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The spatial distribution of particulate organic carbon and microorganisms on seamounts of the South West Indian Ridge

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ABSTRACT[1]

The ecology and biogeochemistry of oceanic seamounts is not very well understood and explored. Pelagic ecosystems above the summits and flanks of seamounts have been observed to show different biological or biogeochemical properties to off-seamount areas, such as enhanced chlorophyll concentrations, a phenomenon referred to as the “seamount effect”. In addition, seamount biogeography has been hypothesised to be similar to islands where community structure differences in multiple organisms have been shown to change between seamounts and across frontal systems.

We used elemental analysis, to measure particulate organic carbon (POC), and flow cytometry, to estimate abundance of microorganisms from above four seamounts (Coral, Melville, Middle of What and Atlantis) along the Southwest Indian Ridge (SWIR) from latitude 32.6°S to 41.3°S, longitude 57.1°E to 42.7°E. Samples were collected from the surface to the bottom using a CTD fitted with optical sensors. POC was predicted from models created from in-situ transmission (optical) data (c_p). The high resolution predicted POC in the euphotic zone showed a heterogeneous distribution both above individual and between seamounts. The shallow penetration of two of the seamounts displayed an effect on the POC concentration in the euphotic zone depleting the layer around the summit. The transmission data showed higher concentrations of particles towards the surface, caused by primary production, and near to the seabed, probably resulting from re-suspension of sediments. The POC concentrations and microbial abundance were positively correlated to c_p and fluctuated with particle abundance, with microorganisms accounting for ~50% of the observed POC. Based on non-metric multidimensional scaling it is clear that the microbial clusters strongly indicate three separate biological regimes associated with northeastern, central and southwestern zones of the section of the SWIR that was sampled. This biological zonation is associated with physical oceanographic boundaries represented by the Subtropical and Subantarctic Fronts, forming three distinct “biogeographical” regions.

1. Introduction

There are more than one hundred thousand seamounts and knolls in the world's oceans (Rogers, 1994; Yesson et al., 2011). However, little is known about their ecology and influence on ocean biogeochemistry. Although data from seamounts are limited, they are considered unique ecosystems, in terms of the structure and sometimes high biomass of the benthic and pelagic biological communities they host (McClain and Hardy, 2010; McClain et al., 2009; Priede and Froese, 2013; Rowden et al., 2010). Pelagic ecosystems above the summit or flanks of seamounts have been observed to show different biological or biogeochemical properties compared to off-seamount areas (Rogers, 1994), a phenomenon referred to as the “seamount effect” (Dower and Mackas, 1996). For example, observations of chlorophyll concentrations in the waters above individual seamounts or seamount chains have occasionally revealed reduced or enhanced primary production compared to off-seamount sites (Dower et al., 1992; Genin and Boehlert, 1985; Lopukhin, 1986; Meredith et al., 2003; Venrick, 1991), although these have frequently been perceived as temporally unstable. Differences in phytoplankton communities have been explained through the effect of seamounts on current flow, leading to localised hydrodynamic phenomena such as Taylor Columns or Cones, doming of density surfaces or isotherms, closed circulation cells, or enhanced vertical mixing, which in turn affects nutrient availability causing enhanced primary productivity (e.g. White et al., 2008). “Seamount effects” have been observed in other parts of the pelagic community extending from heterotrophic microorganisms (e.g. Mendonça et al., 2012) to zooplankton (Fedosova, 1974; Martin and

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[1] pPOC: Predicted POC.

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Christiansen, 2009; Zaika and Kovalev, 1985), micronekton (Nellen, 1973; Boehlert and Yoklavich, 1984; Genin et al., 1988; Nellen, 1973) and large predators (Holland and Grubbs, 2007; Kaschner and Pitcher, 2007; Litvinov, 2008; Louzao et al., 2011; Morato et al., 2010; Parin and Prut'ko, 1985; Thompson and Campanis, 2007).

Whilst the ecology of seamounts has been subject to relatively little research, studies focusing on lower trophic levels and microbial processes on seamounts, which have a strong influence on biogeochemistry, are notably lacking (Vilas et al., 2009) with a few exceptions (Abell et al., 2013; Bröckel and Meyerhöfer, 1999; Mendonça et al., 2012; Moiseyev, 1986; Smith and Batiza, 1989; Wishner et al., 1995). Most organic matter in open-ocean marine ecosystems originates from primary production by phytoplankton (Hügler and Sievert, 2011; Raven and Giordano, 2009). Organic matter is released into seawater as particulate organic matter (POM) or dissolved organic matter (DOM), the latter being material that passes through a 0.7 μm pore size filter. POM is formed mainly by sinking phytoplankton cells and other microorganisms, as well as messy feeding, faecal pellets, mucous feeding nets, structural materials (i.e. chitin from the exoskeletons of crustaceans) and dead organisms (Herring, 2002; Zsolnay, 2003). The fixation of CO_2 through photosynthesis and passage of this carbon towards the deep ocean is known as the biological carbon pump (Volk and Hoffert., 1985).

DOM is formed mainly as a by-product of carbon fixation by phytoplankton and subsequent food-web interactions, as well as the dissolution of POM from microbial activity (Azam et al., 1983; Hansell, 2013; Hansell and Carlson, 2012). A fraction of the POM sinks through the water column where it predominantly is consumed and remineralised by heterotrophs and possibly laterally advected by ocean currents or re-suspended after it has settled on the seabed. Consequently microbial activity and abundance is greater with higher POM and phytoplankton abundances. In general, the closer the POM is generated to the seabed the greater will be its input into seabed-associated communities.

Explanations for decreased or enhanced densities of planktonic and nektonic organisms around seamounts range from effects arising from the physical obstruction of a seamount on vertically migrating species, hydrodynamic mechanisms that increase nutrients, or enhance densities of pelagic species by entrapment, to active migration to seamounts for foraging purposes (Genin, 2004; Louzao et al., 2011; e.g. Rogers, 1994). Given the relatively few examples of enhancement of primary production around oceanic seamounts, it would seem likely that high densities of benthic and pelagic organisms result from processes other than physical obstruction of ocean currents. An obvious contributory factor is that seamount communities live closer to the surface waters than other deep-sea communities and thus benefit from higher supplies of sinking primary production. The negative correlation between supply of POM with depth and the resultant decrease in faunal biomass moving from shallow to deep waters is well understood (Rex et al., 2006; Smith and Demopoulos, 2003).

Another possible explanation, or at least a contributory factor, could be the enhanced supply or trapping of POM through localised hydrodynamic mechanisms associated with the seamount summit or flanks (Kiriakoulakis et al., 2009). Support for such a mechanism was obtained during the OASIS project, which focused on Seine and Sedlo seamounts in the NE Atlantic. Here, although data showed a high degree of spatial and temporal variability, there was evidence of enhanced concentrations of organic matter in the waters above the seamounts, particularly close to the seabed (Kiriakoulakis et al., 2009; Vilas et al., 2009). In addition to hydrodynamic mechanisms, diel vertical migration of zooplankton and micronekton may play a role through two mechanisms. Firstly, by feeding in surface waters at night and digesting surface-generated POM at mesopelagic depths during the day, migrators may actively transport POM to the mesopelagic zone, repackaging POM as faecal pellets. Secondly, the interception of organisms undertaking diel vertical migration by predators associated with seamounts, through messy feeding and, again digestion and defecation, may also contribute to localised concentration of POM. Evidence of the latter mechanism comes from acoustic and dietary studies of predatory fish that aggregate around seamounts (Fock et al., 2002; Genin et al., 1988, 1994; Gorelova and Prut'ko, 1985; Isaacs and Schwartzlose, 1965) and also from observations of high numbers of carcasses of metazoan plankton over seamounts compared to off-seamount localities (e.g. Haury et al., 1995).

The South West Indian Ridge is an area where the Agulhas Return Current, the Subtropical Front and the Subantarctic front, further to the south, create one of the most energetic and productive hydrographic regions of the global ocean (Read et al., 2000). The NE part of the ridge lies beneath the centre of the South Indian Ocean Gyre in a region of weak currents and low primary production. The central and SW sections of the ridge, however, are influenced by higher current velocities and enhanced primary production. The enhanced primary production results from upwelling in the region of turbulent mixing between the east-going Agulhas Return Current and the Southern Ocean circulation (Longhurst, 1995). This region has so far been poorly studied (Rogers, 1994) but In the frontal zone, peak chlorophyll concentrations of $>1\ \mu g\ l^{-1}$ have been recorded. Outside this region, chlorophyll concentrations have been measured at $<0.9\ \mu g\ l^{-1}$, It is thought that the stability of the water column, the availability of nutrients (especially iron), and the accumulation of phytoplankton cells all contribute to elevated chlorophyll measurements at the Subantarctic front and Subtropical Front (Lutjeharms, 1985; Weeks and Shillington, 1996). Thus, seamounts along the SWIR are likely to be in contrasting productivity regimes and water masses depending on their proximity to the Subtropical convergence zone and the Subantarctic Front.

The present study reports on a quantitative analysis of particulate organic carbon (POC) and microbial community abundance across four seamounts of the South West Indian Ridge (SWIR) (Fig. 1). Specifically we investigated the quantity of suspended POC and microorganisms in the waters around four seamounts during austral summer (November–December) of 2011. The aim was to elucidate how POC supplies and microbial abundance were related and how surface primary produced biomass influenced them; in addition to whether there was evidence of a seamount influenced effect on the distribution of POC quantities above the summit and flanks of each seamount.

2. Methods

2.1. Sampling

All sampling was carried out during the *RRS James Cook* voyage JC66 from November–December 2011. During the fieldwork, a total of 154 samples were collected for POC elemental analysis and 213 samples were collected for quantification of microorganisms through flow cytometry (Table 1). Conductivity, temperature, and depth (CTD) profiles, as well as all water samples, were collected with a SeaBird Electronics SBE *9plus* CTD and rosette fitted with 24, 10 l Niskin bottles across transects of six deployments on the four seamounts Coral, Melville, Middle of What and Atlantis, along the SWIR (Fig. 1). An in-situ fluorometer measured Chlorophyll *a* fluorescence to a maximum depth of about 300 m (Hundahl and Holck, 1980) on all CTD deployments and density was calculated from temperature and salinity. Dissolved oxygen and salinity samples were collected to calibrate the CTD sensors.