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Metabolism of free-living and particle-associated prokaryotes: Consequences for carbon flux around a Southern Ocean archipelago

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ABSTRACT

The sub-Antarctic Prince Edward archipelago lies in the path of the Antarctic Circumpolar Current, giving the islands a distinct upstream/downstream axis. Here we examined the possibility of an Island Mass Effect on the prokaryotic community, comparing prokaryotic metabolism in the upstream, inter-island and downstream regions of the islands. Abundance and flow cytometric community structure, heterotrophic production (PHP) and respiration rates (R-ETS) were investigated separately for the particle-associated (PA) and free-living (FL) prokaryote communities. Temperature, salinity structure and low chlorophyll *a* concentrations ($<0.4\ \mu g\ l^{-1}$) suggested a flow-through hydrological regime prevailed during the study. FL and PA abundances and PHP did not vary significantly over the study area. In contrast, FL and PA R-ETS decreased significantly along the upstream to downstream axis. This decrease in R-ETS resulted in high prokaryotic growth efficiencies (PGE) downstream of the islands. This suggests higher carbon sequestration efficiency downstream than upstream of the islands. No significant differences were observed between FL and PA-PGE downstream. In contrast, PA-PGE was significantly higher than FL-PGE at most upstream stations, suggesting quite different carbon utilisation by free-living and particle-associated prokaryotes with potentially important implications for overall carbon flux around the Archipelago. These findings provide new insights into the metabolic and functional roles of the two prokaryotic fractions within pelagic ecosystems. In particular, the observation that carbon consumption on particles is higher than would be expected from estimates of bulk PGE has important implications for our understanding of carbon cycling in the ocean.

1. Introduction

The uptake of organic matter by heterotrophic prokaryotes constitutes a major carbon-flow pathway in the ocean (Azam and Malfatti 2007) and variability in prokaryotic activity can have important consequences for marine food web structure (Azam et al., 1983), biogeochemical processes (e.g. Azam, 1998; Simo et al., 2002; Williams et al., 1998), export of carbon into the ocean interior (Ducklow et al., 2001) and ultimately for the global climate (e.g. Kirchman et al., 2009). Accordingly, the balance between biomass production and organic matter remineralisation into CO_2, which determines to what extent prokaryotic activity acts as a sink or as a link to higher trophic levels (e.g. del Giorgio and Cole 1998), has received increasing attention in studies of oceanic ecosystems.

Although the Southern Ocean exerts a major control on atmospheric CO_2 concentrations (Denman et al., 2007), the role played by prokaryotes in the regulation of carbon fixation and cycling in this system remains poorly understood (e.g. Anderson and Rivkin 2001; Manganelli et al., 2009). In the open ocean, where productivity is generally low, most organic matter originates from primary production and therefore, prokaryote activity is assumed to be mainly controlled by phytoplankton dynamics (e.g. Cole et al., 1988; Delille et al., 2007; Smith et al., 1995). In contrast, the system is likely to be more complex in the vicinity of oceanic frontal systems, the marginal ice zone and oceanic islands, due to the enhancement of productivity and the importance of non-phytoplankton sources of dissolved and particulate organic matter (e.g. Delille et al., 2007; Smith and Benner 2005). Although the production, degradation and export of organic carbon are likely to be disproportionately high around these very productive zones compared to the open ocean, little is known about the significance of prokaryotic activity to overall carbon flux in these ecosystems.

Elevated biological activity, from plankton to top predators, is characteristic of high latitude oceanic islands (Perissinotto et al., 1992), and may result in an important release of debris/particles in the water column which are known to be sites of highly active microbial processes (e.g. Grossart and Ploug 2000; Simon et al., 2002). In addition, elevated enzymatic activity on freshly colonised particles has been shown to release organic and inorganic nutrients into the surrounding water, creating hot spots (or plumes) that greatly extend the volume of intense decomposition processes (Cho and Azam 1988;

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Grossart and Ploug 2000). Although a significant part of the microbial activity in pelagic ecosystems may take place on or in the vicinity of particles (Azam and Long 2001), the interplay between particle-associated and free-living communities as well as their relative roles in overall carbon fluxes in the vicinity of high latitude oceanic islands remains poorly understood.

In this context we investigated a regional gradient of microbial metabolism in the surface waters surrounding the sub-Antarctic archipelago of the Prince Edward Islands, to test the degree to which modifications of the water column by mid-oceanic islands alter free-living and particle-associated prokaryotic community structure and carbon pathways. The two islands of the archipelago, Marion and Prince Edward, lie directly in the path of the easterly-flowing Antarctic Circumpolar Current (ACC), giving them a west–east or upstream–downstream axis (Ansorge et al., 1999; Froneman et al., 1999). The profusion of seabirds and marine mammals (e.g. Chown and Froneman, 2008), as well as the dense kelp beds associated with the islands (Attwood et al., 1991) represent a potential source of nutrients, organic matter and particles within the inter-islands system (Kaehler et al., 2006, 2000; Pakhomov and Chown, 2003).

The objectives of this study were (i) to investigate free-living (FL) and particle-associated (PA) prokaryote abundances and metabolism in the different regions surrounding the Prince Edward archipelago (i.e. upstream, inter-islands and downstream), (ii) to identify the main factors controlling these processes and (iii) to explore the potential consequences of these changes for carbon cycling and food web structure around the islands.

2. Materials and methods

2.1. Study site

The Prince Edward archipelago (46°38′S-37°57′E) rises from a depth of 3000 m and the two islands, Marion and the smaller Prince Edward are separated (10 nm) by a shallow plateau approximately 200 m deep. The islands lie directly in the path of the easterly-flowing Antarctic Circumpolar Current (ACC) within the Polar Frontal Zone (PFZ), bounded to the north by the Subantarctic Front (SAF) and to the south by the Antarctic Polar Front (APF; e.g. Ansorge and Lutjeharms, 2002). Due to their shallow topography, the islands act as an obstacle to the ACC, resulting in modifications of water mass properties along a west–east or an upstream–downstream axis (Ansorge et al., 1999). In addition, intensive oceanographic surveys have highlighted a high degree of variability in the latitudinal location of the SAF with important consequences for the biological environment of this region (see Durgadoo et al., 2010 for a review). When the SAF lies far to the north of the archipelago, the interaction between the ACC and the islands results in water retention within the inter-island region, favouring the development of algal blooms (Perissinotto and Duncombe Rae, 1990). During these periods, zooplankton species characteristic of Antarctic waters are observed in the vicinity of the islands, suggesting the presence of Antarctic Surface Water (AASW) around the Islands (Pakhomov et al., 2000). In strong contrast, when the SAF lies farther south, closer to the Islands, advective forces prevail and a flow-through system rich in sub-Antarctic and sub-tropical species is established between the islands (Pakhomov et al., 2000). These complex frontal space-time dynamics play an important role in productivity in the vicinity of the Prince Edward Islands with important implications for the entire food web up to the top, land-based predators (Perissinotto and McQuaid, 1992).

2.2. Sampling

Sampling was undertaken at 9 stations in the upstream, inter-island and downstream regions of the archipelago during voyage 145 of the research vessel *S.A. Agulhas,* conducted in early austral autumn (April/May) 2009 (Fig. 1). Temperature and salinity profiles were collected at each sampling station with an XR-620 CTD from the surface to a maximum depth of 400 m. Sub-surface (5 m) water samples were collected using a 5-l Niskin bottle at each station.

Dissolved inorganic nutrients concentrations (nitrate + nitrite, ammonium and orthophosphate) were determined from 20 ml water samples filtered through glass-fibre filters (Whatman GF/F) with a Lachat Flow Injection auto-analyser, following standard protocols (Grasshoff et al., 1999).

Chlorophyll *a* (Chl *a*) concentrations were determined fluorometrically (Turner Designs 10 AU Fluorometer) from 250 ml samples collected in triplicate, following Holm-Hansen and Riemann (1978).

2.3. Dissolved organic carbon (DOC) and organic nitrogen (DON)

For the determination of DOC concentrations, 8 ml of seawater was gently filtered through pre-combusted glass-fibre filters (Whatman GF/F), collected in pre-combusted (450 °C for 12 h) glass ampoules, acidified with 3–4 drops of 45% H_3PO_4 and stored at −20 °C until analysis. DOC analysis was performed on an elemental Hi-TOC analyser following standard protocols (Clesceri et al., 1998).

For DON concentrations, aliquots of 60 ml from each station were gently filtered through pre-combusted glass-fibre filters (Whatman GF/F) in acid-washed polyethylene bottles and stored at −20 °C until analysis. Organic and inorganic dissolved nitrogen were transformed into nitrate following Koroleff's method (1969/1970). The resultant nitrate concentrations were determined photometrically and

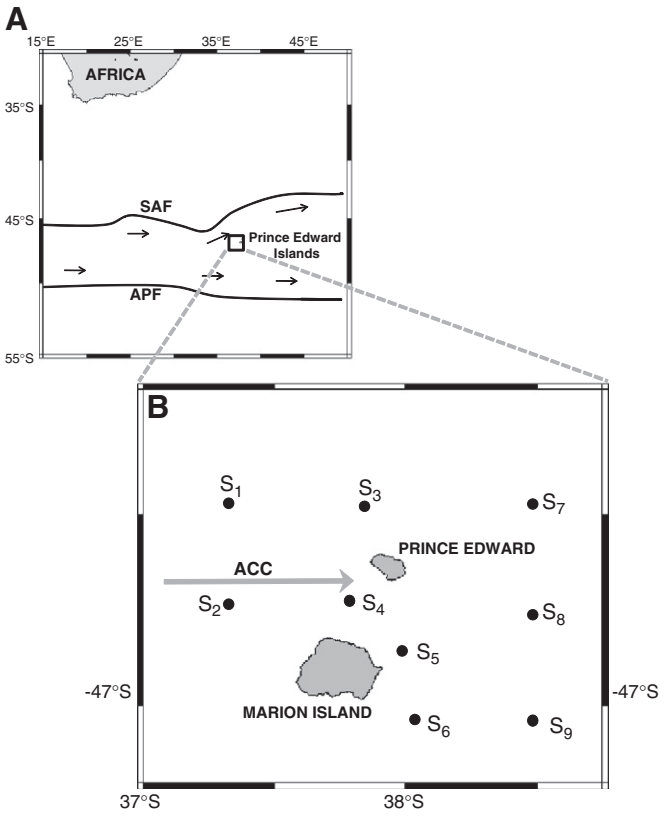

Fig. 1. (A) Positions of Prince Edward Islands Archipelago in relation to African continent and major frontal systems (average position) of the Southern Ocean. SAF: Subantarctic Front; APF: Antarctic Polar Front. (B) Location of the 9 sampling stations (black dots) in the vicinity of Prince Edward Islands archipelago located on the path of the easterly-flowing Antarctic Circumpolar Current (ACC). S_1, S_2 and S_3: upstream area. S_4 and S_5: inter-islands area. S_6, S_7, S_8 and S_9: downstream area.