# Microbial Ecology and Biogeography

OF THE

#### Southern Ocean

David Wilkins

November 20, 2012

# **Contents**

List of Figures	v
List of Tables	vii
List of Acronyms	ix
Acknowledgements	xi
Abstract	xiii
THE SANDBOX	xv
Introduction	1
Physical Oceanography of the Southern Ocean	1
Fronts and zones	1
Water masses and circulation	3
Effect of climate change	4
Microbial ecology of the Southern Ocean	5
Bacteria	5
Alphaproteobacteria	5
Roseobacter	5
SAR11	7
SAR116	8
Betaproteobacteria	9
Gammaproteobacteria	9
SAR86	
OMG group	
Ant4D3	

	GSO-EOSA-1	L
	Deltaproteobacteria	11
	CFB	12
	Cyanobacteria	13
	Verrucomicrobia	14
	Other bacteria	14
	Archaea	15
	Virioplankton	16
	Project questions and hypotheses	17
	Question 1: Is the Polar Front (PF) a major boundary in the biogeography of Southern	
	Ocean (SO) picoplankton?	17
	Question 2: How do the picoplanktonic communities on either side of the PF differ?	17
	Question 3: How do the ecosystem functions performed by picoplankton on either side	
	of the PF differ?	17
	Question 4: To what relative extents do water circulation and physicochemical proper-	
	ties define picoplanktonic biogeography?	17
Г	he Polar Front as a major biogeographic boundary in the Southern Ocean	19
	Summary	
	Introduction	
	Methods	
	Sampling and metagenomic sequencing	
	Phylogenetic analysis of metagenomic data	
	BLAST comparison to RefSeq database	
	Identification of minimal species sets with MINSPEC	
	Operational Taxonomic Unit (OTU) abundances and variance between zones	
	Functional analysis of metagenomic data	
	BLAST comparison to Kyoto Encyclopedia of Genes and Genomes (KEGG) database	
	Analysis of functional potential	
	Results	
	Metagenomic sequencing	
	Phylogenetic analysis of metagenomic data	
	Validation of MINSPEC	
	Functional analysis of metagenomic data	34

Conclusions	51
Mesoscale biogeographic drivers of planktonic diversity	49
Conclusions: Biogeographic role of the Polar Front	46
Functional capacities differentiating the zones	44
Verrucomicrobia	42
Alteromonadales	42
Rhodobacterales	41
Bacteroidetes	41
SAR11 and SAR116 clades	40
Cyanobacteria	39
Ammonia-oxidizing Crenarchaeota	39
GSO-EOSA-1	37
Taxonomic groups differentiating the zones	37
Discussion	37

# **List of Figures**

1	Major fronts and water masses of the Southern Ocean	2
2	Map showing sites of seawater samples used in the Polar Front study	22
3	Rank-abundance curves for OTUs in each zone and size fraction	29
4	Contribution of OTUs to variance between the North and South zones	31
5	Results of minspec validate	33
6	Tree of GSO-EOSA-1 related 16S rRNA genes	38
7	Taxonomic decomposition of KEGG modules	43

# **List of Tables**

1	Details of samples used in Polar Front study	23
2	Twenty most abundant OTUs	28
3	Highest-contributing OTUs to the difference between the North and South zones	30
4	Contributions of KEGG modules to variance between the North and South zones	35
5	Contributions of KEGG ortholog groups to variance between the North and South zones	36



# **List of Acronyms**

**KEGG** Kyoto Encyclopedia of Genes and Genomes.

**OTU** Operational Taxonomic Unit.

**PF** Polar Front.

**SO** Southern Ocean.



# Acknowledgements



### **Abstract**



### THE SANDBOX

I really love "Candidatus Pelagibacter ubique". "Ca. P. ubique" is awesome.

I also love *Escherichia coli*. *E. coli* is really sweet. But its full name is *Escherichia coli*, and its friend is "*Candidatus* Pelagibacter ubique".

# **Conclusions**

#### References

- 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.
- Alonso C. and Pernthaler J. (2006). Roseobacter and SAR11 dominate microbial glucose uptake in coastal North Sea waters. *Environmental Microbiology*, 8(11):2022–2030.
- 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.
- Biastoch A., Böning C. W., Schwarzkopf F. U., and Lutjeharms J. R. E. (2009). Increase in Agulhas leakage due to poleward shift of Southern Hemisphere westerlies. *Nature*, 462(7272):495–498.
- Bidle K. D. and Azam F. (2001). Bacterial control of silicon regeneration from diatom detritus: significance of bacterial ectohydrolases and species identity. *Limnology and Oceanography*, 46(7):1606–1623.
- Biebl H., Allgaier M., Tindall B. J., Koblížek M., Lünsdorf H., Pukall R., and Wagner-Döbler I. (2005). *Dinoroseobacter shibae* gen. nov., sp. nov., a new aerobic phototrophic bacterium isolated from dinoflagellates. *International Journal of Systematic and Evolutionary Microbiology*, 55(Pt 3):1089–1096.
- Bissett A., Richardson A. E., Baker G., Wakelin S., and Thrall P. H. (2010). Life history determines biogeographical patterns of soil bacterial communities over multiple spatial scales. *Molecular Ecology*, 19(19):4315–4327.

- Böning C. W., Dispert A., Visbeck M., Rintoul S. R., and Schwarzkopf F. U. (2008). The response of the Antarctic Circumpolar Current to recent climate change. *Nature Geoscience*, 1(12):864–869.
- Bowman J. P. and McCuaig R. D. (2003). Biodiversity, community structural shifts, and biogeography of prokaryotes within Antarctic continental shelf sediment. *Applied and Environmental Microbiology*, 69(5):2463–2483.
- Bowman J. P., Rea S. M., McCammon S. A., and McMeekin T. A. (2000). Diversity and community structure within anoxic sediment from marine salinity meromictic lakes and a coastal meromictic marine basin, Vestfold Hills, Eastern Antarctica. *Environmental Microbiology*, 2(2):227–237.
- Boyd P. W., Jickells T., Law C. S., Blain S., Boyle E. A., Buesseler K. O., Coale K. H., Cullen J. J., Baar H. J. W.de, Follows M., Harvey M., Lancelot C., Levasseur M., Owens N. P. J., Pollard R., Rivkin R. B., Sarmiento J., Schoemann V., Smetacek V., Takeda S., Tsuda A., Turner S., and Watson A. J. (2007). Mesoscale Iron Enrichment Experiments 1993-2005: Synthesis and Future Directions. *Science*, 315 (5812):612–617.
- Brinkhoff T., Giebel H.-A., and Simon M. (2008). Diversity, ecology, and genomics of the Roseobacter clade: a short overview. *Archives of Microbiology*, 189(6):531–539.
- Brinkmeyer R., Knittel K., Jürgens J., Weyland H., Amann R., and Helmke E. (2003). Diversity and Structure of Bacterial Communities in Arctic versus Antarctic Pack Ice. *Applied and Environmental Microbiology*, 69(11):6610–6619.
- Brown M. V. and Bowman J. P. (2001). A molecular phylogenetic survey of sea-ice microbial communities (SIMCO). *FEMS Microbiology Ecology*, 35(3):267–275.
- Brown M. V., Lauro F. M., DeMaere M. Z., Muir L., Wilkins D., Thomas T., Riddle M. J., Fuhrman J. A., Andrews-Pfannkoch C., Hoffman J. M., McQuaid J. B., Allen A., Rintoul S. R., and Cavicchioli R. (2012). Global biogeography of SAR11 marine bacteria. *Molecular systems biology*, 8.
- Buchan A., González J. M., and Moran M. A. (2005). Overview of the marine Roseobacter lineage. *Applied and Environmental Microbiology*, 71(10):5665–5677.
- Callahan J. E. (1972). The structure and circulation of deep water in the Antarctic. *Deep Sea Research and Oceanographic Abstracts*, 19(8):563–575.
- Campanaro S., Williams T. J., Burg D. W., De Francisci D., Treu L., Lauro F. M., and Cavicchioli R. (2011). Temperature-dependent global gene expression in the Antarctic archaeon *Methanococcoides burtonii*. *Environmental Microbiology*, 13(8):2018–2038.
- Canfield D. E., Stewart F. J., Thamdrup B., De Brabandere L., Dalsgaard T., DeLong E. F., Revsbech N. P., and Ulloa O. (2010). A Cryptic Sulfur Cycle in Oxygen-Minimum-Zone Waters off the Chilean Coast. *Science*, 330(6009):1375–1378.
- 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.
- 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 Warwick R. M. Change in marine communities: an approach to statistical analysis and interpretation. PRIMER-E, Plymoth, 2nd edition, 2001.
- Coleman M. L. M. and Chisholm S. W. S. (2010). Ecosystem-specific selection pressures revealed through comparative population genomics. *Proceedings Of The National Academy Of Sciences Of The United States Of America*, 107(43):18634–18639.
- Cottrell M. T. and Kirchman D. L. (2000). Community Composition of Marine Bacterioplankton Determined by 16S rRNA Gene Clone Libraries and Fluorescence In Situ Hybridization. *Applied and Environmental Microbiology*, 66(12):5116–5122.
- Cottrell M. T., Waidner L. A., Yu L., and Kirchman D. L. (2005). Bacterial diversity of metagenomic and PCR libraries from the Delaware River. *Environmental Microbiology*, 7(12):1883–1895.
- 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 dimethylsul-phoniopropionate: 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.
- 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.
- 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.
- 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.
- Foldvik A. and Gammelsrød T. (1988). Notes on Southern Ocean hydrography, sea-ice and bottom water formation. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 67(1-2):3–17.
- Freitas S., Hatosy S., Fuhrman J. A., Huse S. M., Welch D. B. M., Sogin M. L., and Martiny A. C. (2012). Global distribution and diversity of marine *Verrucomicrobia*. *The ISME Journal*, 6(8):1499–1505.
- Fuhrman J. A., Schwalbach M. S., and Stingl U. (2008). Proteorhodopsins: an array of physiological roles? *Nature Reviews Microbiology*, 6:488–494.
- Fyfe J. C. and Saenko O. A. (2005). Human-induced change in the Antarctic Circumpolar Current. *Journal of Climate*, 18(15):3068–3073.
- 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.
- Giebel H.-A., Brinkhoff T., Zwisler W., Selje N., and Simon M. (2009). Distribution of *Roseobacter* RCA and SAR11 lineages and distinct bacterial communities from the subtropics to the Southern Ocean. *Environmental Microbiology*, 11(8):2164–2178.
- Giebel H.-A., Kalhoefer D., Lemke A., Thole S., Gahl-Janssen R., Simon M., and Brinkhoff T. (2010). Distribution of *Roseobacter RCA* and SAR11 lineages in the North Sea and characteristics of an abundant RCA isolate. *The ISME Journal*, 5:8–19.
- Gille S. T. (2002). Warming of the Southern Ocean Since the 1950s. Science, 295(5558):1275–1277.
- Giovannoni S. J., Tripp H. J., Givan S., Podar M., Vergin K. L., Baptista D., Bibbs L., Eads J., Richardson T. H., Noordewier M., Rappé M. S., Short J. M., Carrington J. C., and Mathur E. J. (2005). Genome streamlining in a cosmopolitan oceanic bacterium. *Science*, 309(5738):1242–1245.
- Giovannoni S. J., Hayakawa D. H., Tripp H. J., Stingl U., Givan S. A., Cho J.-C., Oh H.-M., Kitner J. B., Vergin K. L., and Rappé M. S. (2008). The small genome of an abundant coastal ocean methylotroph. *Environmental Microbiology*, 10(7):1771–1782.
- Glöckner F. O., Fuchs B. M., and Amann R. (1999). Bacterioplankton compositions of lakes and oceans: a first comparison based on fluorescence in situ hybridization. *Applied and Environmental Microbiology*, 65(8):3721–3726.
- González J. M., Fernández-Gómez B., 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.
- 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.
- 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 Biolog*, 138:369–381.
- Huston A. L., Krieger-Brockett B. B., and Deming J. W. (2000). Remarkably low temperature optima for extracellular enzyme activity from Arctic bacteria and sea ice. *Environmental Microbiology*, 2(4): 383–388.
- Ingalls A. E., Shah S. R., Hansman R. L., Aluwihare L. I., Santos G. M., Druffel E. R. M., and Pearson A. (2006). Quantifying archaeal community autotrophy in the mesopelagic ocean using natural radiocarbon. *Proceedings Of The National Academy Of Sciences Of The United States Of America*, 103(17): 6442–6447.
- Iverson V., Morris R. M., Frazar C. D., Berthiaume C. T., Morales R. L., and Armbrust E. V. (2012). Untangling Genomes from Metagenomes: Revealing an Uncultured Class of Marine Euryarchaeota. *Science*, 335(6068):587–590.
- Jacobs S. S. (2004). Bottom water production and its links with the thermohaline circulation. *Antarctic Science*, 16(04):427–437.

- Jamieson R. E., Rogers A. D., Billett D., Smale D. A., and Pearce D. A. (2012). Patterns of marine bacterioplankton biodiversity in the surface waters of the Scotia Arc, Southern Ocean. *FEMS Microbiology Ecology*, 80:452–468.
- Jung S.-Y., Oh T.-K., and Yoon J.-H. (2006). *Colwellia aestuarii* sp. nov., isolated from a tidal flat sediment in Korea. *International Journal of Systematic and Evolutionary Microbiology*, 56(1):33–37.
- Junge K., Eicken H., and Deming J. W. (2003). Motility of *Colwellia psychrerythraea* Strain 34H at Subzero Temperatures. *Applied and Environmental Microbiology*, 69(7):4282–4284.
- Kalanetra K. M., Bano N., and Hollibaugh J. T. (2009). Ammonia-oxidizing *Archaea* in the Arctic Ocean and Antarctic coastal waters. *Environmental Microbiology*, 11(9):2434–2445.
- Kawahata H. and Ishizuka T. (2000). Amino acids in interstitial waters from ODP Sites 689 and 690 on the Maud Rise, Antarctic Ocean. *Geochemical Journal*, 34(4):247–261.
- King G. M. (2003). Molecular and Culture-Based Analyses of Aerobic Carbon Monoxide Oxidizer Diversity. *Applied and Environmental Microbiology*, 69(12):7257–7265.
- Kirchman D. L. (2002). The ecology of Cytophaga–Flavobacteria in aquatic environments. *FEMS Microbiology Ecology*, 39(2):91–100.
- Kirchman D. L. *Microbial ecology of the oceans*. John Wiley & Sons, Inc., Hoboken, New Jersey, second edition, 2008.
- Kjelleberg S., Hermansson M., and Mårdén P. (1987). The transient phase between growth and non-growth of heterotrophic bacteria, with emphasis on the marine environment. *Annual Review of Microbiology*, 41:25–49.
- 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., 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.
- 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.
- 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.
- Merbt S. N., Stahl D. A., Casamayor E. O., Martí E., Nicol G. W., and Prosser J. I. (2012). Differential photoinhibition of bacterial and archaeal ammonia oxidation. *FEMS Microbiology Letters*, 327(1): 41–46.
- Methé B. A., Nelson K. E., Deming J. W., Momen B., Melamud E., Zhang X., Moult J., Madupu R., Nelson W. C., Dodson R. J., Methe B. A., Nelson K. E., Deming J. W., Momen B., Melamud E., Zhang X., Moult J., Madupu R., Nelson W. C., Dodson R. J., Brinkac L. M., Daugherty S. C., Durkin A. S., DeBoy R. T., Kolonay J. F., Sullivan S. A., Zhou L., Davidsen T. M., Wu M., Huston A. L., Lewis M., Weaver B., Weidman J. F., Khouri H., Utterback T. R., Feldblyum T. V., and Fraser C. M. (2005). The psychrophilic lifestyle as revealed by the genome sequence of *Colwellia psychrerythraea* 34H through genomic and proteomic analyses. *Proceedings Of The National Academy Of Sciences Of The United States Of America*, 102(31):10913–10918.
- Meyer B. and Kuever J. (2007). Molecular Analysis of the Diversity of Sulfate-Reducing and Sulfur-Oxidizing Prokaryotes in the Environment, Using *aprA* as Functional Marker Gene. *Applied and Environmental Microbiology*, 73(23):7664–7679.
- Mikaloff Fletcher S. E., Gruber N., Jacobson A. R., Doney S. C., Dutkiewicz S., Gerber M., Follows M., Joos F., Lindsay K., Menemenlis D., Mouchet A., Müller S. A., and Sarmiento J. L. (2006). Inverse estimates of anthropogenic CO<sub>2</sub> uptake, transport, and storage by the ocean. *Global Biogeochemical Cycles*, 20(2):GB2002.
- Miller T. R. and Belas R. (2004). Dimethylsulfoniopropionate Metabolism by *Pfiesteria*-Associated *Roseobacter* spp. *Applied and Environmental Microbiology*, 70(6):3383–3391.
- Mira A., Ochman H., and Moran N. A. (2001). Deletional bias and the evolution of bacterial genomes. *Trends in genetics : TIG*, 17(10):589–596.

- Moore J. K., Abbott M. R., and Richman J. G. (1999). Location and dynamics of the Antarctic Polar Front from satellite sea surface temperature data. *Journal of Geophysical Research*, 104:3052–3073.
- Moran M. A., Belas R., Schell M. A., González J. M., Sun F., Sun S., Binder B. J., Edmonds J., Ye W., Orcutt B., Howard E. C., Meile C., Palefsky W., Goesmann A., Ren Q., Paulsen I., Ulrich L. E., Thompson L. S., Saunders E., and Buchan A. (2007). Ecological Genomics of Marine Roseobacters. *Applied and Environmental Microbiology*, 73(14):4559–4569.
- Moran M. A., González J. M., and Kiene R. P. (2003). Linking a Bacterial Taxon to Sulfur Cycling in the Sea: Studies of the Marine Roseobacter Group. *Geomicrobiology Journal*, 20(4):375–388.
- Moran M. A., Buchan A., González J. M., Heidelberg J. F., Whitman W. B., Kiene R. P., Henriksen J. R., King G. M., Belas R., Fuqua C., Brinkac L., Lewis M., Johri S., Weaver B., Pai G., Eisen J. A., Rahe E., Sheldon W. M., Ye W., Miller T. R., Carlton J., Rasko D. A., Paulsen I. T., Ren Q., Daugherty S. C., Deboy R. T., Dodson R. J., Durkin A. S., Madupu R., Nelson W. C., Sullivan S. A., Rosovitz M. J., Haft D. H., Selengut J., and Ward N. (2004). Genome sequence of *Silicibacter pomeroyi* reveals adaptations to the marine environment. *Nature*, 432(7019):910–913.
- Morris R. M., Rappé M. S., Connon S. A., Vergin K. L., Siebold W. A., Carlson C. A., and Giovannoni S. J. (2002). SAR11 clade dominates ocean surface bacterioplankton communities. *Nature*, 420(6917): 806–810.
- Morris R. M., Longnecker K., and Giovannoni S. J. (2006). *Pirellula* and OM43 are among the dominant lineages identified in an Oregon coast diatom bloom. *Environmental Microbiology*, 8(8):1361–1370.
- Murray A. E. and Grzymski J. J. (2007). Diversity and genomics of Antarctic marine micro-organisms. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 362(1488):2259–2271.
- Murray A. E., Wu K. Y., Moyer C. L., Karl D. M., and DeLong E. F. (1999). Evidence for circumpolar distribution of planktonic Archaea in the Southern Ocean. *Aquatic Microbial Ecology*, 18(3):263–273.
- Murray A. E. A., Preston C. M. C., Massana R. R., Taylor L. T. L., Blakis A. A., Wu K. K., and DeLong E. F. (1998). Seasonal and spatial variability of bacterial and archaeal assemblages in the coastal waters near Anvers Island, Antarctica. *Applied and Environmental Microbiology*, 64(7):2585–2595.
- Murray A. E., Peng V., Tyler C., and Wagh P. (2011). Marine bacterioplankton biomass, activity and community structure in the vicinity of Antarctic icebergs. *Deep Sea Research Part II: Topical Studies in Oceanography*, 58(11-12):1407–1421.
- Newton I. L. G., Woyke T., Auchtung T. A., Dilly G. F., Dutton R. J., Fisher M. C., Fontanez K. M., Lau E., Stewart F. J., Richardson P. M., Barry K. W., Saunders E., Detter J. C., Wu D., Eisen J. A., and Cavanaugh C. M. (2007). The *Calyptogena magnifica* Chemoautotrophic Symbiont Genome. *Science*, 315(5814):998–1000.
- Ng C., DeMaere M. Z., Williams T. J., Lauro F. M., Raftery M., Gibson J. A., Andrews-Pfannkoch C., Lewis M., Hoffman J. M., Thomas T., and Cavicchioli R. (2010). Metaproteogenomic analysis of a dominant green sulfur bacterium from Ace Lake, Antarctica. *The ISME Journal*, 4(8):1002–1019.
- Nikrad M. P., Cottrell M. T., and Kirchman D. L. (2012). Abundance and Single-Cell Activity of Heterotrophic Bacterial Groups in the Western Arctic Ocean in Summer and Winter. *Applied and Environmental Microbiology*, 78(7):2402–2409.
- Obernosterer I., Catala P., Lebaron P., and West N. J. (2011). Distinct bacterial groups contribute to carbon cycling during a naturally iron fertilized phytoplankton bloom in the Southern Ocean. *Limnology and Oceanography*, 56(6):2391–2401.
- Oh H. M., Kwon K. K., Kang I., Kang S. G., Lee J. H., Kim S. J., and Cho J. C. (2010). Complete Genome Sequence of "Candidatus Puniceispirillum marinum" IMCC1322, a Representative of the SAR116 Clade in the Alphaproteobacteria. Journal of Bacteriology, 192(12):3240–3241.

- Oliver J. L., Barber R. T., Smith Jr W. O., and Ducklow H. W. (2004). The heterotrophic bacterial response during the Southern Ocean iron experiment (SOFeX). *Limnology and Oceanography*, 49(6): 2129–2140.
- Orsi A. H., Whitworth T., and Nowlin W. D. (1995). On the meridional extent and fronts of the Antarctic Circumpolar Current. *Deep Sea Research Part I: Oceanographic Research Papers*, 42(5):641–673.
- Orsi A. H., Johnson G. C., and Bullister J. L. (1999). Circulation, mixing, and production of Antarctic Bottom Water. *Progress in Oceanography*, 43(1):55–109.
- O'Sullivan L. A., Fuller K. E., Thomas E. M., Turley C. M., Fry J. C., and Weightman A. J. (2004). Distribution and culturability of the uncultivated 'AGG58 cluster' of the Bacteroidetes phylum in aquatic environments. *FEMS Microbiology Ecology*, 47(3):359–370.
- 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.
- 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.

- Rusch D. B., Halpern A. L., Sutton G., Heidelberg K. B., Williamson S., Yooseph S., Wu D., Eisen J. A., Hoffman J. M., Remington K., Beeson K., Tran B., Smith H., Baden-Tillson H., Stewart C., Thorpe J., Freeman J., Andrews-Pfannkoch C., Venter J. E., Li K., Kravitz S., Heidelberg J. F., Utterback T., Rogers Y.-H., Falcón L. I., Souza V., Bonilla-Rosso G., Eguiarte L. E., Karl D. M., Sathyendranath S., Platt T., Bermingham E., Gallardo V., Tamayo-Castillo G., Ferrari M. R., Strausberg R. L., Nealson K., Friedman R., Frazier M., and Venter J. C. (2007). The Sorcerer II Global Ocean Sampling expedition: northwest Atlantic through eastern tropical Pacific. *PLoS Biology*, 5(3):e77–e77.
- Sabine C. L., Feely R. A., Gruber N., Key R. M., Lee K., Bullister J. L., Wanninkhof R., Wong C. S., Wallace D. W. R., Tilbrook B., Millero F. J., Peng T.-H., Kozyr A., Ono T., and Rios A. F. (2004). The Oceanic Sink for Anthropogenic CO<sub>2</sub>. *Science*, 305(5682):367–371.
- Scanlan D. J., Ostrowski M., Mazard S., Dufresne A., Garczarek L., Hess W. R., Post A. F., Hagemann M., Paulsen I., and Partensky F. (2009). Ecological Genomics of Marine Picocyanobacteria. *Microbiology and Molecular Biology Reviews*, 73(2):249–299.
- Selje N. N., Simon M. M., and Brinkhoff T. T. (2004). A newly discovered *Roseobacter* cluster in temperate and polar oceans. *Nature*, 427(6973):445–448.
- Short C. M. and Suttle C. A. (2005). Nearly Identical Bacteriophage Structural Gene Sequences Are Widely Distributed in both Marine and Freshwater Environments. Applied and Environmental Microbiology, 71(1):480–486.
- Short S. M. and Suttle C. A. (2002). Sequence Analysis of Marine Virus Communities Reveals that Groups of Related Algal Viruses Are Widely Distributed in Nature. *Applied and Environmental Microbiology*, 68(3):1290–1296.
- Simon M., Glöckner F. O., and Amann R. (1999). Different community structure and temperature optima of heterotrophic picoplankton in various regions of the Southern Ocean. *Aquatic Microbial Ecology*, 18(3):275–284.
- Sinha V., Williams J., Meyerhöfer M., Riebesell U., Paulino A. I., and Larsen A. (2007). Air-sea fluxes of methanol, acetone, acetaldehyde, isoprene and DMS from a Norwegian fjord following a phytoplankton bloom in a mesocosm experiment. *Atmospheric Chemistry and Physics*, 7(3):739–755.
- Sokolov S. and Rintoul S. R. (2002). Structure of Southern Ocean fronts at 140°E. *Journal of Marine Systems*, 37(1):151–184.
- Sokolov S. and Rintoul S. R. (2009). Circumpolar structure and distribution of the Antarctic Circumpolar Current fronts: 1. Mean circumpolar paths. *Journal of Geophysical Research*, 114(C11):C11018.
- Sokolov S. and Rintoul S. R. (2009). Circumpolar structure and distribution of the Antarctic Circumpolar Current fronts:âĂÍ2. Variability and relationship to sea surface height. *Journal of Geophysical Research*, 114(C11):C11019.
- 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.
- 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.
- Swan B. K., Martinez-Garcia M., Preston C. M., Sczyrba A., Woyke T., Lamy D., Reinthaler T., Poulton N. J., Masland E. D. P., Gomez M. L., Sieracki M. E., DeLong E. F., Herndl G. J., and Stepanauskas R. (2011). Potential for Chemolithoautotrophy Among Ubiquitous Bacteria Lineages in the Dark Ocean. *Science*, 333(6047):1296–1300.
- Swingley W. D., Sadekar S., Mastrian S. D., Matthies H. J., Hao J., Ramos H., Acharya C. R., Conrad A. L., Taylor H. L., Dejesa L. C., Shah M. K., O'Huallachain M. E., Lince M. T., Blankenship R. E., Beatty J. T., and Touchman J. W. (2007). The Complete Genome Sequence of *Roseobacter denitrificans* Reveals a Mixotrophic Rather than Photosynthetic Metabolism. *Journal of Bacteriology*, 189(3):683–690.
- Teske A., Alm E., Regan J. M., Toze S., Rittmann B. E., and Stahl D. A. (1994). Evolutionary relationships among ammonia- and nitrite-oxidizing bacteria. *Journal of Bacteriology*, 176(21):6623–6630.
- Thomalla S. J., Waldron H. N., Lucas M. I., Read J. F., Ansorge I. J., and Pakhomov E. (2011). Phytoplankton distribution and nitrogen dynamics in the southwest indian subtropical gyre and Southern Ocean waters. *Ocean Science*, 7(1):113–127.
- Thompson D. W. J. and Solomon S. (2002). Interpretation of Recent Southern Hemisphere Climate Change. *Science*, 296(5569):895–899.
- Topping J. N., Heywood J. L., Ward P., and Zubkov M. V. (2006). Bacterioplankton composition in the Scotia Sea, Antarctica, during the austral summer of 2003. *Aquatic Microbial Ecology*, 45(3):229–235.
- 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.
- 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). Dimethylsulfonio-propionate Uptake by Marine Phytoplankton. *Science*, 314(5799):652–654.
- Wagner-Döbler I. and Biebl H. (2006). Environmental Biology of the Marine *Roseobacter Lineage*. *Annual Review of Microbiology*, 60(1):255–280.
- Walker C. B., Torre J. R.de la, Klotz M. G., Urakawa H., Pinel N., Arp D. J., Brochier-Armanet C., Chain P., Chan P. P., Gollabgir A., Hemp J., Hügler M., Karr E. A., Könekke M., Shin M., Lawton T. J., Lowe T., Martens-Habbena W., Sayavedra-Soto L. A., Langf D., Sievert S. M., Rosenzweig A. C., Manning G., and Stahl D. A. (2010). Nitrosopumilus maritimus genome reveals unique mechanisms for nitrification and autotrophy in globally distributed marine crenarchaea. Proceedings Of The National Academy Of Sciences Of The United States Of America, 107(19):8818–8823.
- Walsh D. A., Zaikova E., Howes C. G., Song Y. C., Wright J. J., Tringe S. G., Tortell P. D., and Hallam S. J. (2009). Metagenome of a Versatile Chemolithoautotroph from Expanding Oceanic Dead Zones. *Science*, 326(5952):578–582.

- Ward P., Whitehouse M., Brandon M., Shreeve R., and Woodd-Walker R. (2003). Mesozooplankton community structure across the Antarctic Circumpolar Current to the north of South Georgia: Southern Ocean. *Marine Biology*, 143(1):121–130.
- Weber T. S. and Deutsch C. (2010). Ocean nutrient ratios governed by plankton biogeography. *Nature*, 467(7315):550–554.
- Weinbauer M. G., Arrieta J. M., Griebler C., and Herndl G. J. (2009). Enhanced viral production and infection of bacterioplankton during an iron-induced phytoplankton bloom in the Southern Ocean. *Limnol. Oceanogr*, 54(3):774–784.
- West N. J., Obernosterer I., Zemb O., and Lebaron P. (2008). Major differences of bacterial diversity and activity inside and outside of a natural iron-fertilized phytoplankton bloom in the Southern Ocean. *Environmental Microbiology*, 10(3):738–756.
- Whitworth T. (1980). Zonation and geostrophic flow of the Antarctic Circumpolar Current at Drake Passage. *Deep Sea Research Part I: Oceanographic Research Papers*, 27(7):497–507.
- Whitworth III T. and Nowlin Jr. W. D. (1987). Water masses and currents of the Southern Ocean at the Greenwich Meridian. *Journal of Geophysical Research*, 92(C6):6462–6476.
- Wilhelm S. W. and Suttle C. A. (1999). Viruses and nutrient cycles in the sea. BioScience, 49(10):781–788.
- Wilkins D., Lauro F. M., Williams T. J., DeMaere M. Z., Brown M. V., Hoffman J. M., Andrews-Pfannkoch C., McQuaid J. B., Riddle M. J., Rintoul S. R., and Cavicchioli R. (2012). Biogeographic partitioning of Southern Ocean picoplankton revealed by metagenomics. *Molecular Ecology*.
- 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*, pages n/a-n/a.
- 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*, pages n/a–n/a.
- Wright T. D., Vergin K. L., Boyd P. W., and Giovannoni S. J. (1997). A novel âLC-subdivision proteobacterial lineage from the lower ocean surface layer. *Applied and Environmental Microbiology*, 63 (4):1441–1448.
- Yau S., Lauro F. M., DeMaere M. Z., Brown M. V., Thomas T., Raftery M. J., Andrews-Pfannkoch C., Lewis M., Hoffman J. M., Gibson J. A., and Cavicchioli R. (2011). Virophage control of antarctic algal host-virus dynamics. *Proceedings Of The National Academy Of Sciences Of The United States Of America*, 108(15):6163–6168.
- Ye Y. and Doak T. G. (2009). A parsimony approach to biological pathway reconstruction/inference for genomes and metagenomes. *PLoS Computational Biology*, 5(8):e1000465.

- Yoon J., Yasumoto-Hirose M., Katsuta A., Sekiguchi H., Matsuda S., Kasai H., and Yokota A. (2007). Coraliomargarita akajimensis gen. nov., sp. nov., a novel member of the phylum 'Verrucomicrobia' isolated from seawater in Japan. *International Journal of Systematic and Evolutionary Microbiology*, 57 (5):959–963.
- Zaballos M., López-López A., Ovreas L., Bartual S. G., D'Auria G., Alba J. C., Legault B., Pushker R., Daae F. L., and Rodriguez-Valera F. (2006). Comparison of prokaryotic diversity at offshore oceanic locations reveals a different microbiota in the Mediterranean Sea. *FEMS Microbiology Ecology*, 56(3): 389–405.
- Zhang R., Liu B., Lau S. C. K., Ki J.-S., and Qian P.-Y. (2007). Particle-attached and free-living bacterial communities in a contrasting marine environment: Victoria Harbor, Hong Kong. *FEMS Microbiology Ecology*, 61(3):496–508.
- Zubkov M. V., Sleigh M. A., Tarran G. A., Burkill P. H., and Leakey R. J. G. (1998). Picoplanktonic community structure on an Atlantic transect from 50°N to 50°S. *Deep Sea Research Part I: Oceanographic Research Papers*, 45(8):1339–1355.