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Free-living and particle-associated prokaryote metabolism in giant kelp forests: Implications for carbon flux in a sub-Antarctic coastal area

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ABSTRACT

Extensive beds of large subtidal kelps are characteristic of many temperate and subpolar coastlines. They provide habitats for a wide range of other species and are sites of high primary production that generate large quantities of water-borne particles and dissolved organic compounds that support distinctive communities of prokaryotes. We measured prokaryotic metabolism along transects from the shore to the outside of three giant kelp forests (*Macrocystis pyrifera*) located in the shelf waters of the Prince Edward Islands (Southern Ocean). Abundance, heterotrophic production (PHP), respiration rates (R-ETS) and growth efficiencies (PGE) were investigated within the particle-associated (PA) and the free-living (FL) communities. Temperature, salinity and inorganic nutrient concentrations indicated distinct hydrological differences among the kelp forests that were related to different levels of freshwater input through island run-off. In contrast, detritus and particulate organic matter concentrations showed a common pattern, decreasing from the near-shore to offshore at all sampling sites, suggesting the retention of organically enriched water masses inshore of the kelp forests. While FL and PA abundances did not differ significantly along transects, FL and PA-PHP and PGE all varied significantly across the kelp forests, following the same pattern across each forest. PA-PGE was significantly higher than FL-PGE in the near-shore waters and farther offshore, while FL-PGE was higher or equal to PA-PGE inside the kelp. This shift can be interpreted in terms of gradients in both the age and origins of organic material across the kelp forests. Higher PA-PGE implies that a larger fraction of organic carbon on colonized particles is converted into prokaryotic biomass and so becomes available to higher trophic levels inshore and offshore of *M. pyrifera* forests than inside the kelp bed. In contrast, low PA-PGE suggests that a large quantity of carbon passes through the PA-community and is mainly respired within the kelp forest. These results suggest the retention of particles within giant kelp forests. In controlling the metabolic activity of PA and FL prokaryotes, this retention will influence overall carbon flux around the archipelago. In particular, the observation of a common pattern across different *M. pyrifera* forests has important implications for the role of this species as an autogenic ecological engineer in coastal environments.

1. Introduction

Giant kelp (*Macrocystis pyrifera*) forests are among the most productive ecosystems in the world (Mann, 2000). Kelp forests occur along many temperate coasts and scattered islands in the Southern Ocean (Womersley, 1954; Dayton, 1985), providing habitat, food and refuge for numerous marine organisms (e.g. Foster and Schiel, 1985). *M. pyrifera* therefore plays a vital role in coastal environments and is an important ecosystem engineer (*sensu* Dayton, 1985; Jones et al., 1994). More particularly, kelp forests strongly affect flow, reducing water transport from the shore to the outer edge of the kelp and ultimately alter concentrations in flow-derived substances and particles in near-shore coastal waters (e.g. Gaylord et al., 2007; Rosman et al., 2010). While the potential retention of water masses within giant kelp forests has been widely acknowledged (e.g. Pakhomov et al., 2002; Gaylord et al., 2007; Fram et al., 2008), the consequences of this retention on the structure and functioning of organisms at the base of the marine food web remain unclear.

Heterotrophic prokaryotes are critical components of the carbon cycle and food webs in marine ecosystems (e.g. Azam et al., 1983; Williams et al., 1998; Simo et al., 2002). In particular, the balance between their biomass production and respiration represents a major carbon-flow pathway in these systems (e.g. Azam and

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Malfatti, 2007). The availability of organic matter (e.g. del Giorgio and Scarborough, 1995; del Giorgio et al., 1997) and inorganic nutrients (Rivkin and Anderson, 1997) is known to control prokaryote metabolic activity tightly. Consequently, the retention of enriched water masses within *Macrocystis pyrifera* forests could profoundly affect carbon utilization by prokaryotes and the food web structure of giant kelp forests as well as carbon flux within forests and exchange between them and near-shore waters. Moreover, a substantial amount of suspended debris/particles may accumulate within kelp forests (e.g. Gaylord et al., 2007). Particles are known to be highly active sites of microbial processes (e.g. Grossart and Ploug, 2000; Simon et al., 2002) and elevated enzymatic activity on particles has been shown to release organic and inorganic nutrients into the surrounding water, creating hot spots that greatly extend the volume of intense decomposition processes (Cho and Azam, 1988; Grossart and Ploug, 2001). Therefore, a significant part of overall microbial activity within *M. pyrifera* forests may take place on or in the vicinity of particles.

The Prince Edward Islands comprise Marion and Prince Edward Islands, situated in the Indian sector of the Southern Ocean. The archipelago lies directly in the path of the easterly-flowing Antarctic Circumpolar Current (ACC), giving it a west-east or upstream–downstream axis (Ansorge et al., 1999; Froneman et al., 1999). Like many oceanic islands, the archipelago is seasonally home to up to 5 million breeding pairs of top predators including flying seabirds, penguins and mammals (e.g. Chown and Froneman, 2008). Much of the coastline of the archipelago is occupied by dense *Macrocystis pyrifera* forests, principally in the more sheltered waters of the eastern coast of the larger Marion Island (Attwood et al., 1991). Although the potential for retention of water masses in *M. pyrifera* forests in the near-shore zone around Marion Island has previously been observed (Pakhomov et al., 2002), the consequences for food web structure and carbon flux are still unknown.

Our main hypothesis is that retention of particles and nutrients within kelp forests may enhance microbial processes and the recycling of carbon and organic matter within the canopy and therefore play a major role in carbon cycling and downward flux in near-shore waters. The objectives of this study were to (i) characterize the effect of kelp forests on near-shore water masses, (ii) investigate the variability in free-living (FL) and particle-associated (PA) prokaryote abundances and metabolism across different *Macrocystis pyrifera* forests, (iii) characterize the role of particles and retention of water masses by kelp forests on the patterns observed in the prokaryotic communities, and (iv) explore the potential consequences of these changes for carbon retention and downward flux in the shallow shelf waters of these sub-Antarctic islands.

2. Materials and methods

2.1. Sites and sampling

The Prince Edward Islands (46°38′S–37°57′E) rise from a depth of 3000 m and the two islands (Prince Edward and Marion) are ca. 10 nautical miles apart and separated by a shallow plateau approximately 200 m deep. The archipelago has a hyperoceanic climate (Smith and Steenkamp, 1990) characterized by high precipitation and humidity (e.g. average annual precipitation approximately 1975 mm; le Roux and McGeoch, 2008) so that the near-shore waters of the islands are strongly influenced by freshwater run-off. A substantial part of the coastline of the archipelago is occupied by dense kelp forests; *Durvillaea antarctica* dominates the infra-littoral fringe, while *Macrocystis pyrifera*, formerly *Macrocystis laevis* Hay (see Macaya and Zuccarello, 2010), predominates between the 5 m and 30 m isobaths, particularly in the comparatively sheltered waters of the eastern coast of Marion Island (Attwood et al., 1991; Beckley and Branch, 1992).

Sampling was undertaken in Macaroni and Archway Bays (Fig. 1) during voyage 145 of the research vessel *S.A. Agulhas* in early austral autumn (April/May) 2009, using a small motorized launch (Fig. 1). Macaroni Bay is a relatively large sheltered bay, receiving substantial freshwater input (Fig. 1). Sampling was undertaken at two representative sites in Macaroni Bay: (i) a sheltered site inside the bay (M1) and (ii) a more exposed site located in front of the western cape of the bay (M2) (Fig. 1). In contrast, the smaller Archway Bay receives limited freshwater input and is the site of a large colony of King Penguins (i.e. ~1500 breeding adults; Crawford et al., 2009).

At each site, samples were collected at 3 stations perpendicular to the coast located (i) in the near-shore kelp-free waters (i.e. <5 m deep), (ii) inside the kelp forest and (iii) offshore of the forest. These stations are hereafter referred to as 'inshore', 'kelp' and 'offshore', respectively (Fig. 1). Temperature and salinity profiles were collected at each sampling station with an XR-620 CTD (conductivity, temperature, depth metre) from the surface to the bottom or a maximum depth of 50 m. Water samples were taken from the sub-surface (1 m) using a 5-L Niskin bottle.

2.2. Dissolved inorganic nutrients

For the determination of dissolved inorganic nutrient concentrations (nitrate + nitrite, ammonium and orthophosphate) 20 mL water samples were filtered through glass-fibre filters (Whatman GF/F) and immediately frozen (−20 °C). Concentrations were determined in the laboratory with a Lachat Flow Injection auto-analyser, following standard protocols (Grasshoff et al., 1999).

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 using the high temperature combustion method 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 determined photometrically following Koroleff's method (1969). DON concentrations were obtained by subtracting the sum of inorganic nitrogen species (i.e. ammonium + nitrite + nitrate) from the corresponding total dissolved N concentrations.

2.4. Particulate organic carbon (POC) and organic nitrogen (PON)

Samples for POC and PON (1–1.5 L) were filtered through pre-combusted (450 °C; 12 h) and pre-weighed glass-fibre filters (Whatman GF/F) and stored at −20 °C until analysis. In the laboratory, filters were rinsed with MilliQ water, dried at 60 °C for 24 h, and re-weighed to determine the mass of Suspended Particular Matter (SPM) on the filter (Hewson et al., 2001). Analyses were performed on a Thermo Finnigan Delta XP Plus mass spectrometer interfaced with a Conflo III device to a thermo Flash EA 1112 Elemental Analyser.