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

Publications

Papers

- (Chapter 1) Wilkins D., Yau S., Williams T. J., Allen M. A., Brown M. V., DeMaere M. Z., Lauro F. M., and Cavicchioli R. (2013). Key microbial drivers in Antarctic aquatic environments. *FEMS Microbiology Reviews*, 37(3):303–335
- (Chapter 3) 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. (2013). Biogeographic partitioning of Southern Ocean microorganisms revealed by metagenomics. *Environmental Microbiology*, 15(5):1318–1333
- (Chapter 5) Wilkins D., van Sebille E., Rintoul S. R., Lauro F. M., and Cavicchioli R. (2013). Advection shapes Southern Ocean microbial assemblages independent of distance and environment effects. *Submitted*.
- Siddiqui K. S., Williams T. J., Wilkins D., Yau S., Allen M. A., Brown M. V., Lauro F. M., and Cavicchioli R. (2013). Psychrophiles. *Annual Review of Earth and Planetary Sciences*, 41(1)
- Williams T. J., Wilkins D., Long E., Evans F., DeMaere M. Z., Raftery M. J., and Cavicchioli R. (2013). The role of planktonic Flavobacteria in processing algal organic matter in coastal East Antarctica revealed using metagenomics and metaproteomics. Environmental Microbiology, 15(5):1302–1317
- 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*, 8:595
- 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

Conference abstracts

Wilkins D. Biogeographic partitioning of Southern Ocean picoplankton. In *ISME 13*, Copenhagen, 2012

Contents

Publications List of Figures List of Tables x List of Acronyms 1 Introduction 1.1 Physical oceanography of the Southern Ocean 1.1.1 Fronts and zones 1.1.2 Water masses and circulation 1.1.3 Effect of climate change 1.2 Microbial ecology of the Southern Ocean 1.2.1 Bacteria 1.2.1.1 Roseobacteria 1.2.1.1 Roseobacteria 1.2.1.1.2 SAR11 1.2.1.1.3 SAR16 1.2.1.2 Betaproteobacteria 1.2.1.3 Gammaproteobacteria 1.2.1.3 Gammaproteobacteria 1.2.1.3.1 SAR86 1.2.1.3.2 OMG group 1.2.1.3.3 Ant4D3 1.2.1.3.4 GSO-EOSA-1 1.2.1.4 Deltaproteobacteria 1.2.1.5 CFB 1.2.1.6 Cyanobacteria 1.2.1.7 Verrucomicrobia 1.2.1.8 Other bacteria 1.2.2 Virioplankton 1.3 Project aims 1.3.1 The Polar Front 1.3.1.1 Biogeographic role 1.3.1.2 Differences in community composition 1.3.1.3 Differences in functional potential	A۱	ostra	ct				v
List of Tables x List of Acronyms 1 Introduction 1.1 Physical oceanography of the Southern Ocean 1.1.1 Fronts and zones 1.1.2 Water masses and circulation 1.1.3 Effect of climate change 1.2 Microbial ecology of the Southern Ocean 1.2.1 Bacteria 1.2.1.1 Alphaproteobacteria 1.2.1.1 Roseobacter clade 1.2.1.1.2 SAR11 1.2.1.1.3 SAR116 1.2.1.2 Betaproteobacteria 1.2.1.3 Gammaproteobacteria 1.2.1.3 Gammaproteobacteria 1.2.1.3 SAR86 1.2.1.3.2 OMG group 1.2.1.3.3 Ant4D3 1.2.1.3 Ant4D3 1.2.1.4 Deltaproteobacteria 1.2.1.5 CFB 1.2.1.6 Cyanobacteria 1.2.1.7 Verrucomicrobia 1.2.1.8 Other bacteria 1.2.2 Archaea 1.2.3 Virioplankton 1.3 Project aims 1.3.1 The Polar Front 1.3.1.1 Biogeographic role 1.3.1.2 Differences in community composition 1.3.1.3 Differences in functional potential	A	cknov	wledge	ments			vii
List of Acronyms 1 Introduction 1.1 Physical oceanography of the Southern Ocean 1.1.1 Fronts and zones 1.1.2 Water masses and circulation 1.1.3 Effect of climate change 1.2 Microbial ecology of the Southern Ocean 1.2.1 Bacteria 1.2.1.1 Roseobacter clade 1.2.1.1.1 Roseobacter clade 1.2.1.1.2 SAR11 1.2.1.1.3 SAR116 1.2.1.2 Betaproteobacteria 1.2.1.3 Gammaproteobacteria 1.2.1.3 Gammaproteobacteria 1.2.1.3 Gammaproteobacteria 1.2.1.3 Gammaproteobacteria 1.2.1.3 SAR86 1.2.1.3.1 SAR86 1.2.1.3.2 OMG group 1.2.1.3.3 Ant4D3 1.2.1.3.4 GSO-EOSA-1 1.2.1.4 Deltaproteobacteria 1.2.1.5 CFB 1.2.1.6 Cyanobacteria 1.2.1.7 Verrucomicrobia 1.2.1.8 Other bacteria 1.2.1.9 Virioplankton 1.3 Project aims 1.3.1 The Polar Front 1.3.1.1 Biogeographic role 1.3.1.2 Differences in community composition 1.3.1.3 Differences in functional potential	Pι	ıblica	itions				ix
1 Introduction 1.1 Physical oceanography of the Southern Ocean 1.1.1 Fronts and zones 1.1.2 Water masses and circulation 1.1.3 Effect of climate change 1.2 Microbial ecology of the Southern Ocean 1.2.1 Bacteria 1.2.1.1 Alphaproteobacteria 1.2.1.1 Roseobacter clade 1.2.1.1.2 SAR11 1.2.1.1.3 SAR116 1.2.1.2 Betaproteobacteria 1.2.1.3 Gammaproteobacteria 1.2.1.3 Gammaproteobacteria 1.2.1.3 COMG group 1.2.1.3.1 AN4D3 1.2.1.3.2 OMG group 1.2.1.3.3 An4D3 1.2.1.4 Deltaproteobacteria 1.2.1.5 CFB 1.2.1.6 Cyanobacteria 1.2.1.7 Verrucomicrobia 1.2.1.8 Other bacteria 1.2.2 Archaea 1.2.3 Virioplankton 1.3 Project aims 1.3.1 The Polar Front 1.3.1.1 Biogeographic role 1.3.1.2 Differences in community composition 1.3.1.3 Differences in functional potential	Li	st of	Figures	3			xv
1. Introduction 1.1 Physical oceanography of the Southern Ocean 1.1.1 Fronts and zones 1.1.2 Water masses and circulation 1.1.3 Effect of climate change 1.2 Microbial ecology of the Southern Ocean 1.2.1 Bacteria 1.2.1.1 Alphaproteobacteria 1.2.1.1.1 Roseobacter clade 1.2.1.1.2 SAR11 1.2.1.3 SAR116 1.2.1.3 Gammaproteobacteria 1.2.1.3 Gammaproteobacteria 1.2.1.3.1 SAR86 1.2.1.3.2 OMG group 1.2.1.3.3 Ant4D3 1.2.1.3.4 GSO-EOSA-1 1.2.1.4 Deltaproteobacteria 1.2.1.5 CFB 1.2.1.6 Cyanobacteria 1.2.1.7 Verrucomicrobia 1.2.1.8 Other bacteria 1.2.2 Archaea 1.2.3 Virioplankton 1.3 Project aims 1.3.1 Biogeographic role 1.3.1.2 Differences in community composition 1.3.1.3 Differences in functional potential	Li	st of	Tables				xvii
1.1 Physical oceanography of the Southern Ocean 1.1.1 Fronts and zones 1.1.2 Water masses and circulation 1.1.3 Effect of climate change 1.2 Microbial ecology of the Southern Ocean 1.2.1 Bacteria 1.2.1.1 Alphaproteobacteria 1.2.1.1.1 Roseobacter clade 1.2.1.1.2 SAR11 1.2.1.1.3 SAR116 1.2.1.2 Betaproteobacteria 1.2.1.3 Gammaproteobacteria 1.2.1.3 Gammaproteobacteria 1.2.1.3.1 SAR86 1.2.1.3.2 OMG group 1.2.1.3.3 Ant4D3 1.2.1.3.4 GSO-EOSA-1 1.2.1.4 Deltaproteobacteria 1.2.1.5 CFB 1.2.1.6 Cyanobacteria 1.2.1.7 Verrucomicrobia 1.2.1.8 Other bacteria 1.2.2 Archaea 1.2.3 Virioplankton 1.3 Project aims 1.3.1 The Polar Front 1.3.1.1 Biogeographic role 1.3.1.2 Differences in community composition 1.3.1.3 Differences in functional potential	Li	st of	Acrony	rms			xix
1.2.1 Microbial ecology of the Southern Ocean 1.2.1 Bacteria 1.2.1.1 Alphaproteobacteria 1.2.1.1.1 Roseobacter clade 1.2.1.1.2 SAR11 1.2.1.1.3 SAR116 1.2.1.2 Betaproteobacteria 1.2.1.3 Gammaproteobacteria 1.2.1.3 Gammaproteobacteria 1.2.1.3.1 SAR86 1.2.1.3.2 OMG group 1.2.1.3.3 Ant4D3 1.2.1.3.4 GSO-EOSA-1 1.2.1.4 Deltaproteobacteria 1.2.1.5 CFB 1.2.1.6 Cyanobacteria 1.2.1.7 Verrucomicrobia 1.2.1.8 Other bacteria 1.2.2 Archaea 1.2.3 Virioplankton 1.3 Project aims 1.3.1 The Polar Front 1.3.1.1 Biogeographic role 1.3.1.2 Differences in community composition 1.3.1.3 Differences in functional potential	1		Physic 1.1.1	cal oceanography of the Southern Ocean			1 1 1 3
1.2.1.1.1 Roseobacter clade 1.2.1.1.2 SAR11 1.2.1.3 SAR116 1.2.1.2 Betaproteobacteria 1.2.1.3 Gammaproteobacteria 1.2.1.3.1 SAR86 1.2.1.3.2 OMG group 1.2.1.3.3 Ant4D3 1.2.1.3.4 GSO-EOSA-1 1.2.1.4 Deltaproteobacteria 1.2.1.5 CFB 1.2.1.6 Cyanobacteria 1.2.1.7 Verrucomicrobia 1.2.1.8 Other bacteria 1.2.2 Archaea 1.2.3 Virioplankton 1.3 Project aims 1.3.1 The Polar Front 1.3.1.1 Biogeographic role 1.3.1.2 Differences in community composition 1.3.1.3 Differences in functional potential		1.2	Micro	bial ecology of the Southern Ocean			3 4 4
1.2.1.2 Betaproteobacteria 1.2.1.3 Gammaproteobacteria 1.2.1.3.1 SAR86 1.2.1.3.2 OMG group 1.2.1.3.3 Ant4D3 1.2.1.3.4 GSO-EOSA-1 1.2.1.4 Deltaproteobacteria 1.2.1.5 CFB 1.2.1.6 Cyanobacteria 1.2.1.7 Verrucomicrobia 1.2.1.8 Other bacteria 1.2.2 Archaea 1.2.3 Virioplankton 1.3 Project aims 1.3.1 The Polar Front 1.3.1.1 Biogeographic role 1.3.1.2 Differences in community composition 1.3.1.3 Differences in functional potential				1.2.1.1.1 Roseobacter clade			4 4 6 7
1.2.1.3.2 OMG group 1.2.1.3.3 Ant4D3 1.2.1.3.4 GSO-EOSA-1 1.2.1.4 Deltaproteobacteria 1.2.1.5 CFB 1.2.1.6 Cyanobacteria 1.2.1.7 Verrucomicrobia 1.2.1.8 Other bacteria 1.2.2 Archaea 1.2.3 Virioplankton 1.3 Project aims 1.3.1 The Polar Front 1.3.1.1 Biogeographic role 1.3.1.2 Differences in community composition 1.3.1.3 Differences in functional potential				1.2.1.2Betaproteobacteria			7 8 8
1.2.1.4 Deltaproteobacteria 1.2.1.5 CFB 1.2.1.6 Cyanobacteria 1.2.1.7 Verrucomicrobia 1.2.1.8 Other bacteria 1.2.2 Archaea 1.2.3 Virioplankton 1.3 Project aims 1.3.1 The Polar Front 1.3.1.1 Biogeographic role 1.3.1.2 Differences in community composition 1.3.1.3 Differences in functional potential				1.2.1.3.2 OMG group			8 9 9
1.2.1.7 Verrucomicrobia 1.2.1.8 Other bacteria 1.2.2 Archaea 1.2.3 Virioplankton 1.3 Project aims 1.3.1 The Polar Front 1.3.1.1 Biogeographic role 1.3.1.2 Differences in community composition 1.3.1.3 Differences in functional potential				1.2.1.4 Deltaproteobacteria			9 10 11
1.2.3 Virioplankton			100	1.2.1.7 Verrucomicrobia			11 11
1.3.1 The Polar Front		1.3	1.2.3	Virioplankton			12 13 13
1 (1 (1 - (1))) a maja lahi adapatkan kalangkan kati bilah kalangan kan		1.0	,	The Polar Front	 	 	13 13 14

xii CONTENTS

2	MINS	SPEC				15
	2.1	Abstra	act			15
	2.2	Introd	uction .			15
		2.2.1	Metagen	omic analysis of microbial assemblages		15
		2.2.2		imum parsimony approach		
	2.3	Metho				
		2.3.1		entation of MINSPEC		
		2.3.2		on of MINSPEC		
	2.4					
	2.5					
	2.6	Concl	usions .			22
2	771	D-11	C			22
3		Polar l				23
	3.1 3.2					
	3.3					
	3.3	3.3.1		g and metagenomic sequencing		
		3.3.2		netic analysis of metagenomic data		
		3.3.2	3.3.2.1	BLAST comparison to RefSeq database		
			3.3.2.1	OTU abundances and variance between zones		
			3.3.2.3	Fragment recruitment to verify Operational		20
			3.3.2.3	Unit (OTU) identification		29
			3.3.2.4	Additional samples to test "polynya hypothesis		
		3.3.3		al analysis of metagenomic data	,	30
		5.5.5	3.3.3.1	BLAST comparison to KEGG database		
			3.3.3.2	Analysis of functional potential		
				Taxonomic decomposition		
	3.4	Result				
	0.1	3.4.1		omic sequencing		
		3.4.2		netic analysis of metagenomic data		
		3.4.3		at recruitment to verify OTU identification		
		3.4.4		nal samples to test alternative "polynya hypothe		
		3.4.5		al analysis of metagenomic data		
	3.5					
		3.5.1		nic groups differentiating the zones		
				GSO-EOSA-1		
			3.5.1.2	Ammonia-oxidizing Crenarchaeota		43
				Cyanobacteria		
			3.5.1.4	SAR11 and SAR116 clades		
			3.5.1.5	Bacteroidetes		44
			3.5.1.6	Rhodobacterales		45
			3.5.1.7	Alteromonadales		46
			3.5.1.8	Verrucomicrobia		46
		3.5.2	Function	al capacities differentiating the zones		46
			3.5.2.1	Conclusions		49
_	_					_
4			r formatio			51
	4.1					
	4.2					
	4.3	Metho		· · · _: · · · · · · · · · · · · · · · · · · ·		
	4.4	Kesult	s and Dis	cussion		52

CONTENTS	xiii

5 The advection effect							
	5.1	Abstra	act	57			
	5.2	Introd	uction	57			
		5.2.1	Distance and environment effects in microbial biogeography	57			
		5.2.2	Water mass endemicity and advection of marine microorganisms	58			
		5.2.3	Aims and approach of this study	59			
	5.3	Metho		60			
		5.3.1	Sampling	60			
		5.3.2	DNA extraction	61			
		5.3.3	Sequencing	62			
		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	Result		67			
	0.1	5.4.1	Sequencing and taxonomic assignment	67			
		5.4.2	Environment and distance effects	71			
		5.4.3	Testing the advection effect	73			
		5.4.4	Testing advection effect mechanisms	77			
		5.4.5	Differential effect of advection on OTU subsets	79			
	5.5		ssion	79			
	5.5	5.5.1	Taxonomic resolution	79			
		5.5.2	Differential influence of advection on OTU subsets	81			
		5.5.3	Future work	81			
		3.3.3	Tuture work	01			
6	Gen	eral dis	scussion	83			
	6.1	Contri	ibutions 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			
			6.1.1.3 Future work	85			
		6.1.2	The advection effect	86			
		0.1.2	6.1.2.1 Future work	87			
		6.1.3	MINSPEC	88			
	6.2		icrobial species concept in the "omics" age	89			
	6.3		usions	91			
Re	feren	ices		92			

List of Figures

1.1	Major fronts and water masses of the Southern Ocean	2
2.1	Results of MINSPEC validation	21
3.1	Map showing sites of seawater samples used in the Polar Front study	26
3.2	Summing relative abundances across size fractions	29
3.3	Rank-abundance curves for OTUs in each zone and size fraction	34
3.4	Contribution of OTUs to variance between the North and South zones	36
3.5	Read recruitment to reference genomes	38
3.6	Tree of GSO-EOSA-1 related 16S rRNA genes	42
3.7	Taxonomic decomposition of KEGG modules	47
4.1	Map showing sites of preliminary Antarctic Bottom Water (AABW) samples	53
4.2	Non-Metric Multidimensional Scaling (nMDS) of AABW, North Zone (NZ)	
	and South Zone (SZ) samples	55
5.1	Map showing sites of samples used in the advection study	
5.2	OTU assignments in the advection study	
5.3	nMDS of advective distances between samples	
5.4	nMDS of advective distances between samples	
5.5	dbRDA ordination of relationship between environment and community	
5.6	Encounter times for all samples in advection model	
5.7	nMDS of advective distances between samples	
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	17
3.1	Details of samples used in Polar Front study	27
3.2	Additional samples used to test polynya hypothesis	
3.3	Twenty most abundant OTUs	
3.4	Highest-contributing OTUs to the difference between the North and South	
	zones	35
3.5	Contributions of KEGG modules to variance between the North and South	
	zones	39
3.6	Contributions of KEGG ortholog groups to variance between the North and	
	South zones	40
4.1	AABW samples used in the preliminary analysis	52
4.2	Twenty most abundant OTUs in preliminary AABW samples	
1.2	Twenty most abundant of 03 in premimary 111511 samples	51
5.1	Full sample data for advection study	68
5.1	(cont.) Full sample data for advection study	
5.1	(cont.) Full sample data for advection study	70
5.2	Correlations between dbRDA axes and physicochemical variables	
5.3	_ ·	

List of Acronyms

AABW Antarctic Bottom Water.

nMDS Non-Metric Multidimensional Scaling.

NZ North Zone.

OTU Operational Taxonomic Unit.

SZ South Zone.

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.
- 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., de Baar H. J. W., 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*, 8:595.
- 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.
- Caro-Quintero A. and Konstantinidis K. T. (2011). Bacterial species may exist, metagenomics reveal. *Environmental Microbiology*, 14(2):347–355.
- 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 endemicity of fluorescent Pseudomonas strains in soil. *Applied and Environmental Microbiology*, 66(12):5448–5456.
- Chou H. H. and Holmes M. H. (2001). DNA sequence quality trimming and vector removal. *Bioinformatics*, 17(12):1093–1104.
- 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, Plymoth, 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.
- **CSIRO** microbial diagnostics monitor-Autonomous, in situ and ing for microbial oceanography workshop 2012 summary, 2012. URL http://www.csiro.au/en/Organisation-Structure/Divisions/ Marine--Atmospheric-Research/HiResMicroOceanography-Hobart-workshop-2012/ ${\tt HiResMicroOceanography-Hobart-workshop-2012-summary.aspx.}$
- 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.
- de Wit R. 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., van den Enden R., 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.
- Feng H., Cochran J. K., and Hirschberg D. J. (1999). ²³⁴Th and ⁷Be as tracers for the transport and dynamics of suspended particles in a partially mixed estuary. *Geochimica et Cosmochimica Acta*, 63(17):2487–2505.
- 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., 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.
- 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.
- Grossart H.-P., Kiørboe T., Tang K., and Ploug H. (2003). Bacterial colonization of particles: growth and interactions. *Applied and Environmental Microbiology*, 69(6):3500–3509.
- Grote J., Bayindirli C., Bergauer K., Carpintero de Moraes P., 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.
- Hales T. C. (2005). A Proof of the Kepler Conjecture. *Annals of Mathematics*, 162(3):1065–1185.
- Hambly E. and Suttle C. A. (2005). The viriosphere, diversity, and genetic exchange within phage communities. *Current Opinion in Microbiology*, 8(4):444–450.
- 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.
- Huang J., Su Z., and Xu Y. (2005). The evolution of microbial phosphonate degradative pathways. *Journal of Molecular Evolution*, 61(5):682–690.
- 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 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 nongrowth 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 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 Grzymski 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 *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 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., van Sebille E., 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 crenar-chaeon 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.
- Sauer K., Camper A. K., Ehrlich G. D., Costerton J. W., and Davies D. G. (2002). Pseudomonas aeruginosa displays multiple phenotypes during development as a biofilm. *Journal of Bacteriology*, 184(4):1140–1154.
- Savoye N., Benitez-Nelson C. R., Burd A. B., and Cochran J. K. (2005). ²³⁴Th sorption and export models in the water column: a review.
- 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.

Siddiqui K. S., Williams T. J., Wilkins D., Yau S., Allen M. A., Brown M. V., Lauro F. M., and Cavicchioli R. (2013). Psychrophiles. *Annual Review of Earth and Planetary Sciences*, 41(1).

- 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 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.
- 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.

- Suttle C. A. (2005). Viruses in the sea. Nature, 437(7057):356–361.
- 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.
- Tettelin H., Masignani V., Cieslewicz M. J., Donati C., Medini D., Ward N. L., Angiuoli S. V., Crabtree J., Jones A. L., Durkin A. S., Deboy R. T., Davidsen T. M., Mora M., Scarselli M., Margarit y Ros I., Peterson J. D., Hauser C. R., Sundaram J. P., Nelson W. C., Madupu R., Brinkac L. M., Dodson R. J., Rosovitz M. J., Sullivan S. A., Daugherty S. C., Haft D. H., Selengut J., Gwinn M. L., Zhou L., Zafar N., Khouri H., Radune D., Dimitrov G., Watkins K., O'Connor K. J. B., Smith S., Utterback T. R., White O., Rubens C. E., Grandi G., Madoff L. C., Kasper D. L., Telford J. L., Wessels M. R., Rappuoli R., and Fraser C. M. (2005). Genome analysis of multiple pathogenic isolates of Streptococcus agalactiae: Implications for the microbial "pan-genome". *Proceedings Of The National Academy Of Sciences Of The United States Of America*, 102(39):13950–13955.
- 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.
- van Sebille E., 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). Dimethyl-sulfoniopropionate 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., de la Torre J. R., 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). Mesozoo-plankton community structure across the Antarctic Circumpolar Current to the north of South Georgia: Southern Ocean. *Marine Biology*, 143(1):121–130.
- Waterbury J. B., Willey J. M., Franks D. G., Valois F. W., and Watson S. W. (1985). A cyanobacterium capable of swimming motility. *Science*, 230(4721):74–76.
- 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. Biogeographic partitioning of Southern Ocean picoplankton. In *ISME 13*, Copenhagen, 2012.
- 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. (2013). Biogeographic partitioning of Southern Ocean microorganisms revealed by metagenomics. *Environmental Microbiology*, 15(5):1318–1333.

Wilkins D., van Sebille E., Rintoul S. R., Lauro F. M., and Cavicchioli R. (2013). Advection shapes Southern Ocean microbial assemblages independent of distance and environment effects. *Submitted*.

- Wilkins D., Yau S., Williams T. J., Allen M. A., Brown M. V., DeMaere M. Z., Lauro F. M., and Cavicchioli R. (2013). Key microbial drivers in Antarctic aquatic environments. *FEMS Microbiology Reviews*, 37(3):303–335.
- 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. (2013). The role of planktonic Flavobacteria in processing algal organic matter in coastal East Antarctica revealed using metagenomics and metaproteomics. *Environmental Microbiology*, 15(5):1302–1317.
- 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.
- 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.
- 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.