Microbial Ecology and Biogeography

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Southern Ocean

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List of Acronyms

PASSAGE 2 Pattern Analysis, Spatial Statistics and Geographic Exegesis version 2.

QIIME Quantitative Insights Into Microbial Ecology.

AABW Antarctic Bottom Water.

AAIW Antarctic Intermediate Water.

ANOSIM Analysis of Similarities.

AZ Antarctic Zone.

CDW Circumpolar Deep Water.

CMS Connectivity Modeling System.

CTD Conductivity, Temperature and Depth.

dbRDA Distance-based Redundancy Analysis.

DCM Deep Chlorophyll Maximum.

distLM Distance-based Linear Models.

ECCO Estimating the Circulation and Climate of the Ocean.

KEGG Kyoto Encyclopedia of Genes and Genomes.

LCD Lower Circumpolar Deep.

nMDS Non-Metric Multidimensional Scaling.

NZ North Zone.

OTU Operational Taxonomic Unit.

PF Polar Front.

PFZ Polar Frontal Zone.

SAF Subantarctic Front.

SAMW Subantarctic Mode Water.

SO Southern Ocean.

SOSE Southern Ocean State Estimate.

SZ South Zone.

UCD Upper Circumpolar Deep.

Acknowledgements

The advection effect as a driver of microbial biogeography

Sections of this chapter have been previously published in

Summary

Introduction

The central goal of microbial biogeography is to understand how the distribution and abundance of microorganisms are shaped by their physical context. The Baas Becking hypothesis — that "*everything is everywhere*, but, *the environment selects* (Baas Becking, 1934; de Wit and Bouvier, 2006)" — posits that the rapid dispersal of microorganisms means microbial community structure is determined entirely by environmental selection. This stands in contrast to macroorganism biogeography, which has long been recognised as being under the control of historical (in addition to contemporary environmental) factors, particularly spatial influences such as barriers to dispersal. Microbial biogeography studies have begun to show that historical factors may also shape the distribution of microorganisms (Martiny *et al.*, 2006), e.g. a correlation between spatial and genetic distance (a "distance effect") in fluorescent *Pseudomonas* strains in soils (Cho and Tiedje, 2000). This study, among others (Ramette and Tiedje, 2007; Storch and Sizling), also demonstrated the importance of taxonomic resolution in describing such biogeographic patterns. Other studies have found that dispersal potential varies between microbial species, leading to different or absent distance effects (Bissett *et al.*, 2010). When combined with contemporary environmental selection ("environment effect"), distance effects explain some but not all variation between microbial communities, and the mechanism(s) by which a distance effect arises are not always clear (Hanson *et al.*, 2012).

In the ocean, several recent studies have found that microbial communities can be endemic to hydrographically distinct water masses. Surveys in the Arctic (Galand *et al.*, 2009) and North Atlantic (Agogué *et al.*, 2011) oceans have found that bacterial assemblages within the same water mass can be similar across a range of thousands of kilometres, but assemblages can differ between water masses across a range of hundreds of meters. Water masses are defined by their distinct physicochemical properties, so such patterns do not directly imply the existence of factors beyond environmental selection. However, in some cases a water mass-community relationship has been shown to persist even when environment effects are statistically controlled for (Hamilton *et al.*, 2008; Hamdan *et al.*, 2013).

During the study on the biogeographic effect of the Polar Front (PF) described earlier in this volume, it was found that microbial communities in surface waters of the Mertz Glacier region, a site of deep water formation, were very similar to those at the bottom of the water column, despite the very different environmental conditions (see "*Preliminary analysis of Antarctic Bottom Water (AABW) samples*"). One hypothesis explaining both this observation and water mass endemicity is that microbial assemblages are influenced by the advection (physical transport) of cells by ocean currents. Higher dispersal rates cause the microbial community composition at a given site to increasingly resemble the dispersed colonisers, and less reflect local environmental selection and stochastic effects such as genetic drift (Hanson *et al.*, 2012). Hence, it would be expected that locations that are closely connected by advection (e.g. those within the same water mass, or different levels of the water column at a site of deep water formation) would have more similar compositions than those that are not, even when

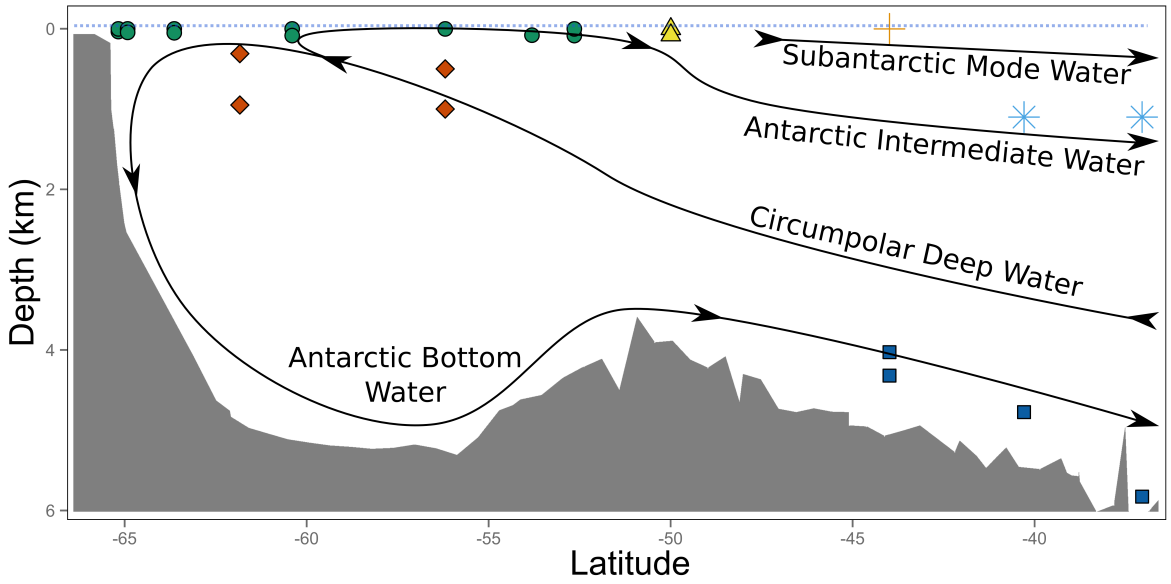

Figure 9: Antarctic Intermediate Waters (AAIW), light blue stars; Subantarctic Mode Water (SAMW), orange crosses; Antarctic Bottom Water (AABW), dark blue squares; Antarctic Zone (AZ), green circles; Polar Frontal Zone (PFZ), yellow triangles; Circumpolar Deep Water (CDW), red diamonds; sea surface, blue dashed horizontal line. Bathymetry is an approximate representation for 115° E, and is indicative only.

the environment effect is accounted for. Indeed, advection is often invoked to explain observations of microbial diversity or abundance which do not seem attributable to environmental selection (e.g. Sul *et al.*, 2013; Ghiglione *et al.*, 2012; Giebel *et al.*, 2009; Lauro *et al.*, 2007). The exchange of very small volumes of water between marine microbial mesocosms has been found to greatly reduce their β-diversity even under consistent environmental conditions (Declerck *et al.*, 2013). This suggests that advection of even small numbers of cells could have a large homogenizing effect independent of environmental selection. However, the existence of a relationship between advection and community composition that is independent of environment and distance effects has not been directly tested.

The Southern Ocean (SO) is composed of several water masses, which are physicochemically distinct but linked by circulation (see "*Introduction*" for a full description; see also Figure 9). This study aimed to determine whether advection shapes the community structure of bacteria and archaea, independent of environment and distance effects. By sampling each of the SO water masses (depths from surface to ∼6 km), dissimilarity between microbial communities over a large spatial distance (∼3000 km) and range of environments could be determined, in order to test whether advection played a role in shaping their composition.

Methods

Sampling

Sampling[5] was conducted on board the RSV *Aurora Australis* during cruise V3 from January 20th–February 7th 2012. This cruise occupied a latitudinal transect from waters north of Cape Poinsett, Antarctica (65° S) to south of Cape Leeuwin, Australia (37° S) within a longitudinal range of 113–115° E.

Sampling was performed as described in Wilkins *et al.* (2012a), with sites and depths selected to provide coverage of all major SO water masses. At each surface station, ∼250–560 L of seawater was pumped from ∼1.5–2.5 m depth. At some surface stations, an additional sample was taken from the Deep Chlorophyll Maximum (DCM), as determined by chlorophyll fluorescence measurements taken

[5]Sampling was performed by David Wilkins, Timothy J. Williams and Sheree Yau.

from a Conductivity, Temperature and Depth (CTD) cast at each station. Samples of mesopelagic and deeper waters (∼120–240 L) were also collected at some stations using Niskin bottles attached to the CTD. Sampling depths were selected based on temperature, salinity and dissolved oxygen profiles to capture water from the targeted water masses. Profiles were generated on the CTD descent, and samples collected on the ascent at the selected depths. Deep water masses were identified by the following criteria: Circumpolar Deep Water (CDW) = oxygen minimum (Upper Circumpolar Deep (UCD)) or salinity maximum (Lower Circumpolar Deep (LCD)); AABW = deep potential temperature minimum; Antarctic Intermediate Water (AAIW) = salinity minimum (Foldvik and Gammelsrød, 1988). Surface zones were identified relative to the major fronts of the SO, which are marked by strong latitudinal gradients in temperature and salinity (Sokolov and Rintoul, 2002; Orsi *et al.*, 1995). The Antarctic Zone (AZ) lies south of the PF (∼51° S at the time of sampling), while the Polar Frontal Zone (PFZ) lies between the PF and the Subantarctic Front (SAF). Subantarctic Mode Water (SAMW) overlays AAIW north of the SAF. In total, 25 samples from the AZ, PFZ, SAMW, AAIW, CDW and AABW were collected for this study (Figure 9).

Seawater samples were prefiltered through a 20 µm plankton net, then filtrate was captured on sequential 3.0 µm 0.8 µm and 0.1 µm 293 mm polyethersulfone membrane filters (Pall, Port Washington, USA), and immediately stored at −20 °C (Rusch *et al.*, 2007; Ng *et al.*, 2010).

DNA extraction

DNA extraction was performed using a modified version of the phenol-chloroform method described in Rusch *et al.* (2007). Samples were thawed in a 37 °C water bath. Half of the storage buffer (∼10 mL) was decanted into a clean 50 mL centrifuge tube. If the volume decanted was less than 10 mL, the difference was made with sterile water (Sigma-Aldrich, St. Louis, USA). An equal volume of 50% sucrose lysis buffer (50 mM TRIS-HCl, 40 mM EDTA, 0.75 M Sucrose, pH 8) was added such that the final concentration was 25% sucrose lysis buffer. A small pinch of lysozyme (Sigma-Aldrich, St. Louis, USA) (final concentration ∼2.5 mg/mL) and 1 mL TRIS-EDTA (10 mM TRIS, 1 mM EDTA, pH 8) was added.

The filter membrane was removed from the storage tube and cut in half aseptically. One half was returned to the storage tube, which was refrozen at −80 °C. The remaining half was cut in half again, and one quarter-filter placed atop the other such that the biomass (filtrand) on each piece was facing outwards. Keeping the filters together, they were cut into very fine (∼3 mm by 10 mm) strips, which were placed in the 50 mL centrifuge tube containing the buffer and lysozyme mixture. This tube was mixed by gentle inversion, then tapped such that all filter strips collected at the bottom of the tube and were covered by lysis buffer. The tube was then incubated in a 37 °C shaking water bath at 275 RPM for 30–60 min.

200 µL of 20 mg/mL Proteinase K (Sigma-Aldrich, St. Louis, USA) was added to the tube, which was mixed by gentle inversion. The tube was gently tapped such that all filter strips collected at the bottom covered by lysis buffer. The tube was then subjected to three freeze-thaw cycles, each cycle consisting of 20–30 min in a −80 °C freezer followed by 20–30 min in a 55 °C water bath. After the final complete thaw, 200 µL of 20 mg/mL Proteinase K and 2 mL of 10% SDS (Sigma-Aldrich, St. Louis, USA) were added to the tube. The tube was mixed by gentle inversion then gently tapped such that all filter strips collected at the bottom covered by lysis buffer. It was then incubated in a 55 °C shaking water bath at 175 RPM for two hours.

The supernatant was pipetted from the tube using a genomic tip and split evenly into two new 50 mL centrifuge tubes. An equal volume of buffer-saturated (10 mM TRIS HCl, 1 mM EDTA, pH 8) phenol (Sigma-Aldrich, St. Louis, USA) was added to each of the tubes, which were mixed by gentle inversion. The mixtures were then fractionated in a fixed-angle rotor centrifuge for 15 min at 3700 RPM at room temperature. The bottom layer of each tube was removed by pipette into a new 50 mL centrifuge tube. Each of these two tubes was then made to 50 mL with sterile water (Sigma-Aldrich, St. Louis, USA). After mixing by gentle inversion, each 50 mL mixture was then split evenly into two new 50 mL centrifuge tubes, resulting in four tubes each containing 25 mL of mixture. These tubes were then made to 50 mL with 1-propanol (Sigma-Aldrich, St. Louis, USA). The mixtures were homogenised by gentle inversion and incubated at 4 °C overnight.

Following incubation, the tubes were centrifuged using a fixed-angle rotor for 30 min at 7500 RPM and room temperature. The majority of the supernatant was removed by decanting, and the tubes left

to sit until the remaining supernatant (∼1 mL) collected at the bottom over the precipitated pellet. The pellet was then resuspended by gentle pipetting with a genomic tip, and the suspension placed in a new 1.5 mL microcentrifuge tube (four tubes total). These tubes were then centrifuged in a microcentrifuge for 10 minutes at 13,000 RPM and room temperature. The supernatant was removed by pipette and the tubes placed in a 37 °C heat block with the lids opened and covered by a sterile KimWipe (Kimberly-Clark, Irving, USA) for 10 min, or longer if the supernatant did not evaporate completely in that time. 93.75 µL of TRIS-EDTA was added to each tube, and the tubes were incubated at 4 °C for one hour to allow the DNA pellet to redissolve.

After this incubation, the pellets were gently pipetted with a genomic tip to ensure complete resuspension. The suspensions from all four tubes were combined, and an additional 750 µL of TRIS-EDTA added. This was then split evenly into two new 1.5 mL microcentrifuge tubes (∼562.5 µL per tube).

750 µL of buffer-saturated phenol was added to each tube, and the tubes mixed gently by inversion until a visible emulsion formed. Phase separation was performed by centrifugation for 5 min at 13,000 RPM and room temperature. The upper (aqueous) phase was removed to a new 1.5 mL microcentrifuge tube using a genomic tip.

750 µL of phenol-chloroform-isoamyl alcohol (25:24:1) mixture (Sigma-Aldrich, St. Louis, USA) was added to each tube, and the tubes mixed by gentle inversion until a visible emulsion formed. Phase separation was performed by centrifugation for 5 min at 13,000 RPM and room temperature. The upper (aqueous) phase was removed to a new 1.5 mL microcentrifuge tube using a genomic tip.

75 µL of 3 M sodium acetate (pH 8) and 750 µL of 1-propanol was added to each tube. The tubes were centrifuged at 13,000 RPM and room temperature for 30 min to precipitate the DNA. The supernatant was removed by pipetting, and 100 µL of 70% ethanol added. The tubes were centrifuged again at 13,000 RPM and room temperature for 5 min. The supernatant was removed by pipetting and the DNA pellet dried in a 37 °C heat block. The DNA was dissolved overnight in 40–200 µL of TRIS-EDTA, depending on the expected yield.

Sequencing

Tag pyrosequencing was performed by Research and Testing Laboratory (Lubbock, USA) on a GS FLX+ platform (Roche, Branford, USA), using a modification of the standard 926F/1392R primers targeting the V6–V8 hypervariable regions of bacterial and archaeal 16S rRNA genes (926wF: AAA-CTY-AAA-KGA-ATT-GRC-GG, 1392R: ACG-GGC-GGT-GTG-TRC). The additional wobble bases have been found to amplify a greater range of environmental bacteria and archaea, particularly Euryarchaeota, than the standard primers (Federico M. Lauro, personal communication). Denoising, chimera removal and trimming of poor quality read ends were performed by the sequencing facility.

Taxonomic assignment

Using Quantitative Insights Into Microbial Ecology (QIIME) 1.6.0 (Caporaso *et al.*, 2010), tag pyrosequencing reads were clustered at the 97% sequence similarity level against the SILVA database of rRNA sequences (release 108, eukaryote and chloroplast sequences removed) (Quast *et al.*, 2013), with non-clustering reads discarded. QIIME was used to assign to each Operational Taxonomic Unit (OTU) cluster a description representing the most detailed lineage common to at least 90% of the clustered reads, with ranks labelled "uncultured" or "other" ignored. To generate a taxonomic profile for each sample, the relative abundances of reads assigned to each OTU in each size fraction were encoded as variables. To account for the reads discarded during clustering, abundances in each size fraction were standardised by the proportion of reads retained from that fraction. The abundances were square root transformed and Bray-Curtis dissimilarity indices between samples calculated in PRIMER 6 (PRIMER-E, Lutton, UK).)

Physicochemical and spatial distances

Environmental data were collected from CTD casts at each sample site. Pressure, dissolved oxygen concentration and water temperature measurements were collected with CTD instruments. Salinity and concentrations of dissolved phosphate, nitrate and silicate were obtained from hydrochemical

analysis of seawater samples collected in Niskin bottles during CTD casts (Rosenberg and Rintoul, 2012). These samples were collected at discrete depths, and the hydrochemical sample closest to the depth of the relevant biological sample was selected. The exceptions were samples 32 and 33 (49.5° S, 115° E), for which nitrate concentrations were not available, and sample 29 (53.2° S, 115° E) for which phosphate concentration was not available. In these cases, a reading from the appropriate depth was substituted from the nearest available cast (50.0° S, 115° E for samples 32 and 33; 53.8° S, 115° E for sample 29). Pressure values were $log(x + 1)$ transformed to reduce right-skew (Clarke and Gorley, 2006) and the combined instrument and hydrochemical data were used to create environmental profiles for each sample. The variables were normalised and a Euclidean distance matrix generated in PRIMER 6.

Distance-based Linear Models (distLM) multivariate analysis (Legendre and Anderson, 1999) was performed to confirm the selection of physicochemical variables and explore their relationship with taxonomic composition. In PRIMER 6, all possible combinations of variables ("BEST selection") were explored by distLM, and the models (sets of variables) that best fit the taxonomic dissimilarity matrix (adjusted R^2 as the fitness measure) were selected. The relationship between the resulting model and the taxonomic dissimilarity between samples was visualised by Distance-based Redundancy Analysis (dbRDA) ordination.

To generate a spatial distance matrix, pairwise ellipsoidal distances between samples (including difference in depth) were calculated using INVERS3D (National Oceanic and Atmospheric Administration, Silver Springs, USA).

Generation of advection distance matrix

Erik van Sebille contributed to writing the following paragraph.

Advection distances between the sites were computed using three-dimensional velocity data from a hydrodynamic numerical ocean model in combination with a Lagrangian trajectory toolset[6]. The ocean model used was the Southern Ocean State Estimate (SOSE) (Mazloff *et al.*, 2010), a numerical model of the SO based on the Estimating the Circulation and Climate of the Ocean (ECCO) machinery (Wunsch and Heimbach, 2007) and constrained by a large set of in situ and remote-sensed observations. SOSE has been validated in the SO (Cerovečki *et al.*, 2011; Firing *et al.*, 2011). Here, the five-day averaged three-dimensional velocity fields for the period January 2005–December 2007 were used, on a 1/6° horizontal resolution and with 42 vertical levels. The Connectivity Modeling System (CMS) (Paris *et al.*, 2013) 1.1 was used to integrate virtual Lagrangian particles within the SOSE velocity fields. For each site, 100 particles were released every 5 days (total of 2.2×10^4 per site). The particles were released at the latitude and depth of the site, evenly spaced in a 1° longitudinal line centred at the site longitudes. The particles were then advected for 100 years, looping through the 3 years of available velocity fields as described in van Sebille *et al.* (2012). Three-dimensional locations of the particles were saved every 5 days.

The trajectory of each particle was analysed to detect encounters between particles and sample sites. An encounter was defined as the vector between any two consecutive 5 day particle locations intersecting a box bounded by ±0.2° of latitude, ±0.5° of longitude and ±50 m of depth from a sample site. Only the first encounter between any particle and sample was counted. Four pairs of samples (10/11; 12/13; 16/17; 21/22), where a DCM sample was taken directly below a surface sample within the mixed layer, were too close to act as separate particle release sites. For these samples, simulated particle releases were performed for only one of the pair, and the generated encounters were attributed to both. For all samples, the mean time in seconds between a particle being released from one sample and encountering another was calculated. Pairwise advective distance between samples was defined as the mean of the two directional mean times between each sample in the pair. This metric was selected to ensure advective flows which may be of high biological relevance, such as a small number of particles quickly transported between sites, were appropriately weighted when paired with flows of lower biological relevance, such as a large number of particles transported between sites over decades. To ensure the results were robust to the choice of metric, subsequent statistical tests were repeated with pairwise advective distance redefined as the mean time for all pairwise encounters. The pairwise distance between the surface/DCM samples discussed above was set to zero. For pairs of samples that

[6]Modelling was performed by Erik van Sebille.

did not yield mutual encounters (47 pairs, all including at least one AABW sample; see Results), this was set to the maximum run time of the simulation (100 years). Subsequent statistical tests were rerun with the DCM and AABW samples excluded to ensure these constraints were not unduly influencing the results (see "Testing of advection effect", below).

Ordination of distance matrices and comparison to water masses

Ordinations of the taxonomic, environmental and advection distance matrices were produced by Non-Metric Multidimensional Scaling (nMDS) in PRIMER 6. Analysis of Similarities (ANOSIM) was also performed in PRIMER 6 to test for statistically significant differences between water masses in each of these three factors. Right-tailed p-values for each test were computed using 999 random label permutations of one of the test matrices.

Testing of advection effect

Mantel tests were performed using Pattern Analysis, Spatial Statistics and Geographic Exegesis version 2 (PASSAGE 2) (Rosenberg and Anderson, 2011). To test for and quantify distance and environment effects, partial Mantel tests were performed comparing the taxonomic matrix to the spatial then environmental matrices, with the remaining matrix held constant. To test the hypothesis that advection shapes SO microbial assemblages independent of distance and environment effects, a partial Mantel test was performed comparing the taxonomic and advection matrices, with both the spatial and environmental matrices held constant. Right-tailed p-values for all tests were calculated using 999 random label permutations of one the test matrices.

To ensure that the result was not unduly influenced by the samples to which the 100 year ceiling was applied (all AABW, see Results) and those for which particle releases were not simulated (samples 11, 13, 17 and 22), the test was repeated with these samples removed.

To confirm that the advection effect was directional, i.e. that "upstream" sites were acting as sources of diversity to "downstream" sites, SOURCETRACKER (Knights *et al.*, 2011) was used to identify sources of OTUs in each sample. Each sample was sequentially designated a sink, with the remaining samples as potential sources, and the most probable proportion of OTUs originating from each potential source determined over 100 randomised trials per sample. Spearman's rank correlation was then calculated between the SOURCETRACKER predicted source proportions and particle encounter source proportions for each sample pairwise, with right-tailed p-value determined by permutation.

Results

Sequencing and taxonomic assignment

After trimming, denoising and chimera removal, the 25 samples (each with three separately sequenced size fractions) yielded 1,008,963 pyrosequencing reads of length 251–561 bp (mean 426 bp). Individual fractions yielded 3,687–52,192 reads (mean 13,453). After clustering against the SILVA database, 2,295–30,760 (mean 9,618) reads per fraction were retained for taxonomic assignment.

1417 unique OTUs were identified across all fractions of all samples. The Chao 1 statistic was calculated, and estimated OTU were under-sequenced by 0–50% across all samples (mean 26%) (Table 8). In all water masses, decreasing numbers of reads yielded OTU assignments as size fraction increased (Figure 10). This probably reflects an increasing number of eukaryotic cells (which were excluded from OTU assignment) on the higher fractions.

Table 8: Full location, summary of taxonomic assignments and full physicochemical data for each of the 25 samples in this study. Units are given in column headers. Water mass abbreviations are Antarctic Intermediate Waters (AAIW); Subantarctic Mode Water (SAMW); Antarctic Bottom Water (AABW); Antarctic Zone (AZ); Polar Frontal Zone (PFZ); Circumpolar Deep Water (CDW).

Sample	Fraction (µm)	Date	Latitude (°)	Longitude (°)	Depth (m)	Water mass	OTU count	Chao 1	Pressure (dbar)	Dissolved O_2 (µmol/L)	Temperature) (°C)	Phosphate (µmol/L)	Nitrate (µmol/L)	Silicate (µmol/L)	Salinity (PSU)
10	0.1	2012-01-20	−65.17	113.1	35	AZ	431	570	36	348.1	−1.125	1.82	26.73	60.6	33.6
10	0.8	2012-01-20	−65.17	113.1	35	AZ	444	593	36	348.1	−1.125	1.82	26.73	60.6	33.6
10	3.0	2012-01-20	−65.17	113.1	35	AZ	148	293	36	348.1	−1.125	1.82	26.73	60.6	33.6
11	0.1	2012-01-20	−65.17	113.1	2	AZ	433	655	2	365.7	−0.798	1.66	25.13	57.8	33.4
11	0.8	2012-01-20	−65.17	113.1	2	AZ	241	422	2	365.7	−0.798	1.66	25.13	57.8	33.4
11	3.0	2012-01-20	−65.17	113.1	2	AZ	145	202	2	365.7	−0.798	1.66	25.13	57.8	33.4
12	0.1	2012-01-21	−64.92	113.3	2	AZ	294	387	2	356.4	−0.358	1.70	25.87	55.0	33.7
12	0.8	2012-01-21	−64.92	113.3	2	AZ	68	79	2	356.4	−0.358	1.70	25.87	55.0	33.7
12	3.0	2012-01-21	−64.92	113.3	2	AZ	158	232	2	356.4	−0.358	1.70	25.87	55.0	33.7
13	0.1	2012-01-21	−64.92	113.3	45	AZ	259	363	46	314.9	−1.604	2.05	30.17	65.8	34.2
13	0.8	2012-01-21	−64.92	113.3	45	AZ	299	418	46	314.9	−1.604	2.05	30.17	65.8	34.2
13	3.0	2012-01-21	−64.92	113.3	45	AZ	115	160	46	314.9	−1.604	2.05	30.17	65.8	34.2
16	0.1	2012-01-22	−63.64	113.3	2	AZ	245	338	2	355.9	0.500	1.62	24.60	47.1	33.8
16	0.8	2012-01-22	−63.64	113.3	2	AZ	210	307	2	355.9	0.500	1.62	24.60	47.1	33.8
16	3.0	2012-01-22	−63.64	113.3	2	AZ	135	222	2	355.9	0.500	1.62	24.60	47.1	33.8
17	0.1	2012-01-22	−63.64	113.3	50	AZ	169	219	50	319.1	−1.352	2.06	29.69	63.3	34.2
17	0.8	2012-01-22	−63.64	113.3	50	AZ	227	315	50	319.1	−1.352	2.06	29.69	63.3	34.2
17	3.0	2012-01-22	−63.64	113.3	50	AZ	199	290	50	319.1	−1.352	2.06	29.69	63.3	34.2
18	0.1	2012-01-24	−61.84	113.5	310	CDW	474	666	314	186.8	1.909	2.35	34.09	83.2	34.6
18	0.8	2012-01-24	−61.84	113.5	310	CDW	466	676	314	186.8	1.909	2.35	34.09	83.2	34.6
18	3.0	2012-01-24	−61.84	113.5	310	CDW	136	172	314	186.8	1.909	2.35	34.09	83.2	34.6
19	0.1	2012-01-24	−61.84	113.5	950	CDW	138	205	962	202.4	1.624	2.18	31.59	95.1	34.7
19	0.8	2012-01-24	−61.84	113.5	950	CDW	124	153	962	202.4	1.624	2.18	31.59	95.1	34.7
19	3.0	2012-01-24	−61.84	113.5	950	CDW	214	315	962	202.4	1.624	2.18	31.59	95.1	34.7
21	0.1	2012-01-25	−60.40	115.0	2	AZ	287	385	2	335.8	2.462	1.75	26.62	16.2	33.9
21	0.8	2012-01-25	−60.40	115.0	2	AZ	217	296	2	335.8	2.462	1.75	26.62	16.2	33.9
21	3.0	2012-01-25	−60.40	115.0	2	AZ	153	240	2	335.8	2.462	1.75	26.62	16.2	33.9
22	0.1	2012-01-25	−60.40	115.0	85	AZ	318	458	86	336.4	1.724	1.96	28.52	24.7	33.9
22	0.8	2012-01-25	−60.40	115.0	85	AZ	298	418	86	336.4	1.724	1.96	28.52	24.7	33.9
22	3.0	2012-01-25	−60.40	115.0	85	AZ	323	420	86	336.4	1.724	1.96	28.52	24.7	33.9
25	0.1	2012-01-27	−56.19	115.0	500	CDW	297	423	506	187.7	2.296	2.39	35.09	72.9	34.5
25	0.8	2012-01-27	−56.19	115.0	500	CDW	595	736	506	187.7	2.296	2.39	35.09	72.9	34.5
25	3.0	2012-01-27	−56.19	115.0	500	CDW	307	396	506	187.7	2.296	2.39	35.09	72.9	34.5
26	0.1	2012-01-27	−56.19	115.0	1000	CDW	257	316	1012	190.1	2.107	2.23	32.90	80.7	34.7
26	0.8	2012-01-27	−56.19	115.0	1000	CDW	438	510	1012	190.1	2.107	2.23	32.90	80.7	34.7
26	3.0	2012-01-27	−56.19	115.0	1000	CDW	380	584	1012	190.1	2.107	2.23	32.90	80.7	34.7
27	0.1	2012-01-27	−56.19	115.0	2	AZ	368	491	2	324.8	4.159	1.64	25.32	9.60	33.8
27	0.8	2012-01-27	−56.19	115.0	2	AZ	318	454	2	324.8	4.159	1.64	25.32	9.60	33.8
27	3.0	2012-01-27	−56.19	115.0	2	AZ	288	394	2	324.8	4.159	1.64	25.32	9.60	33.8

Continued on following page.

Table 8: (cont.) Full sample data for advection study.

Sample	Fraction (µm)	Date	Latitude (°)	Longitude (°)	Depth (m)	Water mass	OTU count	Chao 1	Pressure (dbar)	Dissolved O_2 (µmol/L)	Temperature) (°C)	Phosphate (µmol/L)	Nitrate (µmol/L)	Silicate (µmol/L)	Salinity (PSU)
29	0.1	2012-01-28	−53.81	115.0	80	AZ	281	394	80	324.4	4.399	1.66	24.78	7.80	33.8
29	0.8	2012-01-28	−53.81	115.0	80	AZ	261	377	80	324.4	4.399	1.66	24.78	7.80	33.8
29	3.0	2012-01-28	−53.81	115.0	80	AZ	271	403	80	324.4	4.399	1.66	24.78	7.80	33.8
30	0.1	2012-01-29	−52.65	115.0	85	AZ	217	341	86	330.8	3.517	1.73	26.27	15.7	33.8
30	0.8	2012-01-29	−52.65	115.0	85	AZ	244	358	86	330.8	3.517	1.73	26.27	15.7	33.8
30	3.0	2012-01-29	−52.65	115.0	85	AZ	269	393	86	330.8	3.517	1.73	26.27	15.7	33.8
31	0.1	2012-01-29	−52.65	115.0	2	AZ	392	486	2	332.2	3.941	1.70	26.15	15.4	33.8
31	0.8	2012-01-29	−52.65	115.0	2	AZ	317	470	2	332.2	3.941	1.70	26.15	15.4	33.8
31	3.0	2012-01-29	−52.65	115.0	2	AZ	332	425	2	332.2	3.941	1.70	26.15	15.4	33.8
32	0.1	2012-01-30	−49.99	115.0	2	PFZ	297	407	2	306.9	7.412	1.40	22.74	4.00	33.9
32	0.8	2012-01-30	−49.99	115.0	2	PFZ	269	337	2	306.9	7.412	1.40	22.74	4.00	33.9
32	3.0	2012-01-30	−49.99	115.0	2	PFZ	225	304	2	306.9	7.412	1.40	22.74	4.00	33.9
33	0.1	2012-01-30	−49.99	115.0	80	PFZ	325	422	80	300.3	7.061	1.39	23.02	4.20	34.0
33	0.8	2012-01-30	−49.99	115.0	80	PFZ	352	547	80	300.3	7.061	1.39	23.02	4.20	34.0
33	3.0	2012-01-30	−49.99	115.0	80	PFZ	326	473	80	300.3	7.061	1.39	23.02	4.20	34.0
38	0.1	2012-02-03	−43.99	115.0	2	SAMW	383	494	2	279.1	13.02	0.59	4.540	1.40	34.7
38	0.8	2012-02-03	−43.99	115.0	2	SAMW	215	220	2	279.1	13.02	0.59	4.540	1.40	34.7
38	3.0	2012-02-03	−43.99	115.0	2	SAMW	177	181	2	279.1	13.02	0.59	4.540	1.40	34.7
39	0.1	2012-02-03	−43.99	115.0	4320	AABW	520	682	4400	217.5	0.8497	2.30	32.92	127	34.7
39	0.8	2012-02-03	−43.99	115.0	4320	AABW	158	215	4400	217.5	0.8497	2.30	32.92	127	34.7
39	3.0	2012-02-03	−43.99	115.0	4320	AABW	129	152	4400	217.5	0.8497	2.30	32.92	127	34.7
40	0.1	2012-02-03	−43.99	115.0	4028	AABW	77	102	4100	216.9	0.8503	2.29	32.94	126	34.7
40	0.8	2012-02-03	−43.99	115.0	4028	AABW	156	203	4100	216.9	0.8503	2.29	32.94	126	34.7
40	3.0	2012-02-03	−43.99	115.0	4028	AABW	42	48	4100	216.9	0.8503	2.29	32.94	126	34.7
44	0.1	2012-02-05	−40.29	115.0	4775	AABW	248	303	4866	217.9	0.8716	2.28	33.15	130	34.7
44	0.8	2012-02-05	−40.29	115.0	4775	AABW	405	497	4866	217.9	0.8716	2.28	33.15	130	34.7
44	3.0	2012-02-05	−40.29	115.0	4775	AABW	370	442	4866	217.9	0.8716	2.28	33.15	130	34.7
45	0.1	2012-02-05	−40.29	115.0	1100	AAIW	601	779	1112	199.4	4.321	2.12	31.29	33.9	34.4
45	0.8	2012-02-05	−40.29	115.0	1100	AAIW	150	151	1112	199.4	4.321	2.12	31.29	33.9	34.4
45	3.0	2012-02-05	−40.29	115.0	1100	AAIW	118	124	1112	199.4	4.321	2.12	31.29	33.9	34.4
46	0.1	2012-02-07	−37.05	115.0	1100	AAIW	166	176	1112	201.7	5.233	2.20	32.12	39.5	34.4
46	0.8	2012-02-07	−37.05	115.0	1100	AAIW	227	312	1112	201.7	5.233	2.20	32.12	39.5	34.4
46	3.0	2012-02-07	−37.05	115.0	1100	AAIW	251	360	1112	201.7	5.233	2.20	32.12	39.5	34.4
47	0.1	2012-02-07	−37.05	115.0	5827	AABW	138	248	5952	217.2	1.030	2.29	33.00	129	34.7
47	0.8	2012-02-07	−37.05	115.0	5827	AABW	379	509	5952	217.2	1.030	2.29	33.00	129	34.7
47	3.0	2012-02-07	−37.05	115.0	5827	AABW	106	123	5952	217.2	1.030	2.29	33.00	129	34.7

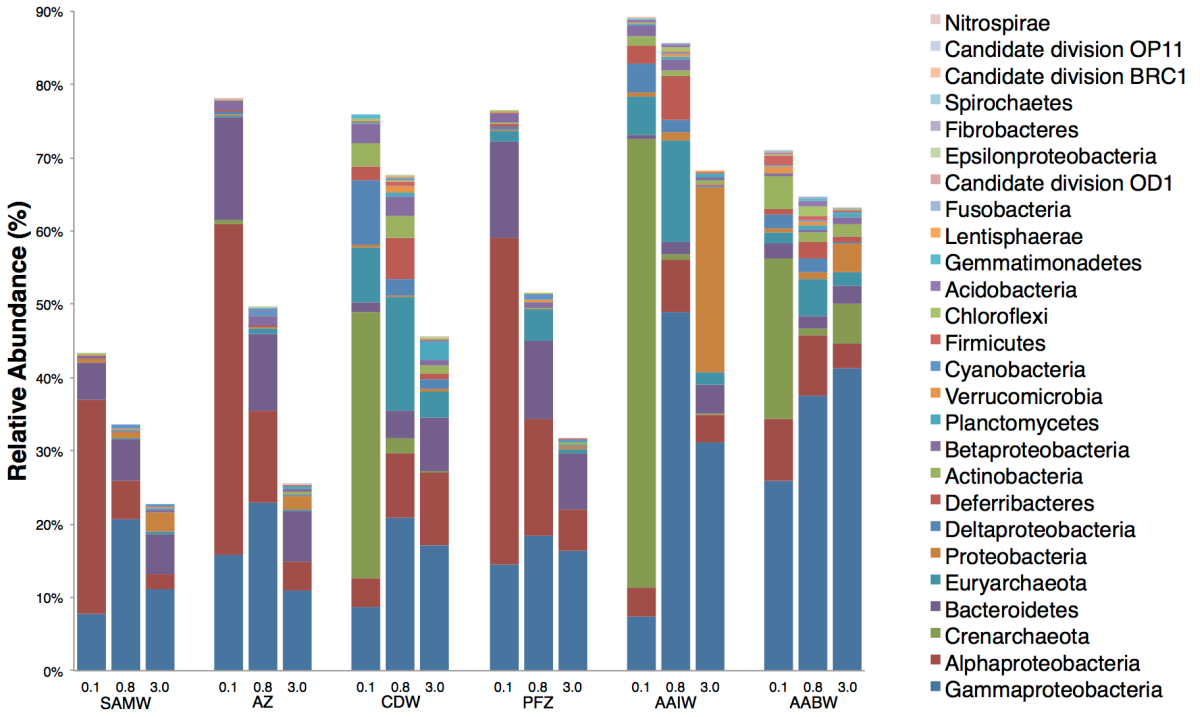

Figure 10: Taxonomic assignments for each sampled water mass. Water masses (x-axis): Subantarctic Mode Water (SAMW); Antarctic Zone (AZ); Circumpolar Deep Water (CDW); Polar Frontal Zone (PFZ); Antarctic Intermediate Water (AAIW); Antarctic Bottom Water (AABW). Size fractions are given in µm. All OTUs aggregated to phylum, except for members of the Proteobacteria which were aggregated to class when known. Relative abundance is percentage of all reads assigned to a given taxonomic group and has been scaled to account for unassigned reads.

nMDS ordination showed that the sampled water masses could be distinguished on the basis of taxonomic distance (Figure 11). This was supported by ANOSIM analysis ($R = 0.77$, $p = 0.001$). While each water mass had a distinct taxonomic profile, some broad differences between surface and deep masses were observed (Figure 10). Surface waters (AZ, PFZ, SAMW) were dominated by representatives of the Alphaproteobacteria, Bacteroidetes and Gammaproteobacteria. The high abundance of Bacteroidetes at the surface reflects their association with phytoplankton, as many species in this lineage specialise in the degradation of high molecular weight products of primary production (Williams *et al.*, 2012b). Alphaproteobacteria were represented primarily by the SAR11 clade, abundant in ocean surface communities (Morris *et al.*, 2002) including the SO (Brown *et al.*, 2012), and Roseobacter clades, which have also been associated with degradation of phytoplankton products (Williams *et al.*, 2012b; Giebel *et al.*, 2009). The dominant Gammaproteobacterial orders were the Alteromonadales and Oceanospirillales, typical of SO surface waters (Wilkins *et al.*, 2012b). Few archaeal OTUs were detected, consistent with their well-described decline in abundance during summer (Murray *et al.*, 1998; Grzymski *et al.*, 2012). The deep water masses (CDW, AAIW, AABW) were dominated by Crenarchaeota, Euryarchaeota and Gammaproteobacteria, again consistent with previous findings (López-García *et al.*, 2001).

Environment and distance effects

nMDS ordination showed that the sampled water masses clustered well on the basis of environmental distance (Figure 12). This was supported by ANOSIM ($R = 0.84$, $p = 0.001$). A partial Mantel test, comparing the taxonomic to environmental matrices with the spatial matrix held constant, found a correlation of $r = 0.48$ ($p = 0.001$), indicating a strong environment effect.

distLM analysis of the individual physicochemical variables found that considered separately, each of phosphate, silicate, nitrate, oxygen, salinity and pressure explained 17–35% of the taxonomic variance between samples ($p = 0.001$). Temperature had no significant effect on taxonomic composition when considered separately ($p > 0.05$). When all combinations of variables were considered (BEST

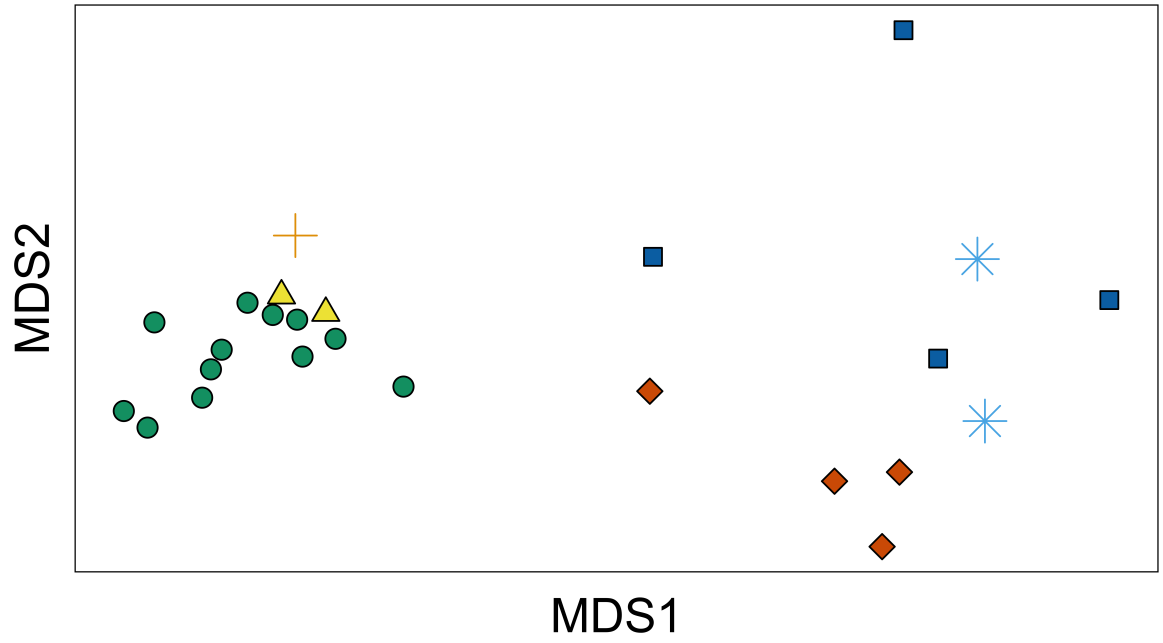

Figure 11: nMDS ordination of the taxonomic distance matrix (2D stress = 0.08). Antarctic Intermediate Waters (AAIW), light blue stars; Subantarctic Mode Water (SAMW), orange crosses; Antarctic Bottom Water (AABW), dark blue squares; Antarctic Zone (AZ), green circles; Polar Frontal Zone (PFZ), yellow triangles; Circumpolar Deep Water (CDW), red diamonds.

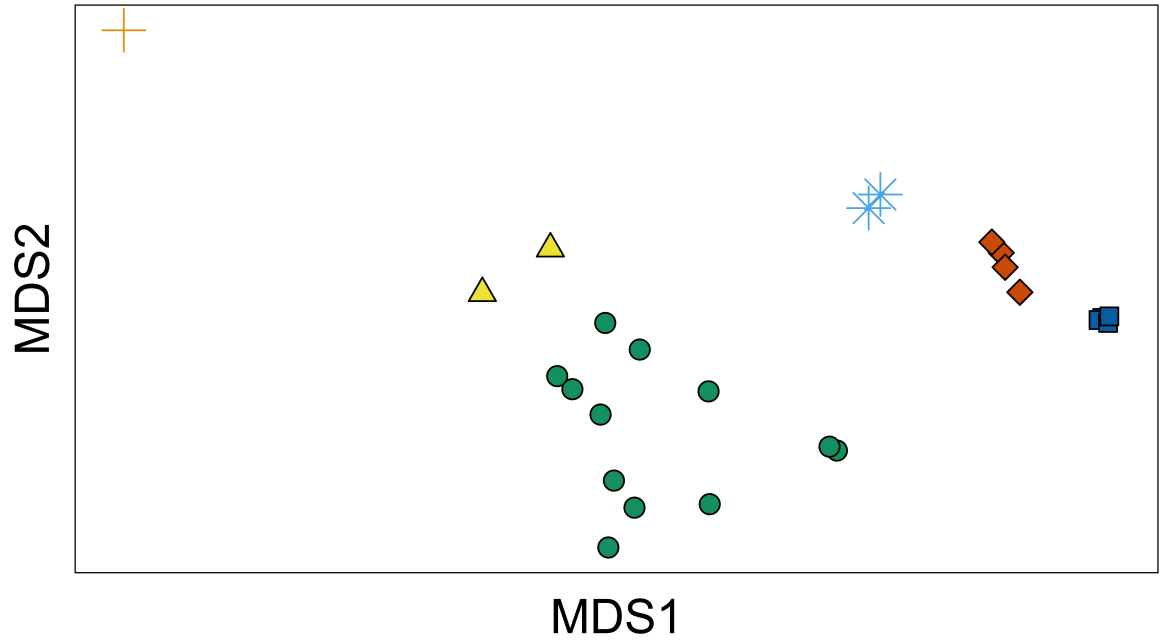

Figure 12: nMDS ordination of the environmental distance matrix (2D stress = 0.02). Antarctic Intermediate Waters (AAIW), light blue stars; Subantarctic Mode Water (SAMW), orange crosses; Antarctic Bottom Water (AABW), dark blue squares; Antarctic Zone (AZ), green circles; Polar Frontal Zone (PFZ), yellow triangles; Circumpolar Deep Water (CDW), red diamonds.

modelling), the best model consisted of all variables with the exception of phosphate (adjusted R^2 = 0.44), with the full set of variables only marginally worse (adjusted R^2 = 0.43). The rejection of phosphate may reflect a redundancy in the measurement of both phosphate and nitrate; these are often held to be constant throughout the ocean at the Redfield ratio of N:P ∼16:1 (Anderson and Sarmiento, 1994). However, deviation from this ratio has been observed in the SO and related to iron concentration (which was not measured in this study) and to phytoplankton abundance (Weber and Deutsch, 2010). For these reasons, and because of the marginal effect of discarding phosphate from the variable selection, it was retained when generating the environmental distance matrix.

The dbRDA plot showed the six variables retained by the distLM model (i.e. all except phosphate) structured the samples first along an axis separating surface and deep samples (dbRDA1), strongly related to dissolved oxygen (r = 0.79) (Figure 13). The second axis was best correlated with temperature (r = −0.75). All six retained variables had a moderate correlation with at least one of the first two axes (Table 9). As with the nMDS ordinations (TODO ref to all nMDS figures), the water masses were generally well separated by the first two dbRDA axes. Samples from the AABW and AAIW, which were not separated by the first two axes, were clearly separated along the third (Table 9), which was best correlated with pressure (r = −0.79). This suggests that these two masses had similar physicochemical properties, and were mainly distinguished by depth, consistent with their common origin in sinking Antarctic Surface Waters (Foldvik and Gammelsrød, 1988).

Table 9: Correlations between dbRDA coordinate axes and physicochemical variables (multiple partial correlations).

Variable	dbRDA1	dbRDA2	dbRDA3	dbRDA4	dbRDA5	dbRDA6
Pressure	− 0.316	− 0.485	− 0.787	− 0.148	− 0.144	− 0.048
Oxygen	0.792	− 0.171	− 0.125	0.069	− 0.567	0.050
Temperature	− 0.025	− 0.750	0.366	0.236	0.180	0.463
Nitrate	− 0.311	0.007	0.325	− 0.636	− 0.561	0.281
Silicate	− 0.303	0.341	− 0.166	0.615	− 0.371	0.498
Salinity	− 0.290	− 0.239	0.311	0.368	− 0.417	− 0.673

A distance effect was detected by comparing the taxonomic and spatial matrices with the environmental matrix held constant (partial Mantel; r = 0.38, p = 0.003). This indicated that a process other than contemporary environmental selection was appreciably affecting variation in microbial community composition.

Discussion

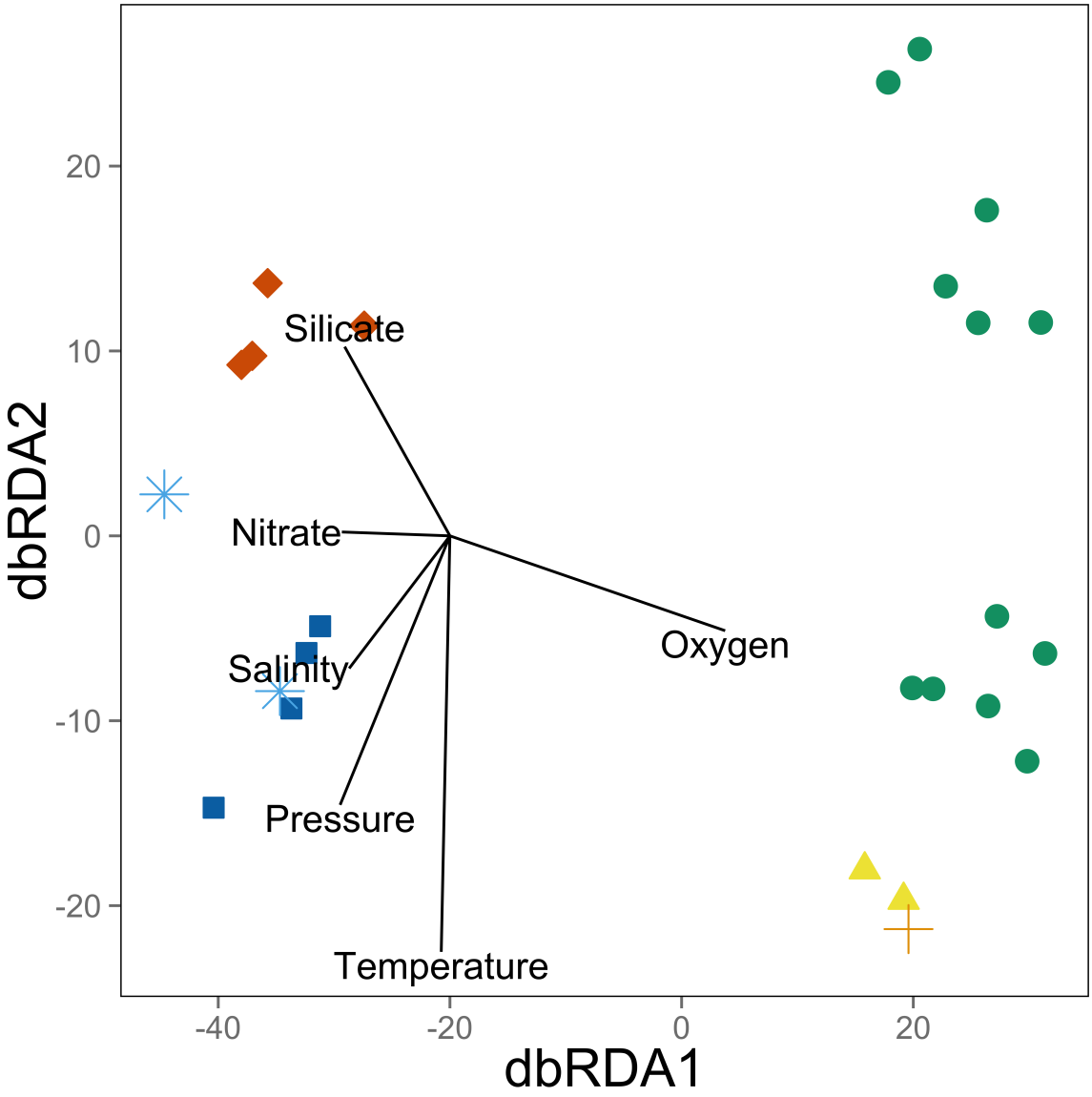

Figure 13: dbRDA ordination of the distLM model describing the relationship between the BEST-selected set of predictor physicochemical variables (pressure, oxygen, temperature, salinity, silicate, and nitrate) and the taxonomic dissimilarity between samples. Vectors represent the effect of each predictor variable on the two visualised axes. Vector length corresponds to the relative size of the effect, while direction represents the correlations to the two displayed axes. The first axis (dbRDA1) captures 64% of fitted and 37% of total variation between the samples' taxonomic profiles; the second (dbRDA2) captures 14% of fitted and 8% of total variation. Antarctic Intermediate Waters (AAIW), light blue stars; Subantarctic Mode Water (SAMW), orange crosses; Antarctic Bottom Water (AABW), dark blue squares; Antarctic Zone (AZ), green circles; Polar Frontal Zone (PFZ), yellow triangles; Circumpolar Deep Water (CDW), red diamonds.

References

Abell G. C. J. and Bowman J. P. (2005). Colonization and community dynamics of class *Flavobacteria* on diatom detritus in experimental mesocosms based on Southern Ocean seawater. *FEMS Microbiology Ecology*, 53(3):379–391.

Abell G. G. J. and Bowman J. P. (2005). Ecological and biogeographic relationships of class Flavobacteria in the Southern Ocean. *FEMS Microbiology Ecology*, 51:265–277.

Agogué H., Lamy D., Neal P. R., Sogin M. L., and Herndl G. J. (2011). Water mass-specificity of bacterial communities in the North Atlantic revealed by massively parallel sequencing. *Molecular Ecology*, 20(2):258–274.

Alonso C. and Pernthaler J. (2006). Roseobacter and SAR11 dominate microbial glucose uptake in coastal North Sea waters. *Environmental Microbiology*, 8(11):2022–2030.

Anderson L. A. and Sarmiento J. L. (1994). Redfield ratios of remineralization determined by nutrient data analysis. *Global Biogeochemical Cycles*, 8(1):65–80.

André J. M., Navarette C., Blanchot J., and Radenac M. H. (1999). Picophytoplankton dynamics in the equatorial Pacific: Growth and grazing rates from cytometric counts. *Journal of Geophysical Research*, 104(C2):3369–3380.

Angly F. E., Felts B., Breitbart M., Salamon P., Edwards R. A., Carlson C., Chan A. M., Haynes M., Kelley S., Liu H., Mahaffy J. M., Mueller J. E., Nulton J., Olson R., Parsons R., Rayhawk S., Suttle C. A., and Rohwer F. (2006). The marine viromes of four oceanic regions. *PLoS Biology*, 4(11):e368.

Angly F. E., Willner D., Prieto-Davó A., Edwards R. A., Schmieder R., Vega-Thurber R., Antonopoulos D. A., Barott K., Cottrell M. T., Desnues C., Dinsdale E. A., Furlan M., Haynes M., Henn M. R., Hu Y., Kirchman D. L., McDole T., McPherson J. D., Meyer F., Miller R. M., Mundt E., Naviaux R. K., Rodriguez-Mueller B., Stevens R., Wegley L., Zhang L., Zhu B., and Rohwer F. (2009). The GAAS Metagenomic Tool and Its Estimations of Viral and Microbial Average Genome Size in Four Major Biomes. *PLoS Computational Biology*, 5(12):e1000593.

Aoki S., Yoritaka M., and Masuyama A. (2003). Multidecadal warming of subsurface temperature in the Indian sector of the Southern Ocean. *Journal of Geophysical Research*, 108(C4):8081–8088.

Baas Becking L. G. M. *Geobiologie Of Inleiding Tot De Milieukunde*. W.P. Van Stockum & Zoon, The Hague, 1934.

Beja O., Aravind L., Koonin E. V., Suzuki M. T., Hadd A., Nguyen L. P., Jovanovich S. B., Gates C. M., Feldman R. A., Spudich J. L., Spudich E. N., and DeLong E. F. (2000). Bacterial rhodopsin: evidence for a new type of phototrophy in the sea. *Science*, 289(5486):1902–1906.

Béjà O., Suzuki M. T., Heidelberg J. F., Nelson W. C., Preston C. M., Hamada T., Eisen J. A., Fraser C. M., and DeLong E. F. (2002). Unsuspected diversity among marine aerobic anoxygenic phototrophs. *Nature*, 415(6872):630–633.

Berg I. A., Kockelkorn D., Buckel W., and Fuchs G. (2007). A 3-Hydroxypropionate/4-Hydroxybutyrate Autotrophic Carbon Dioxide Assimilation Pathway in Archaea. *Science*, 318(5857):1782–1786.

Bidle K. D. and Azam F. (2001). Bacterial control of silicon regeneration from diatom detritus: significance of bacterial ectohydrolases and species identity. *Limnology and Oceanography*, 46(7):1606–1623.

Biebl H., Allgaier M., Tindall B. J., Koblížek M., Lünsdorf H., Pukall R., and Wagner-Döbler I. (2005). *Dinoroseobacter shibae* gen. nov., sp. nov., a new aerobic phototrophic bacterium isolated from dinoflagellates. *International Journal of Systematic and Evolutionary Microbiology*, 55(Pt 3):1089–1096.

Bissett A., Richardson A. E., Baker G., Wakelin S., and Thrall P. H. (2010). Life history determines biogeographical patterns of soil bacterial communities over multiple spatial scales. *Molecular Ecology*, 19(19):4315–4327.

Böning C. W., Dispert A., Visbeck M., Rintoul S. R., and Schwarzkopf F. U. (2008). The response of the Antarctic Circumpolar Current to recent climate change. *Nature Geoscience*, 1(12):864–869.

Bowman J. P. and McCuaig R. D. (2003). Biodiversity, community structural shifts, and biogeography of prokaryotes within Antarctic continental shelf sediment. *Applied and Environmental Microbiology*, 69(5):2463–2483.

Bowman J. P., Rea S. M., McCammon S. A., and McMeekin T. A. (2000). Diversity and community structure within anoxic sediment from marine salinity meromictic lakes and a coastal meromictic marine basin, Vestfold Hills, Eastern Antarctica. *Environmental Microbiology*, 2(2):227–237.

Boyd P. W., Jickells T., Law C. S., Blain S., Boyle E. A., Buesseler K. O., Coale K. H., Cullen J. J., Baar H. J. W.de, Follows M., Harvey M., Lancelot C., Levasseur M., Owens N. P. J., Pollard R., Rivkin R. B., Sarmiento J., Schoemann V., Smetacek V., Takeda S., Tsuda A., Turner S., and Watson A. J. (2007). Mesoscale Iron Enrichment Experiments 1993-2005: Synthesis and Future Directions. *Science*, 315(5812):612–617.

Brinkhoff T., Giebel H.-A., and Simon M. (2008). Diversity, ecology, and genomics of the Roseobacter clade: a short overview. *Archives of Microbiology*, 189(6):531–539.

Brinkmeyer R., Knittel K., Jürgens J., Weyland H., Amann R., and Helmke E. (2003). Diversity and Structure of Bacterial Communities in Arctic versus Antarctic Pack Ice. *Applied and Environmental Microbiology*, 69(11):6610–6619.

Brown M. V. and Bowman J. P. (2001). A molecular phylogenetic survey of sea-ice microbial communities (SIMCO). *FEMS Microbiology Ecology*, 35(3):267–275.

Brown M. V., Lauro F. M., DeMaere M. Z., Muir L., Wilkins D., Thomas T., Riddle M. J., Fuhrman J. A., Andrews-Pfannkoch C., Hoffman J. M., McQuaid J. B., Allen A., Rintoul S. R., and Cavicchioli R. (2012). Global biogeography of SAR11 marine bacteria. *Molecular systems biology*, 8.

Buchan A., González J. M., and Moran M. A. (2005). Overview of the marine Roseobacter lineage. *Applied and Environmental Microbiology*, 71(10):5665–5677.

Callahan J. E. (1972). The structure and circulation of deep water in the Antarctic. *Deep Sea Research and Oceanographic Abstracts*, 19(8):563–575.

Campanaro S., Williams T. J., Burg D. W., De Francisci D., Treu L., Lauro F. M., and Cavicchioli R. (2011). Temperature-dependent global gene expression in the Antarctic archaeon *Methanococcoides burtonii*. *Environmental Microbiology*, 13(8):2018–2038.

Canfield D. E., Stewart F. J., Thamdrup B., De Brabandere L., Dalsgaard T., DeLong E. F., Revsbech N. P., and Ulloa O. (2010). A Cryptic Sulfur Cycle in Oxygen-Minimum-Zone Waters off the Chilean Coast. *Science*, 330(6009):1375–1378.

Caporaso J. G., Kuczynski J., Stombaugh J., Bittinger K., Bushman F. D., Costello E. K., Fierer N., Pena A. G., Goodrich J. K., and Gordon J. I. (2010). QIIME allows analysis of high-throughput community sequencing data. *Nature methods*, 7(5):335–336.

Carlson C. A., Morris R., Parsons R., Treusch A. H., Giovannoni S. J., and Vergin K. (2009). Seasonal dynamics of SAR11 populations in the euphotic and mesopelagic zones of the northwestern Sargasso Sea. *The ISME Journal*, 3(3):283–295.

Cavicchioli R. (2006). Cold-adapted archaea. *Nature Reviews Microbiology*, 4(5):331–343.

Cerovečki I., Talley L. D., and Mazloff M. R. (2011). A comparison of Southern Ocean air-sea buoyancy flux from an ocean state estimate with five other products. *Journal of Climate*, 24:6283–6306.

Chiba S., Ishimaru T., Hosie G. W., and Fukuchi M. (2001). Spatio-temporal variability of zooplankton community structure off east Antarctica (90 to 160°E). *Marine Ecology Progress Series*, 216:95–108.

Cho J. C. and Giovannoni S. J. (2004). Cultivation and Growth Characteristics of a Diverse Group of Oligotrophic Marine Gammaproteobacteria. *Applied and Environmental Microbiology*, 70(1):432–440.

Cho J.-C. and Tiedje J. M. (2000). Biogeography and degree of endemicity of fluorescent Pseudomonas strains in soil. *Applied and Environmental Microbiology*, 66(12):5448–5456.

Christaki U., Obernosterer I., Van Wambeke F., Veldhuis M., Garcia N., and Catala P. (2008). Microbial food web structure in a naturally iron-fertilized area in the Southern Ocean (Kerguelen Plateau). *Deep Sea Research Part II: Topical Studies in Oceanography*, 55(5-7):706–719.

Church M. J., DeLong E. F., Ducklow H. W., Karner M. B., Preston C. M., and Karl D. M. (2003). Abundance and distribution of planktonic Archaea and Bacteria in the waters west of the Antarctic Peninsula. *Limnology and Oceanography*, 48(5):1893–1902.

Clarke K. R. and Gorley R. N. *PRIMER v6: User Manual / Tutorial*, 1st edition edition, 2006.

Clarke K. R. and Warwick R. M. *Change in marine communities: an approach to statistical analysis and interpretation*. PRIMER-E, Plymoth, 2nd edition, 2001.

Coleman M. L. M. and Chisholm S. W. S. (2010). Ecosystem-specific selection pressures revealed through comparative population genomics. *Proceedings Of The National Academy Of Sciences Of The United States Of America*, 107(43):18634–18639.

Cottrell M. T. and Kirchman D. L. (2000). Community Composition of Marine Bacterioplankton Determined by 16S rRNA Gene Clone Libraries and Fluorescence In Situ Hybridization. *Applied and Environmental Microbiology*, 66(12):5116–5122.

Cottrell M. T., Waidner L. A., Yu L., and Kirchman D. L. (2005). Bacterial diversity of metagenomic and PCR libraries from the Delaware River. *Environmental Microbiology*, 7(12):1883–1895.

Cox P. M., Betts R. A., Jones C. D., Spall S. A., and Totterdell I. J. (2000). Acceleration of global warming due to carbon-cycle feedbacks in a coupled climate model. *Nature*, 408(6809):184–187.

Crump B. C., Armbrust E. V., and Baross J. A. (1999). Phylogenetic analysis of particle-attached and free-living bacterial communities in the Columbia River, its estuary, and the adjacent coastal ocean. *Applied and Environmental Microbiology*, 65(7):3192–3204.

Curson A. R. J., Todd J. D., Sullivan M. J., and Johnston A. W. B. (2011). Catabolism of dimethylsulphoniopropionate: microorganisms, enzymes and genes. *Nature Reviews Microbiology*, 9(12):849–859.

Wit R.de and Bouvier T. (2006). *'Everything is everywhere*, but, *the environment selects*'; what did Baas Becking and Beijerinck really say? *Environmental Microbiology*, 8(4):755–758.

Deacon G. E. R. (1982). Physical and biological zonation in the Southern Ocean. *Deep Sea Research Part A. Oceanographic Research Papers*, 29(1):1–15.

Declerck S. A. J., Winter C., Shurin J. B., Suttle C. A., and Matthews B. (2013). Effects of patch connectivity and heterogeneity on metacommunity structure of planktonic bacteria and viruses. *The ISME Journal*, 7(3):533–542.

DeLong E. F., Franks D. G., and Alldredge A. L. (1993). Phylogenetic Diversity of Aggregate-Attached vs. Free-Living Marine Bacterial Assemblages. *Limnology and Oceanography*, 38(5):924–934.

DeLong E. F., Wu K. Y., Prézelin B. B., and Jovine R. V. (1994). High abundance of Archaea in Antarctic marine picoplankton. *Nature*, 371(6499):695–697.

Dinsdale E. A., Edwards R. A., Hall D., Angly F., Breitbart M., Brulc J. M., Furlan M., Desnues C., Haynes M., Li L., McDaniel L., Moran M. A., Nelson K. E., Nilsson C., Olson R., Paul J., Brito B. R., Ruan Y., Swan B. K., Stevens R., Valentine D. L., Thurber R. V., Wegley L., White B. A., and Rohwer F. (2008). Functional metagenomic profiling of nine biomes. *Nature*, 452(7187):629–632.

Dixon J. L., Beale R., and Nightingale P. D. (2011). Rapid biological oxidation of methanol in the tropical Atlantic: significance as a microbial carbon source. *Biogeosciences Discussions*, 8(2):3899–3921.

Ducklow H. W., Myers K., Erickson M., Ghiglione J. F., and Murray A. E. (2011). Response of a summertime Antarctic marine -bacterial community to glucose and ammonium enrichment. *Aquatic Microbial Ecology*, 64(3):205–220.

Dupont C. L., Rusch D. B., Yooseph S., Lombardo M.-J., Richter R. A., Valas R., Novotny M., Yee-Greenbaum J., Selengut J. D., Haft D. H., Halpern A. L., Lasken R. S., Nealson K., Friedman R., and Venter J. C. (2011). Genomic insights to SAR86, an abundant and uncultivated marine bacterial lineage. pages 1–14.

Eilers H., Pernthaler J., Glöckner F. O., and Amann R. (2000). Culturability and In Situ Abundance of Pelagic Bacteria from the North Sea. *Applied and Environmental Microbiology*, 66(7):3044–3051.

El-Sayed S. Z. (2005). History and evolution of primary productivity studies of the Southern Ocean. *Polar Biology*, 28(6):423–438.

Esper O. and Zonneveld K. A. F. (2002). Distribution of organic-walled dinoflagellate cysts in surface sediments of the Southern Ocean (eastern Atlantic sector) between the Subtropical Front and the Weddell Gyre. *Marine Micropaleontology*, 46(1):177–208.

Evans C., Pearce I., and Brussaard C. P. D. (2009). Viral-mediated lysis of microbes and carbon release in the sub-Antarctic and Polar Frontal zones of the Australian Southern Ocean. *Environmental Microbiology*, 11(11):2924–2934.

Evans C., Thomson P. G., Davidson A. T., Bowie A. R., Enden R.van den, Witte H., and Brussaard C. P. D. (2011). Potential climate change impacts on microbial distribution and carbon cycling in the Australian Southern Ocean. *Deep Sea Research Part II: Topical Studies in Oceanography*, 58(21-22): 2150–2161.

Fandino L. B., Riemann L., Steward G. F., Long R. A., and Azam F. (2001). Variations in bacterial community structure during a dinoflagellate bloom analyzed by DGGE and 16S rDNA sequencing. *Aquatic Microbial Ecology*, 23:119.

Feller G. and Gerday C. (2003). Psychrophilic enzymes: hot topics in cold adaptation. *Nature Reviews Microbiology*, 1(3):200–208.

Firing Y. L., Chereskin T. K., and Mazloff M. R. (2011). Vertical structure and transport of the Antarctic Circumpolar Current in Drake Passage from direct velocity observations. *Journal of Geophysical Research*, 116(C8):C08015.

Foldvik A. and Gammelsrød T. (1988). Notes on Southern Ocean hydrography, sea-ice and bottom water formation. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 67(1-2):3–17.

Freitas S., Hatosy S., Fuhrman J. A., Huse S. M., Welch D. B. M., Sogin M. L., and Martiny A. C. (2012). Global distribution and diversity of marine *Verrucomicrobia*. *The ISME Journal*, 6(8):1499–1505.

Fuhrman J. A., Schwalbach M. S., and Stingl U. (2008). Proteorhodopsins: an array of physiological roles? *Nature Reviews Microbiology*, 6:488–494.

Fyfe J. C. and Saenko O. A. (2005). Human-induced change in the Antarctic Circumpolar Current. *Journal of Climate*, 18(15):3068–3073.

Galand P. E., Potvin M., Casamayor E. O., and Lovejoy C. (2009). Hydrography shapes bacterial biogeography of the deep Arctic Ocean. *Nature*, 4(4):564–576.

García-Martínez J. and Rodríguez-Valera F. (2000). Microdiversity of uncultured marine prokaryotes: the SAR11 cluster and the marine Archaea of Group I. *Molecular Ecology*, 9(7):935–948.

Gentile G., Giuliano L., D'Auria G., Smedile F., Azzaro M., De Domenico M., and Yakimov M. M. (2006). Study of bacterial communities in Antarctic coastal waters by a combination of 16S rRNA and 16S rDNA sequencing. *Environmental Microbiology*, 8(12):2150–2161.

Ghiglione J. F. and Murray A. E. (2011). Pronounced summer to winter differences and higher wintertime richness in coastal Antarctic marine bacterioplankton. *Environmental Microbiology*, 14(3): 617–629.

Ghiglione J.-F., Galand P. E., Pommier T., Pedrós-Alió C., Maas E. W., Bakker K., Bertilson S., Kirchmanj D. L., Lovejoy C., Yager P. L., and Murray A. E. (2012). Pole-to-pole biogeography of surface and deep marine bacterial communities. *Proceedings Of The National Academy Of Sciences Of The United States Of America*, 109(43):17633–17638.

Giebel H.-A., Brinkhoff T., Zwisler W., Selje N., and Simon M. (2009). Distribution of *Roseobacter* RCA and SAR11 lineages and distinct bacterial communities from the subtropics to the Southern Ocean. *Environmental Microbiology*, 11(8):2164–2178.

Giebel H.-A., Kalhoefer D., Lemke A., Thole S., Gahl-Janssen R., Simon M., and Brinkhoff T. (2010). Distribution of *Roseobacter* RCA and SAR11 lineages in the North Sea and characteristics of an abundant RCA isolate. *The ISME Journal*, 5:8–19.

Gille S. T. (2002). Warming of the Southern Ocean Since the 1950s. *Science*, 295(5558):1275–1277.

Giovannoni S. J., Tripp H. J., Givan S., Podar M., Vergin K. L., Baptista D., Bibbs L., Eads J., Richardson T. H., Noordewier M., Rappé M. S., Short J. M., Carrington J. C., and Mathur E. J. (2005). Genome streamlining in a cosmopolitan oceanic bacterium. *Science*, 309(5738):1242–1245.

Giovannoni S. J., Hayakawa D. H., Tripp H. J., Stingl U., Givan S. A., Cho J.-C., Oh H.-M., Kitner J. B., Vergin K. L., and Rappé M. S. (2008). The small genome of an abundant coastal ocean methylotroph. *Environmental Microbiology*, 10(7):1771–1782.

Glöckner F. O., Fuchs B. M., and Amann R. (1999). Bacterioplankton compositions of lakes and oceans: a first comparison based on fluorescence in situ hybridization. *Applied and Environmental Microbiology*, 65(8):3721–3726.

González J. M., Fernández-Gómez B., Fernàndez-Guerra A., Gómez-Consarnau L., Sánchez O., Coll-Lladó M., Del Campo J., Escudero L., Rodríguez-Martínez R., Alonso-Sáez L., Latasa M., Paulsen I., Nedashkovskaya O., Lekunberri I., Pinhassi J., and Pedrós-Alió C. (2008). Genome analysis of the proteorhodopsin-containing marine bacterium *Polaribacter* sp. MED152 (Flavobacteria). *Proceedings Of The National Academy Of Sciences Of The United States Of America*, 105(25):8724–8729.

Grossart H. P., Schlingloff A., Bernhard M., Simon M., and Brinkhoff T. (2004). Antagonistic activity of bacteria isolated from organic aggregates of the German Wadden Sea. *FEMS Microbiology Ecology*, 47(3):387–396.

Grote J., Bayindirli C., Bergauer K., Moraes P.Carpintero de, Chen H., D'Ambrosio L., Edwards B., Fernández-Gómez B., Hamisi M., Logares R., Nguyen D., Rii Y. M., Saeck E., Schutte C., Widner B., Church M. J., Steward G. F., Karl D. M., DeLong E. F., Eppley J. M., Schuster S. C., Kyrpides N. C., and Rappé M. S. (2011). Draft genome sequence of strain HIMB100, a cultured representative of the SAR116 clade of marine *Alphaproteobacteria*. *Standards in Genomic Sciences*, 5(3):269–278.

Grzymski J. J., Carter B. J., DeLong E. F., Feldman R. A., Ghadiri A., and Murray A. E. (2006). Comparative Genomics of DNA Fragments from Six Antarctic Marine Planktonic Bacteria. *Applied and Environmental Microbiology*, 72(2):1532–1541.

Grzymski J. J., Riesenfeld C. S., Williams T. J., Dussaq A. M., Ducklow H., Erickson M., Cavicchioli R., and Murray A. E. (2012). A metagenomic assessment of winter and summer bacterioplankton from Antarctica Peninsula coastal surface waters. *The ISME Journal*, 6(10):1901–1915.

Guixa-Boixereu N., Vaqué D., Gasol J. M., Sánchez-Cámara J., and Pedrós-Alió C. (2002). Viral distribution and activity in Antarctic waters. *Deep Sea Research Part II: Topical Studies in Oceanography*, 49 (4):827–845.

Hamdan L. J., Coffin R. B., Sikaroodi M., Greinert J., Treude T., and Gillevet P. M. (2013). Ocean currents shape the microbiome of Arctic marine sediments. *The ISME Journal*, 7(4):685–696.

Hamilton A. K., Lovejoy C., Galand P. E., and Ingram R. G. (2008). Water masses and biogeography of picoeukaryote assemblages in a cold hydrographically complex system. *Limnology and Oceanography*, pages 922–935.

Hanson C. A., Fuhrman J. A., Horner-Devine M. C., and Martiny J. B. H. (2012). Beyond biogeographic patterns: processes shaping the microbial landscape. *Nature Reviews Microbiology*, 10(7):497–506.

Head I. M., Hiorns W. D., Embley T. M., McCarthy A. J., and Saunders J. R. (1993). The phylogeny of autotrophic ammonia-oxidizing bacteria as determined by analysis of 16S ribosomal RNA gene sequences. *Journal of General Microbiology*, 139(6):1147–1153.

Heikes B. G., Chang W., Pilson M. E. Q., Swift E., Singh H. B., Guenther A., Jacob D. J., Field B. D., Fall R., Riemer D., and Brand L. (2002). Atmospheric methanol budget and ocean implication. *Global Biogeochemical Cycles*, 16(4):1133.

Hessen D. O., Ågren G. I., Anderson T. R., Elser J. J., and de Ruiter, P.C. (2004). Carbon sequestration in ecosystems: the role of stoichiometry. *Ecology*, 85(5):1179–1192.

Hollibaugh J. T., Bano N., and Ducklow H. W. (2002). Widespread Distribution in Polar Oceans of a 16S rRNA Gene Sequence with Affinity to *Nitrosospira*-Like Ammonia-Oxidizing Bacteria. *Applied and Environmental Microbiology*, 68(3):1478–1484.

Howard E. C., Sun S., Biers E. J., and Moran M. A. (2008). Abundant and diverse bacteria involved in DMSP degradation in marine surface waters. *Environmental Microbiology*, 10(9):2397–2410.

Hunt B. P. V., Pakhomov E. A., and McQuaid C. D. (2001). Short-term variation and long-term changes inthe oceanographic environment and zooplankton community in the vicinity of a sub-Antarctic archipelago. *Marine Biolog*, 138:369–381.

Huntley M. E., Lopez M. D., and Karl D. M. (1991). Top predators in the Southern ocean: a major leak in the biological carbon pump. *Science*, 253(5015):64–66.

Huson D. H., Auch A. F., Qi J., and Schuster S. C. (2007). MEGAN analysis of metagenomic data. *Genome Research*, 17(3):377–386.

Huston A. L., Krieger-Brockett B. B., and Deming J. W. (2000). Remarkably low temperature optima for extracellular enzyme activity from Arctic bacteria and sea ice. *Environmental Microbiology*, 2(4): 383–388.

Ingalls A. E., Shah S. R., Hansman R. L., Aluwihare L. I., Santos G. M., Druffel E. R. M., and Pearson A. (2006). Quantifying archaeal community autotrophy in the mesopelagic ocean using natural radiocarbon. *Proceedings Of The National Academy Of Sciences Of The United States Of America*, 103 (17):6442–6447.

Iverson V., Morris R. M., Frazar C. D., Berthiaume C. T., Morales R. L., and Armbrust E. V. (2012). Untangling Genomes from Metagenomes: Revealing an Uncultured Class of Marine Euryarchaeota. *Science*, 335(6068):587–590.

Jacobs S. S. (2004). Bottom water production and its links with the thermohaline circulation. *Antarctic Science*, 16(04):427–437.

Jamieson R. E., Rogers A. D., Billett D., Smale D. A., and Pearce D. A. (2012). Patterns of marine bacterioplankton biodiversity in the surface waters of the Scotia Arc, Southern Ocean. *FEMS Microbiology Ecology*, 80:452–468.

Jung S.-Y., Oh T.-K., and Yoon J.-H. (2006). *Colwellia aestuarii* sp. nov., isolated from a tidal flat sediment in Korea. *International Journal of Systematic and Evolutionary Microbiology*, 56(1):33–37.

Junge K., Eicken H., and Deming J. W. (2003). Motility of *Colwellia psychrerythraea* Strain 34H at Subzero Temperatures. *Applied and Environmental Microbiology*, 69(7):4282–4284.

Kalanetra K. M., Bano N., and Hollibaugh J. T. (2009). Ammonia-oxidizing *Archaea* in the Arctic Ocean and Antarctic coastal waters. *Environmental Microbiology*, 11(9):2434–2445.

Kawahata H. and Ishizuka T. (2000). Amino acids in interstitial waters from ODP Sites 689 and 690 on the Maud Rise, Antarctic Ocean. *Geochemical Journal*, 34(4):247–261.

King G. M. (2003). Molecular and Culture-Based Analyses of Aerobic Carbon Monoxide Oxidizer Diversity. *Applied and Environmental Microbiology*, 69(12):7257–7265.

Kirchman D. L. (2002). The ecology of *Cytophaga–Flavobacteria* in aquatic environments. *FEMS Microbiology Ecology*, 39(2):91–100.

Kirchman D. L. *Microbial ecology of the oceans*. John Wiley & Sons, Inc., Hoboken, New Jersey, second edition, 2008.

Kjelleberg S., Hermansson M., and Mårdén P. (1987). The transient phase between growth and non-growth of heterotrophic bacteria, with emphasis on the marine environment. *Annual Review of Microbiology*, 41:25–49.

Knights D., Kuczynski J., Charlson E. S., Zaneveld J., Mozer M. C., Collman R. G., Bushman F. D., Knight R., and Kelley S. T. (2011). Bayesian community-wide culture-independent microbial source tracking. *Nature methods*, 8(9):761–763.

Koh E. Y., Phua W., and Ryan K. G. (2011). Aerobic anoxygenic phototrophic bacteria in Antarctic sea ice and seawater. *Environmental Microbiology Reports*, 3(6):710–716.

Kuwahara H., Yoshida T., Takaki Y., Shimamura S., Nishi S., Harada M., Matsuyama K., Takishita K., Kawato M., Uematsu K., Fujiwara Y., Sato T., Kato C., Kitagawa M., Kato I., and Maruyama T. (2007). Reduced Genome of the Thioautotrophic Intracellular Symbiont in a Deep-Sea Clam, *Calyptogena okutanii*. *Current Biology*, 17(10):881–886.

Laubscher R. K., Perissinotto R., and McQuaid C. D. (1993). Phytoplankton production and biomass at frontal zones in the Atlantic sector of the Southern Ocean. *Polar Biology*, 13(7).

Lauro F. M., Chastain R. A., Blankenship L. E., Yayanos A. A., and Bartlett D. H. (2007). The unique 16S rRNA genes of piezophiles reflect both phylogeny and adaptation. *Applied and Environmental Microbiology*, 73(3):838–845.

Lauro F. M., McDougald D., Thomas T., Williams T. J., Egan S., Rice S., DeMaere M. Z., Ting L., Ertan H., Johnson J., Ferriera S., Lapidus A., Anderson I., Kyrpides N., Munk A. C., Detter C., Han C. S., Brown M. V., Robb F. T., Kjelleberg S., and Cavicchioli R. (2009). The genomic basis of trophic strategy in marine bacteria. *Proceedings Of The National Academy Of Sciences Of The United States Of America*, 106(37):15527–15533.

Lauro F. M., DeMaere M. Z., Yau S., Brown M. V., Ng C., Wilkins D., Raftery M. J., Gibson J. A., Andrews-Pfannkoch C., Lewis M., Hoffman J. M., Thomas T., and Cavicchioli R. (2011). An integrative study of a meromictic lake ecosystem in Antarctica. *The ISME Journal*, 5(5):879–895.

Legendre P. and Anderson M. J. (1999). Distance-based redundancy analysis: testing multispecies responses in multifactorial ecological experiments. *Ecological Monographs*, 69(1):1–24.

Liu H., Nolla H. A., and Campbell L. (1997). *Prochlorococcus* growth rate and contribution to primary production in the equatorial and subtropical North Pacific Ocean. *Aquatic Microbial Ecology*, 12(1): 39–47.

Liu H., Campbell L., Landry M. R., Nolla H. A., Brown S. L., and Constantinou J. (1998). *Prochlorococcus* and *Synechococcus* growth rates and contributions to production in the Arabian Sea during the 1995 Southwest and Northeast Monsoons. *Deep Sea Research Part II: Topical Studies in Oceanography*, 45 (10-11):2327–2352.

Lo Giudice A., Caruso C., Mangano S., Bruni V., Domenico M., and Michaud L. (2011). Marine Bacterioplankton Diversity and Community Composition in an Antarctic Coastal Environment. *Microbial Ecology*, 63(1):210–223.

Lomas M. W. and Moran S. B. (2011). Evidence for aggregation and export of cyanobacteria and nano-eukaryotes from the Sargasso Sea euphotic zone. *Biogeosciences*, 8(1):203–216.

López-García P., López-López A., Moreira D., and Rodríguez-Valera F. (2001). Diversity of free-living prokaryotes from a deep-sea site at the Antarctic Polar Front. *FEMS Microbiology Ecology*, 36(2-3): 193–202.

Ludwig W., Strunk O., Westram R., Richter L., Meier H., Yadhukumar , Buchner A., Lai T., Steppi S., Jobb G., Förster W., Brettske I., Gerber S., Ginhart A. W., Gross O., Grumann S., Hermann S., Jost R., König A., Liss T., Lüssmann R., May M., Nonhoff B., Reichel B., Strehlow R., Stamatakis A., Stuckmann N., Vilbig A., Lenke M., Ludwig T., Bode A., and Schleifer K.-H. (2004). ARB: a software environment for sequence data. *Nucleic Acids Research*, 32(4):1363–1371.

Malmstrom R. R., Cottrell M. T., Elifantz H., and Kirchman D. L. (2005). Biomass production and assimilation of dissolved organic matter by SAR11 bacteria in the Northwest Atlantic Ocean. *Applied and Environmental Microbiology*, 71(6):2979–2986.

Marchant H. J., Davidson A. T., and Wright S. W. (1987). The distribution and abundance of chroococcoid cyanobacteria in the Southern Ocean. *Proc. NIPR Symp. Polar Biol*, 1:1–9.

Martiny J. B. H., Bohannan B. J. M., Brown J. H., Colwell R. K., Fuhrman J. A., Green J. L., Horner-Devine M. C., Kane M., Krumins J. A., Kuske C. R., Morin P. J., Naeem S., Ovreas L., Reysenbach A.-L., Smith V. H., and Staley J. T. (2006). Microbial biogeography: putting microorganisms on the map. *Nature Reviews Microbiology*, 4(2):102–112.

Mary I., Heywood J. L., Fuchs B. M., Amann R., Tarran G. A., Burkill P. H., and Zubkov M. V. (2006). SAR11 dominance among metabolically active low nucleic acid bacterioplankton in surface waters along an Atlantic meridional transect. *Aquatic Microbial Ecology*, 45(2):107–113.

Massana R., Taylor L. T., Murray A. E., Wu K. Y., Jeffrey W. H., and DeLong E. F. (1998). Vertical Distribution and Temporal Variation of Marine Planktonic Archaea in the Gerlache Strait, Antarctica, During Early Spring. *Limnology and . . .*, 43(4):607–617.

Massana R., DeLong E. F., and Pedrós-Alió C. (2000). A Few Cosmopolitan Phylotypes Dominate Planktonic Archaeal Assemblages in Widely Different Oceanic Provinces. *Applied and Environmental Microbiology*, 66(5):1777–1787.

Mayali X., Franks P. J. S., and Azam F. (2008). Cultivation and Ecosystem Role of a Marine *Roseobacter* Clade-Affiliated Cluster Bacterium. *Applied and Environmental Microbiology*, 74(9):2595–2603.

Mazloff M. R., Heimbach P., and Wunsch C. (2010). An eddy-permitting Southern Ocean state estimate. *Journal of physical oceanography*, 40:880–899.

Merbt S. N., Stahl D. A., Casamayor E. O., Martí E., Nicol G. W., and Prosser J. I. (2012). Differential photoinhibition of bacterial and archaeal ammonia oxidation. *FEMS Microbiology Letters*, 327(1): 41–46.

Methé B. A., Nelson K. E., Deming J. W., Momen B., Melamud E., Zhang X., Moult J., Madupu R., Nelson W. C., Dodson R. J., Methe B. A., Nelson K. E., Deming J. W., Momen B., Melamud E., Zhang X., Moult J., Madupu R., Nelson W. C., Dodson R. J., Brinkac L. M., Daugherty S. C., Durkin A. S., DeBoy R. T., Kolonay J. F., Sullivan S. A., Zhou L., Davidsen T. M., Wu M., Huston A. L., Lewis M., Weaver B., Weidman J. F., Khouri H., Utterback T. R., Feldblyum T. V., and Fraser C. M.

(2005). The psychrophilic lifestyle as revealed by the genome sequence of *Colwellia psychrerythraea* 34H through genomic and proteomic analyses. *Proceedings Of The National Academy Of Sciences Of The United States Of America*, 102(31):10913–10918.

Meyer B. and Kuever J. (2007). Molecular Analysis of the Diversity of Sulfate-Reducing and Sulfur-Oxidizing Prokaryotes in the Environment, Using *aprA* as Functional Marker Gene. *Applied and Environmental Microbiology*, 73(23):7664–7679.

Mikaloff Fletcher S. E., Gruber N., Jacobson A. R., Doney S. C., Dutkiewicz S., Gerber M., Follows M., Joos F., Lindsay K., Menemenlis D., Mouchet A., Müller S. A., and Sarmiento J. L. (2006). Inverse estimates of anthropogenic CO_2 uptake, transport, and storage by the ocean. *Global Biogeochemical Cycles*, 20(2):GB2002.

Miller T. R. and Belas R. (2004). Dimethylsulfoniopropionate Metabolism by *Pfiesteria*-Associated *Roseobacter* spp. *Applied and Environmental Microbiology*, 70(6):3383–3391.

Mira A., Ochman H., and Moran N. A. (2001). Deletional bias and the evolution of bacterial genomes. *Trends in genetics : TIG*, 17(10):589–596.

Moore J. K., Abbott M. R., and Richman J. G. (1999). Location and dynamics of the Antarctic Polar Front from satellite sea surface temperature data. *Journal of Geophysical Research*, 104:3052–3073.

Moran M. A., Belas R., Schell M. A., González J. M., Sun F., Sun S., Binder B. J., Edmonds J., Ye W., Orcutt B., Howard E. C., Meile C., Palefsky W., Goesmann A., Ren Q., Paulsen I., Ulrich L. E., Thompson L. S., Saunders E., and Buchan A. (2007). Ecological Genomics of Marine Roseobacters. *Applied and Environmental Microbiology*, 73(14):4559–4569.

Moran M. A., González J. M., and Kiene R. P. (2003). Linking a Bacterial Taxon to Sulfur Cycling in the Sea: Studies of the Marine Roseobacter Group. *Geomicrobiology Journal*, 20(4):375–388.

Moran M. A., Buchan A., González J. M., Heidelberg J. F., Whitman W. B., Kiene R. P., Henriksen J. R., King G. M., Belas R., Fuqua C., Brinkac L., Lewis M., Johri S., Weaver B., Pai G., Eisen J. A., Rahe E., Sheldon W. M., Ye W., Miller T. R., Carlton J., Rasko D. A., Paulsen I. T., Ren Q., Daugherty S. C., Deboy R. T., Dodson R. J., Durkin A. S., Madupu R., Nelson W. C., Sullivan S. A., Rosovitz M. J., Haft D. H., Selengut J., and Ward N. (2004). Genome sequence of *Silicibacter pomeroyi* reveals adaptations to the marine environment. *Nature*, 432(7019):910–913.

Morris R. M., Rappé M. S., Connon S. A., Vergin K. L., Siebold W. A., Carlson C. A., and Giovannoni S. J. (2002). SAR11 clade dominates ocean surface bacterioplankton communities. *Nature*, 420(6917): 806–810.

Morris R. M., Longnecker K., and Giovannoni S. J. (2006). *Pirellula* and OM43 are among the dominant lineages identified in an Oregon coast diatom bloom. *Environmental Microbiology*, 8(8):1361–1370.

Murray A. E. and Grzymski J. J. (2007). Diversity and genomics of Antarctic marine micro-organisms. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 362(1488):2259–2271.

Murray A. E., Wu K. Y., Moyer C. L., Karl D. M., and DeLong E. F. (1999). Evidence for circumpolar distribution of planktonic Archaea in the Southern Ocean. *Aquatic Microbial Ecology*, 18(3):263–273.

Murray A. E. A., Preston C. M. C., Massana R. R., Taylor L. T. L., Blakis A. A., Wu K. K., and DeLong E. F. (1998). Seasonal and spatial variability of bacterial and archaeal assemblages in the coastal waters near Anvers Island, Antarctica. *Applied and Environmental Microbiology*, 64(7):2585–2595.

Murray A. E., Peng V., Tyler C., and Wagh P. (2011). Marine bacterioplankton biomass, activity and community structure in the vicinity of Antarctic icebergs. *Deep Sea Research Part II: Topical Studies in Oceanography*, 58(11-12):1407–1421.

Newton I. L. G., Woyke T., Auchtung T. A., Dilly G. F., Dutton R. J., Fisher M. C., Fontanez K. M., Lau E., Stewart F. J., Richardson P. M., Barry K. W., Saunders E., Detter J. C., Wu D., Eisen J. A., and Cavanaugh C. M. (2007). The *Calyptogena magnifica* Chemoautotrophic Symbiont Genome. *Science*, 315(5814):998–1000.

Ng C., DeMaere M. Z., Williams T. J., Lauro F. M., Raftery M., Gibson J. A., Andrews-Pfannkoch C., Lewis M., Hoffman J. M., Thomas T., and Cavicchioli R. (2010). Metaproteogenomic analysis of a dominant green sulfur bacterium from Ace Lake, Antarctica. *The ISME Journal*, 4(8):1002–1019.

Nikrad M. P., Cottrell M. T., and Kirchman D. L. (2012). Abundance and Single-Cell Activity of Heterotrophic Bacterial Groups in the Western Arctic Ocean in Summer and Winter. *Applied and Environmental Microbiology*, 78(7):2402–2409.

Obernosterer I., Catala P., Lebaron P., and West N. J. (2011). Distinct bacterial groups contribute to carbon cycling during a naturally iron fertilized phytoplankton bloom in the Southern Ocean. *Limnology and Oceanography*, 56(6):2391–2401.

Oh H. M., Kwon K. K., Kang I., Kang S. G., Lee J. H., Kim S. J., and Cho J. C. (2010). Complete Genome Sequence of "*Candidatus* Puniceispirillum marinum" IMCC1322, a Representative of the SAR116 Clade in the *Alphaproteobacteria*. *Journal of Bacteriology*, 192(12):3240–3241.

Oliver J. L., Barber R. T., Smith Jr W. O., and Ducklow H. W. (2004). The heterotrophic bacterial response during the Southern Ocean iron experiment (SOFeX). *Limnology and Oceanography*, 49(6): 2129–2140.

Orsi A. H., Whitworth T., and Nowlin W. D. (1995). On the meridional extent and fronts of the Antarctic Circumpolar Current. *Deep Sea Research Part I: Oceanographic Research Papers*, 42(5):641–673.

Orsi A. H., Johnson G. C., and Bullister J. L. (1999). Circulation, mixing, and production of Antarctic Bottom Water. *Progress in Oceanography*, 43(1):55–109.

O'Sullivan L. A., Fuller K. E., Thomas E. M., Turley C. M., Fry J. C., and Weightman A. J. (2004). Distribution and culturability of the uncultivated 'AGG58 cluster' of the *Bacteroidetes* phylum in aquatic environments. *FEMS Microbiology Ecology*, 47(3):359–370.

Paris C. B., Helgers J., Sebille E.van, and Srinivasan A. (2013). Connectivity Modeling System: A probabilistic modeling tool for the multi-scale tracking of biotic and abiotic variability in the ocean. *Environmental Modelling and Software*, 42(C):47–54.

Partensky F., Hess W. R., and Vaulot D. (1999). *Prochlorococcus*, a marine photosynthetic prokaryote of global significance. *Microbiology and Molecular Biology Reviews*, 63(1):106–127.

Paul J. H., DeFlaun M. F., and Jeffrey W. H. (1988). Mechanisms of DNA utilization by estuarine microbial populations. *Applied and Environmental Microbiology*, 54(7):1682–1688.

Pham V. D., Konstantinidis K. T., Palden T., and DeLong E. F. (2008). Phylogenetic analyses of ribosomal DNA-containing bacterioplankton genome fragments from a 4000 m vertical profile in the North Pacific Subtropical Gyre. *Environmental Microbiology*, 10(9):2313–2330.

Pinhassi J., Sala M. M., Havskum H., Peters F., Guadayol Ò., Malits A., and Marrasé C. (2004). Changes in bacterioplankton composition under different phytoplankton regimens. *Applied and Environmental Microbiology*, 70(11):6753–6766.

Piquet A. M. T., Bolhuis H., Meredith M. P., and Buma A. G. J. (2011). Shifts in coastal Antarctic marine microbial communities during and after melt water-related surface stratification. *FEMS Microbiology Ecology*, 76(3):413–427.

Pollard R. T., Lucas M. I., and Read J. F. (2002). Physical controls on biogeochemical zonation in the Southern Ocean. *Deep Sea Research Part II: Topical Studies in Oceanography*, 49(16):3289–3305.

Pommier T., Canbäck B., Riemann L., Boström K. H., Simu K., Lundberg P., Tunlid A., and Hagström Å. (2007). Global patterns of diversity and community structure in marine bacterioplankton. *Molecular Ecology*, 16(4):867–880.

Poorvin L., Rinta-Kanto J. M., Hutchins D. A., and Wilhelm S. W. (2004). Viral release of iron and its bioavailability to marine plankton. *Limnology and Oceanography*, 49(5):1734–1741.

Powell L. M., Bowman J. P., Skerratt J. H., Franzmann P. D., and Burton H. R. (2005). Ecology of a novel *Synechococcus* clade occurring in dense populations in saline Antarctic lakes. *Marine Ecology Progress Series*, 291(28 April):65–80.

Preston C. M., Wu K. Y., Molinski T. F., and DeLong E. F. (1996). A psychrophilic crenarchaeon inhabits a marine sponge: *Cenarchaeum symbiosum* gen. nov., sp. nov. *Proceedings Of The National Academy Of Sciences Of The United States Of America*, 93(13):6241–6246.

Qin J., Li R., Raes J., Arumugam M., Burgdorf K. S., Manichanh C., Nielsen T., Pons N., Levenez F., Yamada T., Mende D. R., Li J., Xu J., Li S., Li D., Cao J., Wang B., Liang H., Zheng H., Xie Y., Tap J., Lepage P., Bertalan M., Batto J.-M., Hansen T., Le Paslier D., Linneberg A., Nielsen H. B., Pelletier E., Renault P., Sicheritz-Ponten T., Turner K., Zhu H., Yu C., Li S., Jian M., Zhou Y., Li Y., Zhang X., Li S., Qin N., Yang H., Wang J., Brunak S., Doré J., Guarner F., Kristiansen K., Pedersen O., Parkhill J., Weissenbach J., MetaHIT Consortium , Bork P., Ehrlich S. D., and Wang J. (2010). A human gut microbial gene catalogue established by metagenomic sequencing. *Nature*, 464(7285):59–65.

Quast C., Pruesse E., Yilmaz P., Gerken J., Schweer T., Yarza P., Peplies J., and Glöckner F. O. (2013). The SILVA ribosomal RNA gene database project: improved data processing and web-based tools. *Nucleic Acids Research*, 41(Database issue):D590–6.

Ramette A. and Tiedje J. M. (2007). Multiscale responses of microbial life to spatial distance and environmental heterogeneity in a patchy ecosystem. *Proceedings Of The National Academy Of Sciences Of The United States Of America*, 104(8):2761–2766.

Rappé M. S., Connon S. A., Vergin K. L., and Giovannoni S. J. (2002). Cultivation of the ubiquitous SAR11 marine bacterioplankton clade. *Nature*, 418(6898):630–633.

Rath J., Wu K. Y., Herndl G. J., and DeLong E. F. (1998). High phylogenetic diversity in a marine-snow-associated bacterial assemblage. *Aquatic Microbial Ecology*, 14(3):261–269.

Reisch C. R., Stoudemayer M. J., Varaljay V. A., Amster I. J., Moran M. A., and Whitman W. B. (2011). Novel pathway for assimilation of dimethylsulphoniopropionate widespread in marine bacteria. *Nature*, 473(7346):208–211.

Rosenberg M. and Rintoul S. R. Aurora Australis Marine Science Cruise AU1203 – Oceanographic Field Measurements and Analysis. Technical report, 2012.

Rosenberg M. S. and Anderson C. D. (2011). PASSaGE: pattern analysis, spatial statistics and geographic exegesis. Version 2. *Methods in Ecology and Evolution*, 2(3):229–232.

Rusch D. B., Halpern A. L., Sutton G., Heidelberg K. B., Williamson S., Yooseph S., Wu D., Eisen J. A., Hoffman J. M., Remington K., Beeson K., Tran B., Smith H., Baden-Tillson H., Stewart C., Thorpe J., Freeman J., Andrews-Pfannkoch C., Venter J. E., Li K., Kravitz S., Heidelberg J. F., Utterback T., Rogers Y.-H., Falcón L. I., Souza V., Bonilla-Rosso G., Eguiarte L. E., Karl D. M., Sathyendranath S., Platt T., Bermingham E., Gallardo V., Tamayo-Castillo G., Ferrari M. R., Strausberg R. L., Nealson K., Friedman R., Frazier M., and Venter J. C. (2007). The Sorcerer II Global Ocean Sampling expedition: northwest Atlantic through eastern tropical Pacific. *PLoS Biology*, 5(3):e77–e77.

Sabine C. L., Feely R. A., Gruber N., Key R. M., Lee K., Bullister J. L., Wanninkhof R., Wong C. S., Wallace D. W. R., Tilbrook B., Millero F. J., Peng T.-H., Kozyr A., Ono T., and Rios A. F. (2004). The Oceanic Sink for Anthropogenic CO_2. *Science*, 305(5682):367–371.

Scanlan D. J., Ostrowski M., Mazard S., Dufresne A., Garczarek L., Hess W. R., Post A. F., Hagemann M., Paulsen I., and Partensky F. (2009). Ecological Genomics of Marine Picocyanobacteria. *Microbiology and Molecular Biology Reviews*, 73(2):249–299.

Selje N. N., Simon M. M., and Brinkhoff T. T. (2004). A newly discovered *Roseobacter* cluster in temperate and polar oceans. *Nature*, 427(6973):445–448.

Short C. M. and Suttle C. A. (2005). Nearly Identical Bacteriophage Structural Gene Sequences Are Widely Distributed in both Marine and Freshwater Environments. *Applied and Environmental Microbiology*, 71(1):480–486.

Short S. M. and Suttle C. A. (2002). Sequence Analysis of Marine Virus Communities Reveals that Groups of Related Algal Viruses Are Widely Distributed in Nature. *Applied and Environmental Microbiology*, 68(3):1290–1296.

Simon M., Glöckner F. O., and Amann R. (1999). Different community structure and temperature optima of heterotrophic picoplankton in various regions of the Southern Ocean. *Aquatic Microbial Ecology*, 18(3):275–284.

Sinha V., Williams J., Meyerhöfer M., Riebesell U., Paulino A. I., and Larsen A. (2007). Air-sea fluxes of methanol, acetone, acetaldehyde, isoprene and DMS from a Norwegian fjord following a phytoplankton bloom in a mesocosm experiment. *Atmospheric Chemistry and Physics*, 7(3):739–755.

Sokolov S. and Rintoul S. R. (2002). Structure of Southern Ocean fronts at 140°E. *Journal of Marine Systems*, 37(1):151–184.

Sokolov S. and Rintoul S. R. (2009). Circumpolar structure and distribution of the Antarctic Circumpolar Current fronts: 1. Mean circumpolar paths. *Journal of Geophysical Research*, 114(C11):C11018.

Sowell S. M., Wilhelm L. J., Norbeck A. D., Lipton M. S., Nicora C. D., Barofsky D. F., Carlson C. A., Smith R. D., and Giovanonni S. J. (2009). Transport functions dominate the SAR11 metaproteome at low-nutrient extremes in the Sargasso Sea. *The ISME Journal*, 3(1):93–105.

Speer K., Rintoul S. R., and Sloyan B. (2000). The Diabatic Deacon Cell. *Journal of physical oceanography*, 30(12):3212–3222.

Steindler L., Schwalbach M. S., Smith D. P., Chan F., and Giovannoni S. J. (2011). Energy Starved *Candidatus* Pelagibacter Ubique Substitutes Light-Mediated ATP Production for Endogenous Carbon Respiration. *PLoS ONE*, 6(5):e19725.

Stingl U., Tripp H. J., and Giovannoni S. J. (2007). Improvements of high-throughput culturing yielded novel SAR11 strains and other abundant marine bacteria from the Oregon coast and the Bermuda Atlantic Time Series study site. *The ISME Journal*, 1:361–371.

). The concept of taxon invariance in ecology: do diversity patterns vary with changes in taxonomic resolution? *Folia Geobotanica*, 43:329–344.

Straza T. R. A., Ducklow H. W., Murray A. E., and Kirchman D. L. (2010). Abundance and single-cell activity of bacterial groups in Antarctic coastal waters. *Limnology and Oceanography*, 55(6):2526–2536.

Strous M., Fuerst J. A., Kramer E. H. M., Logemann S., Muyzer G., Van De Pas-Schoonen K. T., Webb R., Kuenen J. G., and Jetten M. S. M. (1999). Missing lithotroph identified as new planctomycete. *Nature*, 400(6743):446–449.

Strutton P. G., Griffiths F. B., Waters R. L., Wright S. W., and Bindoff N. L. (2000). Primary productivity off the coast of East Antarctica (80- 150°E): January to March 1996. *Deep Sea Research Part II: Topical Studies in Oceanography*, 47:2327–2362.

Sul W. J., Oliver T. A., Ducklow H. W., Amaral-Zettler L. A., and Sogin M. L. (2013). Marine bacteria exhibit a bipolar distribution. *Proceedings Of The National Academy Of Sciences Of The United States Of America*, 110(6):2342–2347.

Swan B. K., Martinez-Garcia M., Preston C. M., Sczyrba A., Woyke T., Lamy D., Reinthaler T., Poulton N. J., Masland E. D. P., Gomez M. L., Sieracki M. E., DeLong E. F., Herndl G. J., and Stepanauskas R. (2011). Potential for Chemolithoautotrophy Among Ubiquitous Bacteria Lineages in the Dark Ocean. *Science*, 333(6047):1296–1300.

Swingley W. D., Sadekar S., Mastrian S. D., Matthies H. J., Hao J., Ramos H., Acharya C. R., Conrad A. L., Taylor H. L., Dejesa L. C., Shah M. K., O'Huallachain M. E., Lince M. T., Blankenship R. E., Beatty J. T., and Touchman J. W. (2007). The Complete Genome Sequence of *Roseobacter denitrificans* Reveals a Mixotrophic Rather than Photosynthetic Metabolism. *Journal of Bacteriology*, 189(3):683–690.

Teske A., Alm E., Regan J. M., Toze S., Rittmann B. E., and Stahl D. A. (1994). Evolutionary relationships among ammonia- and nitrite-oxidizing bacteria. *Journal of Bacteriology*, 176(21):6623–6630.

Thomalla S. J., Waldron H. N., Lucas M. I., Read J. F., Ansorge I. J., and Pakhomov E. (2011). Phytoplankton distribution and nitrogen dynamics in the southwest indian subtropical gyre and Southern Ocean waters. *Ocean Science*, 7(1):113–127.

Thompson D. W. J. and Solomon S. (2002). Interpretation of Recent Southern Hemisphere Climate Change. *Science*, 296(5569):895–899.

Topping J. N., Heywood J. L., Ward P., and Zubkov M. V. (2006). Bacterioplankton composition in the Scotia Sea, Antarctica, during the austral summer of 2003. *Aquatic Microbial Ecology*, 45(3):229–235.

Tréguer P., Nelson D. M., Van Bennekom A. J., DeMaster D. J., Leynaert A., and Quéquiner B. (1995). The silica balance in the world ocean: a reestimate. *Science*, 268(5209):375–379.

Tripp H. J., Kitner J. B., Schwalbach M. S., Dacey J. W. H., Wilhelm L. J., and Giovannoni S. J. (2008). SAR11 marine bacteria require exogenous reduced sulphur for growth. *Nature*, 452(7188):741–744.

Trull T., Rintoul S. R., Hadfield M., and Abraham E. R. (2001). Circulation and seasonal evolution of polar waters south of Australia: implications for iron fertilization of the Southern Ocean. *Deep Sea Research Part II: Topical Studies in Oceanography*, 48(11):2439–2466.

Sebille E.van, Johns W. E., and Beal L. M. (2012). Does the vorticity flux from Agulhas rings control the zonal pathway of NADW across the South Atlantic? *Journal of Geophysical Research*, 117(C5):C05037.

Venter J. C., Remington K., Heidelberg J. F., Halpern A. L., Rusch D., Eisen J. A., Wu D., Paulsen I., Nelson K. E., Nelson W., Fouts D. E., Levy S., Knap A. H., Lomas M. W., Nealson K., White O., Peterson J., Hoffman J., Parsons R., Baden-Tillson H., Pfannkoch C., Rogers Y.-H., and Smith H. O. (2004). Environmental Genome Shotgun Sequencing of the Sargasso Sea. *Science*, 304(5667):66–74.

Vila-Costa M., Simó R., Harada H., Gasol J. M., Slezak D., and Kiene R. P. (2006). Dimethylsulfoniopropionate Uptake by Marine Phytoplankton. *Science*, 314(5799):652–654.

Wagner-Döbler I. and Biebl H. (2006). Environmental Biology of the Marine *Roseobacter* Lineage. *Annual Review of Microbiology*, 60(1):255–280.

Walker C. B., Torre J. R.de la, Klotz M. G., Urakawa H., Pinel N., Arp D. J., Brochier-Armanet C., Chain P., Chan P. P., Gollabgir A., Hemp J., Hügler M., Karr E. A., Könekke M., Shin M., Lawton T. J., Lowe T., Martens-Habbena W., Sayavedra-Soto L. A., Langf D., Sievert S. M., Rosenzweig A. C., Manning G., and Stahl D. A. (2010). *Nitrosopumilus maritimus* genome reveals unique mechanisms for nitrification and autotrophy in globally distributed marine crenarchaea. *Proceedings Of The National Academy Of Sciences Of The United States Of America*, 107(19):8818–8823.

Walsh D. A., Zaikova E., Howes C. G., Song Y. C., Wright J. J., Tringe S. G., Tortell P. D., and Hallam S. J. (2009). Metagenome of a Versatile Chemolithoautotroph from Expanding Oceanic Dead Zones. *Science*, 326(5952):578–582.

Ward P., Whitehouse M., Brandon M., Shreeve R., and Woodd-Walker R. (2003). Mesozooplankton community structure across the Antarctic Circumpolar Current to the north of South Georgia: Southern Ocean. *Marine Biology*, 143(1):121–130.

Weber T. S. and Deutsch C. (2010). Ocean nutrient ratios governed by plankton biogeography. *Nature*, 467(7315):550–554.

Weinbauer M. G., Arrieta J. M., Griebler C., and Herndl G. J. (2009). Enhanced viral production and infection of bacterioplankton during an iron-induced phytoplankton bloom in the Southern Ocean. *Limnol. Oceanogr*, 54(3):774–784.

West N. J., Obernosterer I., Zemb O., and Lebaron P. (2008). Major differences of bacterial diversity and activity inside and outside of a natural iron-fertilized phytoplankton bloom in the Southern Ocean. *Environmental Microbiology*, 10(3):738–756.

Whitworth T. (1980). Zonation and geostrophic flow of the Antarctic Circumpolar Current at Drake Passage. *Deep Sea Research Part I: Oceanographic Research Papers*, 27(7):497–507.

Whitworth III T. and Nowlin Jr. W. D. (1987). Water masses and currents of the Southern Ocean at the Greenwich Meridian. *Journal of Geophysical Research*, 92(C6):6462–6476.

Wilhelm S. W. and Suttle C. A. (1999). Viruses and nutrient cycles in the sea. *BioScience*, 49(10):781–788.

Wilkins D., Lauro F. M., Williams T. J., DeMaere M. Z., Brown M. V., Hoffman J. M., Andrews-Pfannkoch C., McQuaid J. B., Riddle M. J., Rintoul S. R., and Cavicchioli R. (2012). Biogeographic partitioning of Southern Ocean microorganisms revealed by metagenomics. *Environmental Microbiology*.

Wilkins D., Yau S., Williams T. J., Allen M. A., Brown M. V., DeMaere M. Z., Lauro F. M., and Cavicchioli R. (2012). Key microbial drivers in Antarctic aquatic environments. *FEMS Microbiology Reviews*.

Williams G. D., Nicol S., Aoki S., Meijers A. J. S., Bindoff N. L., Iijima Y., Marsland S. J., and Klocker A. (2010). Surface oceanography of BROKE-West, along the Antarctic margin of the south-west Indian Ocean (30–80°E). *Deep Sea Research Part II: Topical Studies in Oceanography*, 57(9-10):738–757.

Williams T. J., Lauro F. M., Ertan H., Burg D. W., Poljak A., Raftery M. J., and Cavicchioli R. (2011). Defining the response of a microorganism to temperatures that span its complete growth temperature range (-2 °C to 28 °C) using multiplex quantitative proteomics. *Environmental Microbiology*, 13 (8):2186–2203.

Williams T. J., Long E., Evans F., DeMaere M. Z., Lauro F. M., Raftery M. J., Ducklow H., Grzymski J. J., Murray A. E., and Cavicchioli R. (2012). A metaproteomic assessment of winter and summer bacterioplankton from Antarctic Peninsula coastal surface waters. *The ISME Journal*, 6(10):1883–1900.

Williams T. J., Wilkins D., Long E., Evans F., DeMaere M. Z., Raftery M. J., and Cavicchioli R. (2012). The role of planktonic Flavobacteria in processing algal organic matter in coastal East Antarctica revealed using metagenomics and metaproteomics. *Environmental Microbiology*.

Wright T. D., Vergin K. L., Boyd P. W., and Giovannoni S. J. (1997). A novel âĹĆ-subdivision proteobacterial lineage from the lower ocean surface layer. *Applied and Environmental Microbiology*, 63 (4):1441–1448.

Wunsch C. and Heimbach P. (2007). Practical global oceanic state estimation. *Physica D: Nonlinear Phenomena*, 230(1):197–208.

Ye Y. and Doak T. G. (2009). A parsimony approach to biological pathway reconstruction/inference for genomes and metagenomes. *PLoS Computational Biology*, 5(8):e1000465.

Yoon J., Yasumoto-Hirose M., Katsuta A., Sekiguchi H., Matsuda S., Kasai H., and Yokota A. (2007). *Coraliomargarita akajimensis* gen. nov., sp. nov., a novel member of the phylum '*Verrucomicrobia*' isolated from seawater in Japan. *International Journal of Systematic and Evolutionary Microbiology*, 57(5): 959–963.

Zaballos M., López-López A., Ovreas L., Bartual S. G., D'Auria G., Alba J. C., Legault B., Pushker R., Daae F. L., and Rodriguez-Valera F. (2006). Comparison of prokaryotic diversity at offshore oceanic locations reveals a different microbiota in the Mediterranean Sea. *FEMS Microbiology Ecology*, 56(3): 389–405.

Zhang R., Liu B., Lau S. C. K., Ki J.-S., and Qian P.-Y. (2007). Particle-attached and free-living bacterial communities in a contrasting marine environment: Victoria Harbor, Hong Kong. *FEMS Microbiology Ecology*, 61(3):496–508.

Zubkov M. V., Sleigh M. A., Tarran G. A., Burkill P. H., and Leakey R. J. G. (1998). Picoplanktonic community structure on an Atlantic transect from 50°N to 50°S. *Deep Sea Research Part I: Oceanographic Research Papers*, 45(8):1339–1355.