

Microbial Ecology and Biogeography

— OF THE —

Southern Ocean

David Wilkins



*Submitted in fulfillment of the requirements for the Degree of Doctor of
Philosophy.*

SCHOOL OF BIOTECHNOLOGY AND BIOMOLECULAR SCIENCES
UNIVERSITY OF NEW SOUTH WALES, SYDNEY

April 2013



Contents

Abstract	iii
List of Figures	ix
List of Tables	xi
List of Acronyms	xiii
Acknowledgements	xv
1 Introduction	1
1.1 Physical oceanography of the Southern Ocean	1
1.1.1 Fronts and zones	1
1.1.2 Water masses and circulation	3
1.1.3 Effect of climate change	4
1.2 Microbial ecology of the Southern Ocean	4
1.2.1 Bacteria	5
1.2.1.1 Alphaproteobacteria	5
1.2.1.1.1 Roseobacter clade	5
1.2.1.1.2 SAR11	6
1.2.1.1.3 SAR116	7
1.2.1.2 Betaproteobacteria	8
1.2.1.3 Gammaproteobacteria	8
1.2.1.3.1 SAR86	8
1.2.1.3.2 OMG group	9
1.2.1.3.3 Ant4D3	9
1.2.1.3.4 GSO-EOSA-1	10
1.2.1.4 Deltaproteobacteria	10
1.2.1.5 CFB	10
1.2.1.6 Cyanobacteria	12
1.2.1.7 Verrucomicrobia	12
1.2.1.8 Other bacteria	12
1.2.2 Archaea	13
1.2.3 Virioplankton	14
1.3 Project aims	15
1.3.1 The Polar Front	15
1.3.1.1 Biogeographic role	15
1.3.1.2 Differences in community composition	15
1.3.1.3 Differences in functional potential	15
1.3.2 The role of advection in microbial biogeography	15

2	MINSPEC	17
2.1	Abstract	17
2.2	Introduction	17
2.2.1	Metagenomic analysis of microbial assemblages	17
2.2.2	The maximum parsimony approach	19
2.3	Methods	20
2.3.1	Implementation of MINSPEC	20
2.3.2	Validation of MINSPEC	21
2.4	Results	22
2.5	Discussion	22
2.6	Conclusions	24
3	The Polar Front	25
3.1	Abstract	25
3.2	Introduction	26
3.3	Methods	27
3.3.1	Sampling and metagenomic sequencing	27
3.3.2	Phylogenetic analysis of metagenomic data	30
3.3.2.1	BLAST comparison to RefSeq database	30
3.3.2.2	OTU abundances and variance between zones	30
3.3.2.3	Fragment recruitment to verify Operational Taxonomic Unit (OTU) identification	31
3.3.2.4	Additional samples to test “polynya hypothesis”	31
3.3.3	Functional analysis of metagenomic data	31
3.3.3.1	BLAST comparison to KEGG database	31
3.3.3.2	Analysis of functional potential	32
3.3.3.3	Taxonomic decomposition	32
3.4	Results	33
3.4.1	Metagenomic sequencing	33
3.4.2	Phylogenetic analysis of metagenomic data	33
3.4.3	Fragment recruitment to verify OTU identification	39
3.4.4	Additional samples to test alternative “polynya hypothesis”	39
3.4.5	Functional analysis of metagenomic data	39
3.5	Discussion	43
3.5.1	Taxonomic groups differentiating the zones	43
3.5.1.1	GSO-EOSA-1	43
3.5.1.2	Ammonia-oxidizing Crenarchaeota	45
3.5.1.3	Cyanobacteria	45
3.5.1.4	SAR11 and SAR116 clades	46
3.5.1.5	Bacteroidetes	47
3.5.1.6	Rhodobacterales	47
3.5.1.7	Alteromonadales	48
3.5.1.8	Verrucomicrobia	48
3.5.2	Functional capacities differentiating the zones	48
3.5.2.1	Conclusions: Biogeographic role of the Polar Front	52
4	Deep water formation	53
4.1	Abstract	53
4.2	Introduction	53
4.3	Methods	54
4.4	Results and Discussion	54

5	The advection effect	57
5.1	Abstract	57
5.2	Introduction	57
5.2.1	Distance and environment effects in microbial biogeography	57
5.2.2	Water mass endemism and advection of marine microorganisms	58
5.2.3	Aims and approach of this study	59
5.3	Methods	60
5.3.1	Sampling	60
5.3.2	DNA extraction	61
5.3.3	Sequencing	63
5.3.4	Taxonomic assignment	63
5.3.5	Physicochemical and spatial distances	63
5.3.6	Generation of advection distance matrix	64
5.3.7	Ordination of distance matrices and comparison to water masses	65
5.3.8	Testing of advection effect	65
5.3.9	Differential influence of advection on OTU subsets	66
5.4	Results	67
5.4.1	Sequencing and taxonomic assignment	67
5.4.2	Environment and distance effects	72
5.4.3	Testing the advection effect	74
5.4.4	Testing advection effect mechanisms	78
5.4.5	Differential effect of advection on OTU subsets	79
5.5	Discussion	79
5.5.1	Taxonomic resolution	80
5.5.2	Differential influence of advection on OTU subsets	81
5.5.3	Future work	81
6	General discussion	83
6.1	Contributions of this thesis	83
6.1.1	The Polar Front	83
6.1.1.1	Biogeographic role of the Polar Front	84
6.1.1.2	The Polar Front and climate change	85
6.1.2	The advection effect	86
6.1.3	MINSPEC	87
6.2	Conceptual units in microbial ecology	88
6.3	Future work	89
6.4	Conclusions	89
	References	90

List of Figures

1.1	Major fronts and water masses of the Southern Ocean	2
2.1	Results of MINSPEC validation	23
3.1	Map showing sites of seawater samples used in the Polar Front study	28
3.2	Rank-abundance curves for OTUs in each zone and size fraction	36
3.3	Contribution of OTUs to variance between the North and South zones	38
3.4	Read recruitment to reference genomes	40
3.5	Tree of GSO-EOSA-1 related 16S rRNA genes	44
3.6	Taxonomic decomposition of KEGG modules	49
4.1	Map showing sites of preliminary Antarctic Bottom Water (AABW) samples	55
4.2	Non-Metric Multidimensional Scaling (nMDS) of AABW, North Zone (NZ) and South Zone (SZ) samples	56
5.1	Map showing sites of samples used in the advection study	60
5.2	OTU assignments in the advection study.	71
5.3	nMDS of advective distances between samples.	72
5.4	nMDS of advective distances between samples.	73
5.5	dbRDA ordination of relationship between environment and community. . .	74
5.6	Encounter times for all samples in advection model.	75
5.7	nMDS of advective distances between samples.	77
5.8	Advection effect at different taxonomic resolutions	78
6.1	Biogeographic effect sizes	87

List of Tables

2.1	Examples of spurious OTU identifications	19
3.1	Details of samples used in Polar Front study	29
3.2	Additional samples used to test polynya hypothesis	31
3.3	Twenty most abundant OTUs	34
3.4	Highest-contributing OTUs to the difference between the North and South zones	37
3.5	Contributions of KEGG modules to variance between the North and South zones	41
3.6	Contributions of KEGG ortholog groups to variance between the North and South zones	42
4.1	AABW samples used in the preliminary analysis	54
4.2	Twenty most abundant OTUs in preliminary AABW samples	56
5.1	Full sample data for advection study	68
5.1	(cont.) Full sample data for advection study.	69
5.1	(cont.) Full sample data for advection study.	70
5.2	Correlations between dbRDA axes and physicochemical variables	73
5.3	Results of BVSTEP	80

List of Acronyms

AABW Antarctic Bottom Water.

ACC Antarctic Circumpolar Current.

AZ Antarctic Zone.

CDW Circumpolar Deep Water.

NADW North Atlantic Deep Water.

nMDS Non-Metric Multidimensional Scaling.

NZ North Zone.

OTU Operational Taxonomic Unit.

PF Polar Front.

RCA Roseobacter Clade Affiliated.

SAM Southern Annular Mode.

SAMW Subantarctic Mode Water.

SAZ Subantarctic Zone.

SO Southern Ocean.

STF Subtropical Front.

SZ South Zone.

Acknowledgements

Chapter 6

General discussion

6.1 Contributions of this thesis

This thesis aimed to investigate the microbial ecology and biogeography of the Southern Ocean (SO). To achieve this, two factors that structure the biogeographic distribution of microorganisms in the SO were selected for study: the Polar Front (PF), a major biogeographic barrier, and advection, a potentially major biogeographic force.

6.1.1 The Polar Front

This project found good evidence that the PF is a major biogeographic barrier in the SO, by demonstrating that the bacterial and archaeal communities in the waters to the south (the Antarctic Zone (AZ)) are significantly different from the waters to the north (the Subantarctic Zone (SAZ) and subtropical waters north of the Subtropical Front (STF), primarily representing Subantarctic Mode Water (SAMW)) (Chapter 3).

This is not the first study on the effect of the PF on the distribution of SO microbiota. Variation in the position of the Antarctic Circumpolar Current (ACC), which determines the location of the PF, has been shown to influence zooplankton composition (e.g. Chiba *et al.*, 2001; Hunt *et al.*, 2001), including dinoflagellates (Esper and Zonneveld, 2002)¹. The ACC and/or PF have similarly been shown to influence the distribution of *Roseobacter* phylotypes (Selje *et al.*, 2004; Giebel *et al.*, 2009), *Flavobacteria* (Abell and Bowman, 2005b), and SAR11 phylotypes (Giebel *et al.*, 2009). However, this thesis provides a significant contribution, presenting the first community-level (metagenomic) survey of SO bacterial and archaeal plankton performed over a latitudinal transect occupying all major SO surface water masses to give an integrated snapshot of the microbial ecology and biogeography of the SO.

As well as the confirming previous findings on the level of individual taxonomic groups, this study found that the effect of the PF extends to the whole community, and even to the distribution of genomically encoded functional potential. The higher abundance south of the PF of Bacteroidetes and Rhodobacterales, associated with the degradation of phytoplanktonic byproducts (e.g. Buchan *et al.*, 2005; Williams *et al.*, 2012b), reflect

¹Interestingly, one study described the biogeographic effect of ACC-associated fronts on zooplankton as being only weakly related to environmental parameters (Ward *et al.*, 2003), suggesting the effect of advection (Chapter 5) on zooplankton as a potential avenue for future research

the higher concentrations of (primarily eukaryotic) phytoplankton in this region. This was also reflected in the functional analysis, with an overrepresentation of high-specificity transporters, suggestive of copiotrophic taxa in a “feast” phase (Lauro *et al.*, 2009). In general, waters south of the PF reflected the upwelling of nutrient-rich North Atlantic Deep Water (NADW) and higher supply of light during the austral summer, which make the region significantly more active and productive than SAZ and even subtropical waters to the north.

These northern waters were characterised by a higher relative abundance of slow-growing, nutrient-scavenging oligotrophs such as SAR11 and SAR116. Functionally, this was reflected in the higher abundance of genes encoding branched-chain amino acid transporters, which both SAR11 and SAR116 possess. The other significant feature of region north of the PF was the higher abundance of the cyanobacterial genera *Prochlorococcus* and *Synechococcus*, and concurrently the photosynthesis functions they encode. This was most likely due to the sensitivity of these genera to temperature.

6.1.1.1 Biogeographic role of the Polar Front

Having shown that the PF is a major biogeographic barrier, and in light of the advection study also presented in this thesis (Chapter 5), it is worth considering the mechanism(s) by which the PF shapes microbial biogeography. It is likely that three main forces are at work.

The first is the role of the PF as a “biogeographic barrier” in the classical sense in which the term is applied to macroorganisms. In other words, it physically prevents or slows the migration of cells between the regions it divides, leading if not to allopatric speciation, at least to some degree of genetic divergence, which is amplified by the differences in environmental properties. Selje *et al.* (2004), who first reported that Roseobacter Clade Affiliated (RCA) phylotypes differed across the PF, offered this mechanism as a likely explanation, an idea corroborated by further reports on RCA (Giebel *et al.*, 2009) and Flavobacteria (Abell and Bowman, 2005b). The advection effect (Chapter 5) supports such a mechanism, by showing that oceanic regions poorly connected by advection (i.e. poorly mixed) have less similar microbial communities.

The second mechanism, complementary to the first, is the difference in physicochemical properties resulting from the same oceanographic forces that create the PF: in particular, the advective distribution of nutrients. The ratio of biological N/P export in SO surface waters increases northwards from the region of upwelling Circumpolar Deep Water (CDW) in the AZ ($N/P_{\text{exp}} < 16$) to the SAZ ($N/P_{\text{exp}} > 16$) (Weber and Deutsch, 2010). This directly contradicts the standard assumption that PO_4^{3-} is exported to the deep ocean in a fixed proportion of $\sim 16:1$ available NO_3^- to PO_4^{3-} (the Redfield ratio). Weber and Deutsch (2010) convincingly showed that this is largely a result of the biogeographic distribution of low cellular N/P diatoms relative to other high cellular N/P plankton. The distribution of diatoms in the SO is in turn controlled by the concentration of silicic acid (Franck *et al.*, 2000), which supplied in abundance south of the PF by upwelling CDW but is limiting further north (widely held, but well summarised by Coale *et al.*, 2004), explaining the observed difference in N/P_{exp} . Further, Weber and Deutsch (2010) showed that advective mixing of organic N and P exported to the deep ocean by sinking organic matter

and remineralised in the aphotic zone was sufficient to counterbalance the differential export of N and P by diatoms and other plankton, leading to an equilibrium approximately equivalent to the Redfield ratio of 16:1 N:P. Advective transport of nutrients and the distribution of plankton are thus intimately connected in the SO, with the PF acting as a key barrier between the nutrient-rich AZ upwelling and the comparatively oligotrophic SAZ. As well as the distribution of these major nutrients (N, P and Si), the waters to the north and south of the PF differ in temperature and salinity due to their different circulatory origins (Foldvik and Gammelsrød, 1988).

The third mechanism by which the PF may act as a biogeographic boundary is more mundane. Being a polar ocean, the SO is subject to strong latitudinal gradients in air temperature and sunlight unrelated to its oceanographic structure. The Antarctic Circle, the latitude at which continuous 24-hour periods of sunlight (and of darkness) become possible, is considerably south of the PF ($\sim 66.5^\circ$ S, although this varies due to slow changes in the Earth's axial tilt). However, the existence of large environmental gradients means that longitudinal features (fronts, currents, divergences and convergences in both the ocean and atmosphere) are almost certain to be associated with biological discontinuities simply by virtue of lying on a particular latitude, without necessarily having any causal relationship. In the case of the PF and its role in the distribution of marine bacteria and archaea, the possibility that this was the only significance of the PF was explicitly tested for and discounted in this study: other arbitrary latitudinal lines do not structure the biological observations as well as the PF (see Chapter 3). Nevertheless, it is likely that latitudinal gradients not directly related to the PF (particularly sunlight) do make some contribution to the biogeographic pattern.

6.1.1.2 The Polar Front and climate change

Global climate change is already having a large effect on the SO. The ACC is largely driven by the strong westerly winds that are characteristic of sub-polar Ferrel cells in atmospheric circulation. The Southern Annular Mode (SAM) (also known as the Antarctic Oscillation) is a complex, low-frequency oscillation in the latitude and speed of this westerly wind belt between "positive" (further south, stronger flow) and "negative" (further north, weaker flow) phases. As a result of climate change, the long-term trend of the SAM may be towards the positive phase (Thompson and Solomon, 2002). Along with an increase in the temperature of ACC waters (also due to climate change (Aoki *et al.*, 2003; Böning *et al.*, 2008)), this may be responsible for the observed southward migration of the mean position of the ACC by ~ 50 km since the 1950s (Gille, 2002). Even with optimistic assumptions about future anthropogenic greenhouse gas emissions, it has been predicted to move a further $\sim 1.4^\circ$ south (~ 150 km) by the year 2100 (Fyfe and Saenko, 2005).

The effects of climate change on marine ecology are often thought of in terms of changes in physicochemical properties such as temperature, salinity, pH, and atmospheric CO_2 . However, changes to the location of biogeographic barriers such as the PF may also be significant. Southward migration of the PF will displace a large surface area of AZ waters enriched by upwelling nutrients, increasing the relative area of the comparatively oligotrophic SAZ. This may result in a net decrease in primary production, although concurrent changes in temperature and other physicochemical properties make this difficult

to predict. As the SO is a major site for sequestration of anthropogenic CO₂ through the biological pump (Thomalla *et al.*, 2011), this raises the possibility of creating a negative feedback loop (Cox *et al.*, 2000) which would further accelerate global climate change. Future metagenomic surveys of the SO with a broader taxonomic scope and increased sampling resolution will be valuable in better predicting such effects.

6.1.2 The advection effect

The second major focus of this thesis was the role of advection in shaping the biogeography of microorganisms in the SO, and by extension the ocean in general. This question is highly topical, given the recent discovery that geographic distance often controls microbial biogeography in contradiction with the Baas Beeking hypothesis (key studies: Cho and Tiedje (2000); Whitaker *et al.* (2003); reviews: Martiny *et al.* (2006); Hanson *et al.* (2012)), and the frequent invocation of circulation to explain observed distributions of marine microbes (e.g. Lauro *et al.*, 2007; Giebel *et al.*, 2009; Ghiglione *et al.*, 2012; Sul *et al.*, 2013).

Previous work addressing this question has focused on water mass endemism and qualitative descriptions of circulation. Galand *et al.* (2009) and Agogu   *et al.* (2011) presented evidence of the specificity of microbial communities to water masses in the Arctic and North Atlantic oceans, even across small geographic distances, suggesting boundaries between water masses act as biogeographic barriers, although these observations do not exclude simple environmental selection. Hamilton *et al.* (2008), also describing the Arctic and North Atlantic oceans, found picoeukaryotic communities clustered by circulatory origin as determined by qualitative analysis of hydrographic properties. The authors noted that quantitative modelling of circulation would be necessary to directly test the role of circulation. Recently, Hamdan *et al.* (2013) demonstrated a similar clustering of prokaryotes Arctic marine sediments with their circulatory origins. Both studies controlled for environmental factors to various degrees.

This thesis (and the associated publication) present the first quantitative test of the effect of advection on microbial biogeography. By employing a high-resolution computational model of SO circulation to determine advective distances between samples, the standard ecological tools of distance matrices and partitioning of variance with the partial Mantel test could be used to isolate the effect of advection from environmental selection and spatial separation. This thesis thus also contributes a replicable method for future studies to evaluate the advection effect in other marine environments and directly compare it to other biogeographic forces.

Together, contemporary environmental selection and geographic distance explain ~ 50% of variation in microbial community composition (Hanson *et al.*, 2012). In this study, advection was estimated to explain 7% of variation (Fig. 6.1). This is a conservative estimate, as higher values were found when alternative distance metrics were considered and problematic samples excluded, and samples which shared a common advective origin but had a large mutual advective distance were not considered. Future work on the advection effect will be valuable not only in confirming its role but in obtaining an accurate measure of its magnitude.

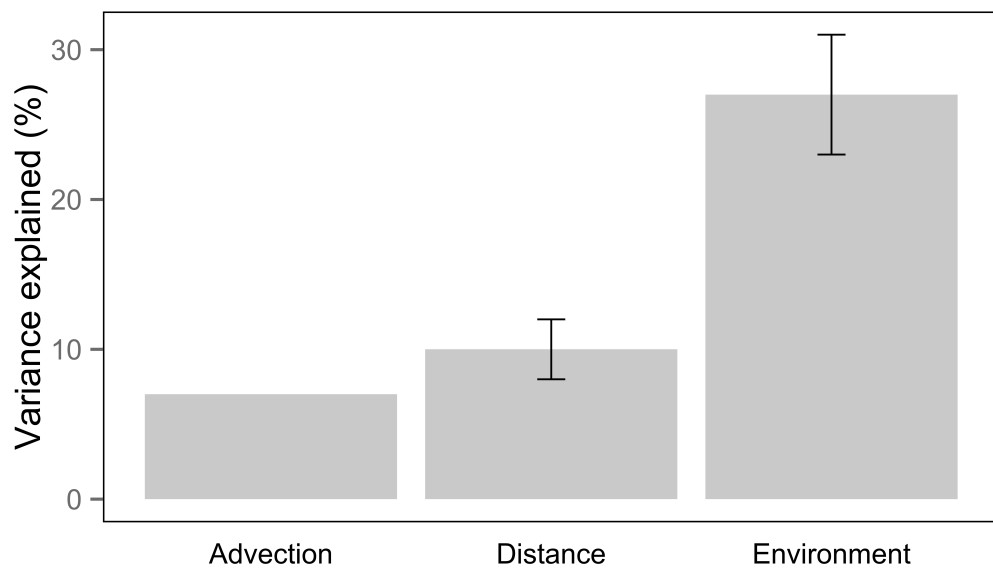


Figure 6.1: Variation in microbial community composition explained by environment and distance effects (data from review of 19 studies by Hanson *et al.* (2012); error bars represent standard error) and by the advection effect (this study).

6.1.3 MINSPEC

This thesis also presents a novel software tool, *MINSPEC*, which contributes to improving the accuracy of Operational Taxonomic Unit (OTU) assignment and calculation of relative abundances in metagenomic studies.

The number of publicly available full genome sequences for microbial species is growing exponentially: over the course of this project, the number of microbial genomes in the RefSeq database increased from 5,500 (May 2010) to 15,000 (March 2013) (<http://www.ncbi.nlm.nih.gov/refseq/statistics/>, accessed 12 April 2013). As more genomes become available, the number of potential high-quality matches to a given metagenomic read will increase as a natural result of genomic identity between related organisms. *MINSPEC* reduces the need to rely on nucleotide identity as the sole objective standard for assigning metagenomic reads to OTUs, making use of the contextual information provided by the full set of reads to inform the assignment of each individual read. While assembly of metagenomic reads can to some extent perform the same function (Temperton and Giovannoni, 2012), *MINSPEC* does not require long or overlapping reads, making it well-suited to the short read lengths of current next-generation sequencing methods and to environments such as the open ocean that have a long tail of low-abundance taxa.

In the long term, single-cell genomic sequencing is the most promising approach for accurate and reliable environmental genomics (Blainey, 2013). Until then, *MINSPEC* may be of use in improving the quality of metagenomic results.

6.2 Conceptual units in microbial ecology

In some fortunate disciplines, the natural ontologies by which humans “carve up” the observed world into conceptual units map well onto the underlying phenomena. In medicine, for example, the object of study (the human body) is physically divided into easily recognised and discrete units (organs) which have likewise discrete and well-defined functions. A physician’s mental model of the human body has familiar and tangible components, and allows them to understand diseases as systematic divergences from the body’s normal form and function. In physics, on the other hand, such intuitive ontologies frequently fail and even mislead. The vision of electrons as discrete spheres orbiting a nucleus like planets around a star holds a strong intuitive appeal, but is contradicted by wave-particle duality, and any physicist who failed to resist this tempting but incorrect view would be at an enormous disadvantage. Physicists, unlike physicians, must either work in new and unfamiliar modes of thinking, or abandon a conceptual grasp of their objects of study altogether and instead investigate them indirectly through mathematical surrogates.

In microbiology, the natural unit of study is the cell, and the natural unit by which cells are categorised is the species. Although defining microbial species is not quite as straightforward as for sexually reproducing macroorganisms, the usual standards of 16S and genomic similarity are sufficient for laboratory experiments involving clonal or simple mixed populations in culture. Environmental microbiologists, in need of a similar unit of categorisation but faced with the diversity and depth of environmental populations, frequently use the OTU as a practical method of categorising cells with properties similar enough for the purposes of the scientific question at hand.

The rapidly emerging “omics” approaches to environmental microbiology have begun to strain the limits of this view. Enormous population sizes, short generation times and the high rate of horizontal gene transfer between bacterial cells mean that rather than discrete numbers of distinct OTUs, environmental assemblages may be better described as “a continuum of genomic possibilities” (Goldenfeld and Woese, 2007). Just as a physicist may know that electrons are not infinitesimal billiard balls, but still struggle to conceptualise the wave function of a fundamental particle as anything other than a mathematical abstraction, attempting to describe the ecological and biogeographic patterns of environmental microbes with the familiar vocabulary of species (or OTUs) and cells can be challenging. This has been illustrated many times during the course of this thesis. In the study of the PF (Chapter 3), a large and statistically significant difference between the communities to the north and south of the front was found to be driven by a long and flat distribution of OTUs, each of which individually contributed only a small amount of variance (Table 3.4). Likewise, the differences in functional potential between the zones were spread thin over a large number of functional gene categories (Tables 3.5 and 3.6) which nevertheless represented a real and important distinction *in toto*. In Chapter 5, the attempt to identify OTUs which differentially contributed to the statistically well-supported advection effect yielded results in the form of subsets of OTUs that were best correlated with the effect. However, the biological relevance of these subsets was not clear. It may simply be unfruitful to try to conceptualise such patterns on the level of individual OTUs.

The recent renewal of activity in microbial biogeography (Ramette and Tiedje, 2006),

the urgency of climate change and other ecological problems and the improvement in technologies for interrogating environmental assemblages all create a need to develop ways of meaningfully describing, categorising and drawing conclusions from environmental data (Goldenfeld and Woese, 2007). As in physics, this may require the reluctant abandonment of intuitive and straightforward conceptual models for a less familiar but more accurate ontology.

TODO this needs some actual proscriptions

6.3 Future work

TODO Future work

SO microbial ecology Current metagenomic methods require only looking at a small part of the community at a time (constrained by primer selection, size fractionation) - would be great to see the whole thing - single cell?

Future studies should seek to confirm the advection results, particularly the advection effect, in other regions.

6.4 Conclusions

This project has demonstrated the role of the PF as a major biogeographic barrier in the SO. It has also provided the first direct evidence that the advection of marine microbes influences their community composition. As well as these results, this thesis contributes methodological advances with the metagenomic tool *MINSPEC* and a replicable method for assessing the advection effect in marine systems. Increased knowledge about fundamental patterns in microbial ecology and biogeography, as well as the specific ecosystem of the SO, will be valuable to shaping our response to ecological challenges such as climate change and expanding our understanding of microbial life on Earth.

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.
- Agogu  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.
- Andr  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-Dav  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.
- B  a 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.
- Blainey P. C. (2013). The future is now: single-cell genomics of bacteria and archaea. *FEMS Microbiology Reviews*, 37(3):407–427.
- 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.
- 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 endemism 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. (1998). Quantifying structural redundancy in ecological communities. *Oecologia*, 113(2):278–289.
- Clarke K. R. and Warwick R. M. *Change in marine communities: an approach to statistical analysis and interpretation*. PRIMER-E, Plymouth, 2nd edition, 2001.
- Coale K. H., Johnson K. S., Chavez F. P., Buesseler K. O., Barber R. T., Brzezinski M. A., Cochlan W. P., Millero F. J., Falkowski P. G., and Bauer J. E. (2004). Southern Ocean iron enrichment experiment: carbon cycling in high-and low-Si waters. *Science*, 304(5669):408–414.
- 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.
- Finlay B. J. (2002). Global Dispersal of Free-Living Microbial Eukaryote Species. *Science*, 296(5570):1061–1063.
- 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.
- Franck V. M., Brzezinski M. A., Coale K. H., and Nelson D. M. (2000). Iron and silicic acid concentrations regulate Si uptake north and south of the Polar Frontal Zone in the Pacific Sector of the Southern Ocean. *Current Opinion in Microbiology*, 47(15-16):3315–3338.
- 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., Kirchman 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 methylophile. *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.
- Goldenfeld N. and Woese C. (2007). Biology's next revolution. *Nature*, 445(7126):369–369.
- González J. M., Fernández-Gómez B., Fernández-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.
- Grzymalski 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.
- Grzymalski 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 in the oceanographic environment and zooplankton community in the vicinity of a sub-Antarctic archipelago. *Marine Biology*, 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 nongrowth of heterotrophic bacteria, with emphasis on the marine environment. *Annual Review of Microbiology*, 41:25–49.
- Knight 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.
- Méthé B. A., Nelson K. E., Deming J. W., Momen B., Melamud E., Zhang X., Moulton J., Madupu R., Nelson W. C., Dodson R. J., Methe B. A., Nelson K. E., Deming J. W., Momen B., Melamud E., Zhang X., Moulton 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 CO₂ 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 Grzyski J. J. (2007). Diversity and genomics of Antarctic marine microorganisms. *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 *Calyptogenia 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 W. O., Jr, 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.
- Ramette A. and Tiedje J. M. (2006). Biogeography: An Emerging Cornerstone for Understanding Prokaryotic Diversity, Ecology, and Evolution. *Microbial Ecology*, 53(2):197–207.
- 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 CO₂. *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.
- Sogin M. L., Morrison H. G., Huber J. A., Welch D. M., Huse S. M., Neal P. R., Arrieta J. M., and Herndl G. J. (2006). Microbial diversity in the deep sea and the underexplored “rare biosphere”. *Proceedings Of The National Academy Of Sciences Of The United States Of America*, 103(32):12115–12120.
- 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 Giovannoni 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.
- Storch D. and Sizling A. L. (2008). 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.
- Tamura T., Williams G. D., Fraser A. D., and Ohshima K. I. (2012). Potential regime shift in decreased sea ice production after the Mertz Glacier calving. *Nature Communications*, 3:826–.
- Temperton B. and Giovannoni S. J. (2012). Metagenomics: microbial diversity through a scratched lens. *Current Opinion in Microbiology*, 15(5):605–612.
- 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.
- Seville 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.
- Whitaker R. J., Grogan D. W., and Taylor J. W. (2003). Geographic barriers isolate endemic populations of hyperthermophilic archaea. *Science*, 301(5635):976–978.
- 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 T., III and Nowlin W. D., Jr. (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., Bindoff N. L., Marsland S. J., and Rintoul S. R. (2008). Formation and export of dense shelf water from the Adélie Depression, East Antarctica. *Journal of Geophysical Research*, 113(C4):C04039.
- 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 α -subdivision proteobacterial lineage from the lower ocean surface layer. *Applied and Environmental Microbiology*, 63(4):1441–1448.
- 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). *Coralimargarita 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.
- Youssef N., Sheik C. S., Krumholz L. R., Najar F. Z., Roe B. A., and Elshahed M. S. (2009). Comparison of species richness estimates obtained using nearly complete fragments and simulated pyrosequencing-generated fragments in 16S rRNA gene-based environmental surveys. *Applied and Environmental Microbiology*.
- 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.