial growth in the bathypelagic zone. However, our limited observations showed that neither POC nor DOC has any significant correlation with bacterial abundance in deep sea. This may be partially attributable to their existence in a non-cultivable form with very low metabolic activities or growth at low temperature. Although mesopelagic and abyssal respiration is assumed as insignificant, it can be comparable to the photic layer if the total volume of the ocean is considered (del Giorgio and Duarte, 2002).

4.4 DOM as an important regulator of bacterial dynamics

Bacterial abundance in the Atlantic is presumably influenced by the concentrations and characteristics of DOM. The observed low DOC/DON ratio (mostly between 9 and

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20) in the ocean's surface reflects the source of DOM from autochthonous plankton. Freshly produced DOM from marine phytoplankton has low C/N values ranging from 4 to 11 (Hopkinson et al., 1997; Conan et al., 2007). Labile DOM is also characterized by lower C/N than refractory DOM (Carlson, 2002). Interestingly, our study has revealed higher *Vibrio* abundance in surface samples having a low C/N of DOM. Vibrios' association with plankton or suspended particulates to utilize released DOM patches can be facilitated by flagella, pili, chemotaxis, and quorum sensing (Yildiz and Visick, 2009). Bacterial metabolic activities may contribute a large portion of long-lived DOM (semi-labile or refractory) and ultimately increase its C/N ratio (Jiao et al., 2010). Exceptional higher occurrences of cultivable bacteria (~20 % of DAPI count) in some tropical mid-Atlantic regions with higher DOC and DON values (e.g. 14.66° N, Fig. 2) indicate their potential to resuscitate from the predominant non-cultivable state probably due to availability of degradable DOM.

Beyond the effect of temperature, variations in bacterial abundance, particularly *Vibrio* spp., can be better explained by the individual or combined changes in DOC and DON (Fig. 2). Microcosm studies have shown that the growth rate of *Vibrio* spp. can be higher than other prokaryotes upon efficient utilization of DOM which may aid in their persistence in particle-free seawater (Mouriño-Pérez et al., 2003; Weinbauer et al., 2006). Temperature alone may not properly explain bacterial dynamics in oceanic surface water unless the effects of DOC, DON and PP are also considered. Occurrences of higher DOC or DON at some eastern Atlantic stations did not correlate with Chl-*a* but coincided with higher Fe values or lower salinity (e.g. stations 13–17). Upwelling events near the equator or ITCZ, offshore transport of riverine discharge (e.g. Senegal river), and recently degraded phytoplankton blooms may contribute to the DOM increase. High Fe concentrations may facilitate fast plankton growth followed by its degradation and production of DOM to support bacterial population. In this context, the bioavailability and solubility of iron, introduced by the atmosphere, may play an important role (Jickells et al., 2005; Boyanapalli et al., 2007). The low abundance of particulate sources of C and N (DOC = 93 ± 3 % of TOC, DON = 85 ± 9 % of TON) in

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the surface suggests the presence of old DOM which may be mostly semi-labile or refractory. However, at regions with higher solar irradiation refractory DOM can be photochemically degraded into more labile and low molecular weight DOC which might be directly used by bacterioplankton (Kieber et al., 1989; Cherrier et al., 1999).

5 Conclusions

Our study illustrates an important role of DOM in regulating marine bacterial population. Most bacteria can survive without being associated with plankton (>20 µm) and seems to be not directly dependent on POC or PON, although phytoplankton or SPM is the primary source of DOM. Therefore, it can be argued that DOC and DON are important sources of carbon and nitrogen for bacterial growth and survival. The correlations between temperature, DOC, DON and bacterial abundance including cultivable *Vibrio* spp. in the Atlantic surface waters support this hypothesis. Bacterial influence on turnover of semi-labile DOM might be very important. Ubiquitous presence of cultivable *Vibrio* spp. in both surface and deep sea indicates this bacterial group as one of the key players in biogeochemical cycles. Temperature rise due to global warming may increase the abundance of bacteria including opportunistic *Vibrio* spp. and facilitate degradation of labile and semi-labile organic matter along with conservation of fixed carbon as refractory DOM. The complex interplay of temperature, DOC, DON and bacterial utilization of DOM clearly needs more research for better understanding the role of organic matter to support bacterial dynamics in the oligotrophic oceanic environment.

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Table 1. Average values of nutrients and selected biogeochemical parameters in different surface water samples[a].

Stations (samples[b])	Latitude/longitude	Salinity	Chl-*a* ($\mu g\,l^{-1}$)	DOC (μM C)	DON (μM N)	DIN[c] (μM N)	C/N of DOM	Silicate (μM Si)	Phosphate (μM P)	N/P inorg.	PON (μM N)	POC (μM C)	Fe (nM)
1 (S)	50.17° N/2.35° W	35.23	0.54	69.6	NM	NM	NM	NM	NM	NM	0.74	9.3	NM
2 (S, P)	48.53° N/6.11° W	35.29	2.25	64.1	4.3	1.51	14.9	1.55	0.15	10.4	1.36	8.5	NM
3 (S, C)	46.33° N/7.84° W	35.65	0.18	65.6	2.6	1.63	25.2	1.24	0.14	11.6	1.10	8.7	NM
4 (S)	44.04° N/10.29° W	35.90	0.78	66.3	4.3	0.68	15.4	0.81	0.10	7.2	1.04	6.7	1.20
5 (S, P)	42.77° N/11.66° W	35.92	0.77	67.8	6.8	0.55	10.0	0.88	0.09	6.4	0.76	4.5	0.66
6 (S)	39.45° N/12.68° W	36.07	0.45	68.4	3.5	0.18	19.5	1.00	0.06	3.0	0.68	4.3	0.54
7 (S, C)	37.12° N/13.36° W	36.30	0.31	70.9	1.8	0.10	41.7	0.78	0.08	1.3	0.41	2.8	0.98
8 (S)	33.70° N/14.43° W	36.86	0.24	70.0	8.0	0.17	8.8	1.38	0.06	2.8	0.30	2.0	0.88
9 (S, P)	30.80° N/14.93° W	36.89	0.15	75.4	6.8	0.11	11.1	0.83	0.06	1.8	0.40	2.7	4.15
10 (S)	26.68° N/16.38° W	36.82	0.31	66.4	4.9	0.06	13.6	0.79	0.05	1.2	0.57	3.4	1.15
11 (S, P, C)	22.50° N/20.50° W	36.90	0.68	69.7	5.5	0.12	12.7	0.67	0.08	1.5	0.91	6.8	2.78
12 (S)	17.72° N/20.81° W	36.46	0.45	66.7	5.8	BDL	11.5	0.73	0.07	0.3	0.68	5.3	2.26
13 (S, P)	14.66° N/20.98° W	35.55	1.42	94.7	10.3	0.23	9.2	0.40	0.07	3.2	0.48	3.3	2.58
14 (S, C)	10.63° N/20.13° W	35.34	0.24	80.9	4.3	0.29	18.8	1.24	0.60	0.5	1.69	11.8	4.33
15 (S)	8.16° N/19.19° W	34.47	0.22	75.3	6.9	0.17	10.9	1.26	0.06	3.1	0.50	5.1	4.74
16 (S, P)	5.43° N/16.46° W	34.21	0.15	81.9	8.1	0.26	10.1	1.60	0.05	5.8	0.51	3.2	5.98
17 (S)	2.47° N/14.15° W	34.65	0.15	79.9	5.0	0.25	15.9	0.96	0.06	4.5	0.74	5.1	4.28
18 (S)	0.15° S/12.19° W	36.03	0.14	74.3	3.1	0.08	24.0	1.06	0.06	1.3	0.55	4.3	1.20
19 (S, P)	3.17° S/9.37° W	36.10	0.24	69.9	4.6	0.07	15.2	1.31	0.06	1.2	0.50	3.0	0.93
20 (S, C)	5.09° S/7.06° W	36.15	0.29	72.8	3.7	BDL	19.8	1.21	0.11	0.2	0.73	3.9	2.44
21 (S)	9.08° S/4.38° W	36.10	0.16	79.6	2.8	BDL	28.4	1.38	0.06	0.3	0.70	3.8	0.88
22 (S, P)	11.70° S/2.14° W	36.41	0.11	81.0	2.2	0.08	36.8	1.17	0.07	1.1	0.46	3.2	1.45
23 (S, P)	14.95° S/0.69° E	36.13	0.30	75.6	4.0	0.48	19.1	1.17	0.24	2.1	0.41	2.6	0.81
24 (S, C)	17.73° S/3.13° E	35.89	0.33	70.6	4.2	2.64	16.8	1.05	0.35	7.5	1.06	6.7	0.59
25 (S)	20.65° S/5.73° E	35.54	0.40	71.9	3.5	3.86	20.5	0.93	0.51	7.6	1.23	6.8	0.55
26 (S, C)	23.72° S/8.52° E	35.56	0.50	65.5	2.2	0.30	29.8	1.28	0.22	1.4	1.14	7.3	0.47

[a] "NM" and "BDL" indicates "not measured" and "below detection limit", respectively; [b] S, P and C indicates sampling events, i.e. surface water, plankton and deep CTD sampling, respectively; [c] DIN includes NO_3^--N, NO_2^--N and NH_4^+-N with dominance of NO_3^--N.

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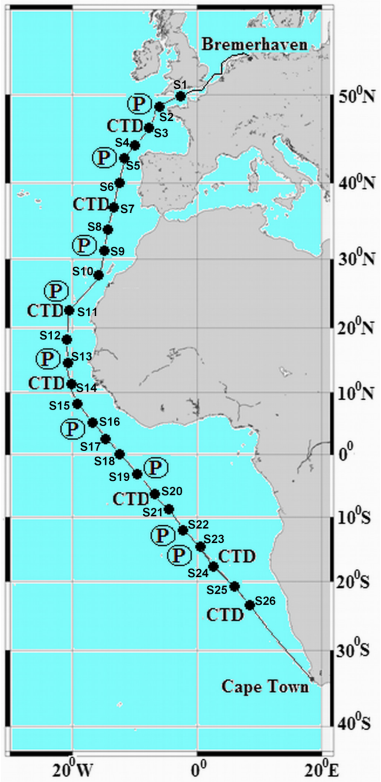

Fig. 1. Sampling stations during the Atlantic expedition with R/V *Polarstern* (ANT 25/1). Closed circles indicate stations (S1 to S26) where surface water samples were collected. "P" and "CTD" indicates the stations where plankton (>20 µm and >55 µm) samples and water samples from various depths (50–200 m, 1500–2500 m and 4000–5500 m) were collected.

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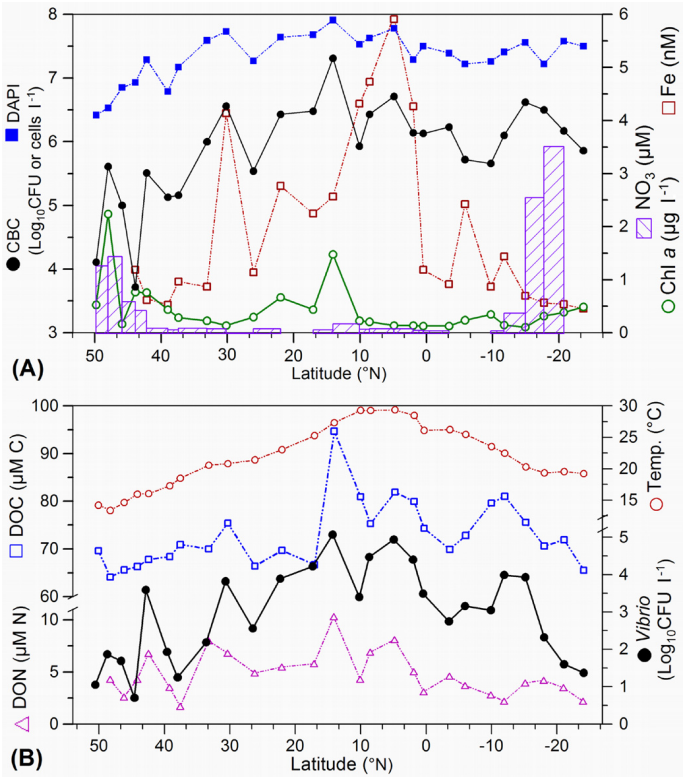

Fig. 2. Fluctuations of bacterial populations and important biogeochemical parameters at various sampling stations. **(A)** Change in culture independent DAPI counts, cultivable bacterial counts (CBC) along with NO_3, Fe and Chl-*a*. **(B)** Change in cultivable *Vibrio* population along with temperature (Temp.), dissolved organic C (DOC) and N (DON). Average values of bacteriological (triplicate) and biogeochemical parameters (quadruplicate) are shown. CBC and cultivable *Vibrio* counts were obtained using marine agar and TCBS agar, respectively.

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Biogeochemical controls on the oceanic bacterial population

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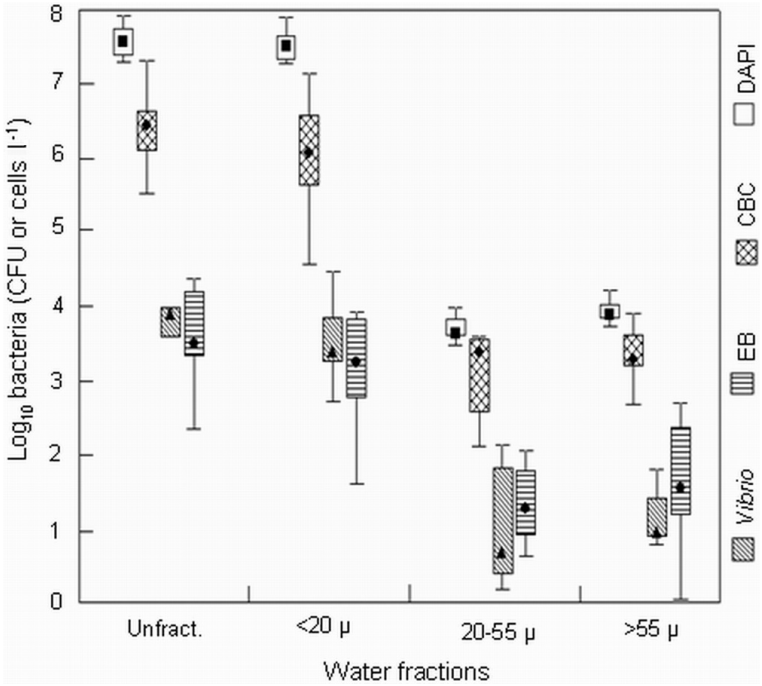

Fig. 3. Comparative abundance of bacteria in surface water fractions (<20 µm, 20–55 µm, >55 µm, unfract.: unfractionated) displayed as Box-Whiskers plots (Statistica). Samples were collected from nine discrete locations in the eastern Atlantic Ocean. The bottom and top of the box plots indicate the 25th and 75th percentile. Closed symbols in the box indicate median values. Vertical bar indicates standard deviation. DAPI and CBC represent culture independent total bacteria and cultivable bacterial count, respectively. *Vibrio* and EB (presumptive Enterobacteriaceae) represent counts on selective TCBS and MacConkey agars, respectively.

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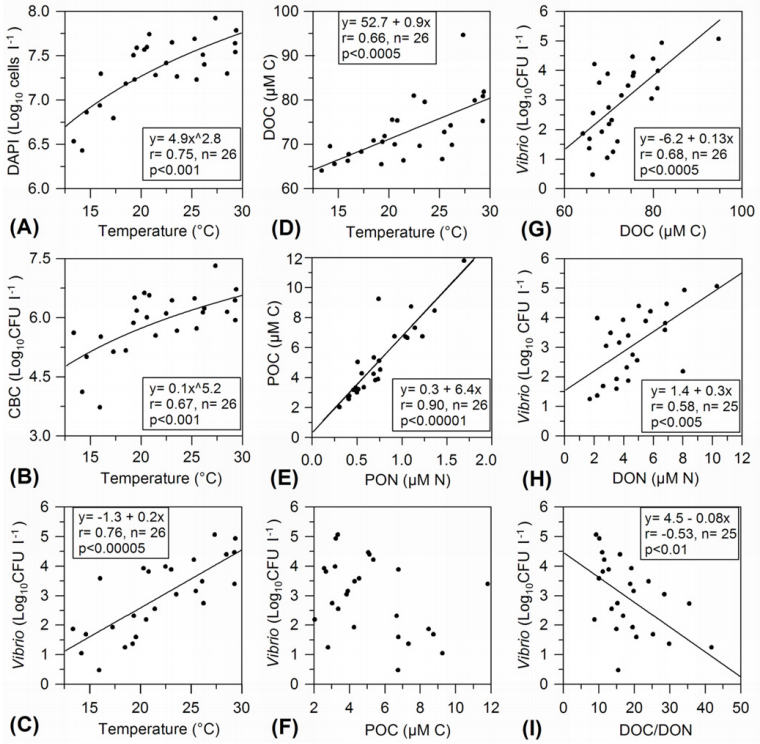

Fig. 4. Correlation among bacterial abundance and various biogeochemical factors. DAPI and CBC represent culture independent total bacteria and cultivable bacterial counts, respectively. DOC and DON represent dissolved organic C and N, while POC and PON represent particulate organic C and N, respectively. Lines represent linear or curvilinear regression between the two parameters. Regression equation and relevant information are shown in each box. There was no significant correlation between POC values and cultivable *Vibrio* counts as shown in **(F)**.

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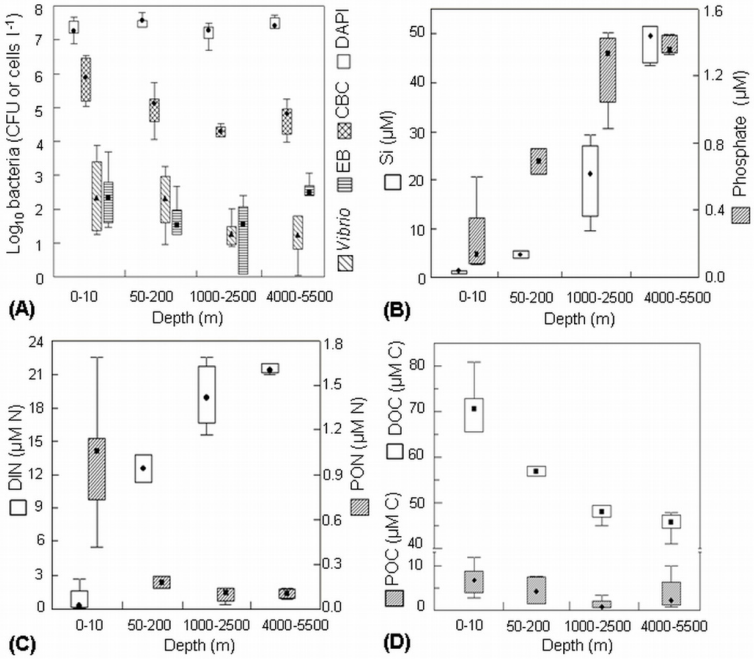

Fig. 5. Depth-wise changes in bacterial abundance and biogeochemical parameters. Samples were collected using a CTD rosette sampler from seven discrete locations in the eastern Atlantic Ocean. Box-Whiskers plots represent the composite scenario at each depth range. The bottom and top of the box indicate the 25th and 75th percentile. Closed symbols in the box indicate median values. Vertical bar indicates standard deviation. DAPI, CBC and EB represent counts of culture independent total bacteria, cultivable bacteria and presumptive Enterobacteriaceae, respectively. DOC represent dissolved organic C, while POC and PON represent particulate organic C and N, respectively. Dissolved inorganic N (DIN) includes NO_3^--N, NO_2^--N and NH_4^+-N with exclusive (mostly >95 %) dominance of NO_3^--N.

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