

Microbial Ecology and Biogeography

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Southern Ocean

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List of Acronyms

AABW Antarctic Bottom Water.

ACC Antarctic Circumpolar Current.

AZ Antarctic Zone.

CDW Circumpolar Deep Water.

NADW North Atlantic Deep Water.

nMDS Non-Metric Multidimensional Scaling.

NZ North Zone.

OTU Operational Taxonomic Unit.

PF Polar Front.

RCA Roseobacter Clade Affiliated.

SAMW Subantarctic Mode Water.

SAZ Subantarctic Zone.

SO Southern Ocean.

STF Subtropical Front.

SZ South Zone.

Acknowledgements

Chapter 6

General discussion

6.1 Contributions of this thesis

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

6.1.1 The Polar Front

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

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

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

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

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

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

6.1.1.1 Biogeographic role of the Polar Front

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

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

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

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

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

6.1.2 The advection effect

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

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

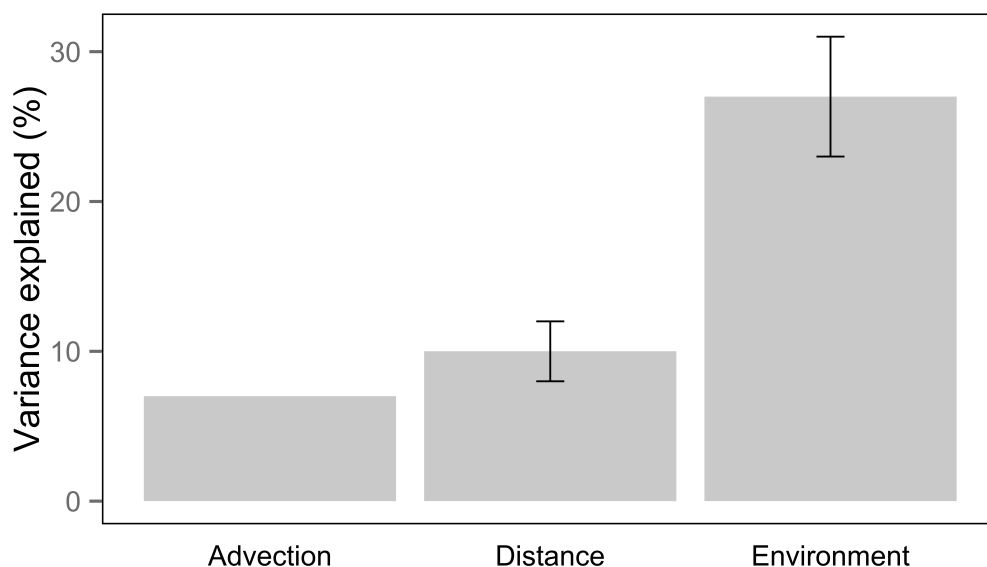


Figure 6.1: Variation in microbial community composition explained by environment and distance effects (data from review of 19 studies by Hanson *et al.* (2012); error bar represents standard error) and by the advection effect (this study).

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

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

6.1.3 MINSPEC

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

The number of publicly available full genome sequences for microbial species is growing exponentially: over the course of this project, the number of microbial genomes in the RefSeq database increased from 5,500 (May 2010) to 15,000 (March 2013) (<http://>

www.ncbi.nlm.nih.gov/refseq/statistics/, accessed 12 April 2013). As more genomes become available, the number of potential high-quality matches to a given metagenomic read will increase as a natural result of genomic identity between related organisms. MINSPEC reduces the need to rely on nucleotide identity as the sole objective standard for assigning metagenomic reads to OTUs, making use of the contextual information provided by the full set of reads to inform the assignment of each individual read. While assembly of metagenomic reads can to some extent perform the same function (Temperton and Giovannoni, 2012), MINSPEC does not require long or overlapping reads, making it well-suited to the short read lengths of current next-generation sequencing methods and to environments such as the open ocean that have a long tail of low-abundance taxa.

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

6.2 Levels of description in microbial ecology and biogeography

"Top down" vs "bottom up": medicine started "top down"; economics started "bottom up"; microbial ecology would like to have started "top down", but methodologically was forced to proceed "bottom up".

'omics finally allows microbial ecology to become a "top down" discipline. But as this perspective is almost brand new, we're struggling with how to meaningfully carve up and interpret what we see. The species concepts seems natural and easily measured on the cells-and-petri-dishes level, but seems to become almost meaningless when examining a whole community. Moreover, the tiny size, incredible diversity and adaptiveness of microbes means enormous amounts of data must be collected and carefully processed to identify even the simplest of biogeographic patterns (e.g. distance effect).

climate change needs a mention here somewhere

Nevertheless, progress is being made: environment effect, distance effect, and now advection effect. The challenge is linking the top to the bottom. It's very hard to disentangle the effects of individual OTUs – give as examples surface vs. DCM; BVSTEP of advection results. Just as it might be misguided for a physician to try to conceptualise a disease in terms of the elemental ratios of diseased vs healthy tissue, it may not even be a fruitful approach to try and think of ecological patterns in terms of their constituent species.

Future work

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

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

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