Pelagic ecology of the South West Indian Ocean Ridge seamounts: introduction and overview

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Introduction and historical context

The Indian Ocean was described by Behrman (1981) as the “Forlorn Ocean”, a region neglected by science up to the late-1950s. For example, the *Challenger* Expedition from 1872 – 1876 largely avoided the Indian Ocean, sailing from Cape Town into Antarctic waters sampling around the Prince Edward Islands, Kerguelen Island and Crozet Islands before heading to Melbourne. From 1876 to the 1950s there were expeditions on several vessels including the *Valdivia*, *Gauss* and *Planet* (Germany), the *Snellius* (Netherlands), *Discovery II*, *MahaBiss* (United Kingdom), *Albatross* (Sweden), *Dana* and *Galathea* (Denmark; Behrman, 1981). There was no coordination between these efforts and overall the Indian Ocean, especially the deep sea remained perhaps the most poorly explored of the world’s oceans. This situation was largely behind the multilateral effort represented by the International Indian Ocean Expedition (IIEO), which was coordinated by the Scientific Committee for Ocean Research (SCOR), and which ran from 1959-1965. Work during this expedition focused on the Arabian Sea, the area to the north west of Australia and the waters over the continental slopes of coastal states in the region. Subsequently several large-scale international oceanographic programmes have included significant components in the Indian Ocean, including the Joint Global Ocean Flux Study (JGOFS) and the World Ocean Circulation Experiment (WOCE). These studies were focused on physical oceanographic measurements and biogeochemistry and whilst the Indian Ocean is still less understood than other large oceans it is now integrated into the major ocean observation systems (Talley et al., 2011). This cannot be said for many aspects of the biology of the region, despite the fact that the Indian Ocean is one of the few places where exploitation of marine living resources is still growing (FAO, 2016). The biology of the deep Indian Ocean outside of the Arabian Sea is particularly poorly understood given the presence of globally significant areas of seamounts, submarine plateaus, continental and island slopes.

Seamounts of the Indian Ocean are perhaps the least explored globally (Demopoulos et al., 2003). This volume is focused on the oceanography and pelagic ecology around five seamounts of the South West Indian Ridge and one on the Madagascar Ridge. Whilst the seamounts of the South West Indian Ridge have been subject to geological investigation as a result of the ultra-slow spreading of the ridge, the thin crust in the region and the formation of massifs through tectonic uplift (e.g. Dick et al., 2003), their biology remains poorly characterised and based on a handful of studies (reviewed in Rogers et al., 2017). Notwithstanding the lack of biological studies, the seamounts of the South West Indian Ocean have been exploited for deep-sea fisheries resources at least since the 1980s (Rogers et al., 2017). Much of this fishing has been undertaken using bottom trawling with a high likelihood of significant adverse impacts on vulnerable marine ecosystems such as cold-water coral habitat which was predicted to occur on the seamounts of the region (Tittensor et al., 2009). More recently a large area of the ridge was licensed for exploration for deep-sea mineral resources by the International Seabed Authority (ISA; Boschen et al., 2016) mainly associated with seabed massive sulphides associated with hydrothermal vents (Tao et al., 2012; 2014). On the basis of the past impacts and present and future risks (Clark & Tittensor, 2010) to the seamounts of the South West Indian Ocean, study of the region remains a high priority. However, the presence seamounts with a variety of summit depths, sizes and shapes that span waters from the Southern Ocean through to sub-tropical waters including the presence of a highly dynamic current regime based around the Agulhas Retroflection and the closely distributed Agulhas, Sub-Tropical and Sub-Antarctic Fronts makes this region a high scientific priority for the understanding of the ecology of seamounts globally. Only an estimated 250-280 seamounts have been subject to biological sampling out of an estimated >170,000 in the global ocean, a proportion of <0.002% (Rogers et al., 2015).

For these reasons the Global Environment Facility (GEF) funded the study: *Applying an ecosystem-based approach to fisheries management: focus on seamounts in the Southern Indian Ocean* (GEF Project ID 3657; Rogers et al., 2017). The papers in this volume are focused mainly on the oceanography and pelagic ecology associated with 5 seamounts on the South West Indian Ridge, Coral Seamount, Melville Bank, Middle of What Seamount, Sapmer Bank and Atlantis Seamount and one un-named seamount on the Madagascar Ridge. This was aimed at understanding how pelagic ecosystems are influenced by the presence of the seamounts and also how pelagic ecosystems may support / interact with seamount resident populations of fish targeted by the deep-sea fishing industry. The focus here was on the hypothesis that seamounts trap diurnally migrating zooplankton and micronekton which are preyed on by these fish, a phenomenon known as topographic blockage (Genin, 2004). There was also the prospect that oceanography and bentho-pelagic interactions would likely influence the distribution and other aspects of the ecology (e.g. dispersal) of the benthic organisms living on the seamounts.

Overview of contributions to the volume

A review of the current knowledge of the seamounts of the South West Indian Ocean, including their underlying geology, the regional oceanography, and what is known of their biology is presented in Rogers et al (2017). Included in this paper is a background to the structure and management of GEF Project 3657. The paper focuses mainly on sampling undertaken during the *Fridtjof Nansen* Cruise 2009-410, the cruise report of which is available at: https://brage.bibsys.no/xmlui/bitstream/handle/11250/107144/2009410%20SWISeaM.pdf?sequence=1 . Full details of the range of oceanographic, acoustic and biological sampling undertaken during the cruise is presented as well as a discussion of general sampling limitations.

The South West Indian Ocean is dominated by the Sub-Tropical Anticyclonic Gyre, the western boundary of which is dominated by the Agulhas Current which represents a strong southward flow of water (~70 Sv; Pollard & Read, 2017). This current retroflects south of the tip of South Africa and forms the southern boundary of the Sub-Tropical Anticyclonic Gyre, meandering between 37°S and 41°S. In this volume Pollard & Read (2017) refine the estimates of transport of these major current systems. They demonstrate that the eastward transport of the Agulhas Return Current accounts for the 70 Sv of transport of the Agulhas Current as far as 50°E. To the east of this the current peels off to the north to complete the circulation of the Sub-Tropical Gyre. Between the Agulhas Return Current and the tip of Madagascar westward-drifting eddies account for ~50 Sv of transport and together with southward flow to the east and west of Madagascar account for the flow of 70 Sv of the Agulhas Current. Mesoscale eddies and meanders of the Agulhas and Sub-Tropical fronts were a dominant feature over the seamounts associated with the Agulhas Front, especially Melville Bank and Middle of What Seamounts which were also subject to the greatest current flow speeds. Sapmer was less effected and Atlantis Bank lay in the waters of the Sub-Tropical Anticyclonic Gyre and as a result the latter showed greater stratification near the surface and was associated with lower current velocities. Coral Seamount lay to the south of the Sub-Tropical Front in colder, more oxygenated waters associated with the Southern Ocean. This seamount showed lower mean surface current speeds that the seamounts associated with the Agulhas Return Current but could still be influenced by its meanders when flow could be accelerated. The seamount on the Madagascar Ridge was influenced by westward drifting eddies and was thus subject to more rapidly-flowing currents than Atlantis Bank to the south.

Read & Pollard (2017) explore the local current regimes around the seamounts studies which were largely driven by mesoscale eddies as described above. The interactions of barotropic tides and the seamounts led to the generation of internal tides (Read & Pollard, 2017). This effect was observed particularly around the summit of the seamounts with either energy downwards from the crest (Coral Seamount) or upwards (Sapmer and Melville banks). This led to enhanced current sheer, increasing the potential for mixing and turbulent flow above several of the seamounts potentially leading to resuspension of material from the seabed. Internal tides led to vertical displacements of isopycnals above the seamounts of up to 200m with exposure of the summits of two seamounts, Coral and Melville Bank, to the fluorescence peak below the surface (Read & Pollard, 2017). Such a phenomenon is likely to provide enhanced food supplies to organisms living on the summits of these seamounts at each tidal cycle. Evidence for tidal rectification was only found at one seamount (Melville Bank) with some similarities to flow observed at Fieberling Guyot (Lavelle, 2006) whilst there was little evidence for Taylor-Column formation in the present study (Read & Pollard, 2017). Overall, these findings add to previous studies which have described interactions between elevated topography and tidal flow leading to enhanced delivery of surface primary production to benthic communities, resuspension of organic matter and circulation that may influence seabed communities in other ways (e.g. White et al., 2007).

Sonnekus et al. (2017) measured the physical parameters (temperature, salinity, oxygen macronutrients) and phytoplankton communities over the six investigated seamounts. They generally find an increase in phytoplankton biomass with increasing latitude with Coral Seamount having significantly higher biomass than the un-named seamount on Madagascar Ridge. Nutrient ratios indicated that nitrate was limiting to phytoplankton growth at all of the seamounts with the exception of Coral Seamount which was silicate-limited. 148 species of phytoplankton were detected across the sampled region with waters over Atlantis Bank showing the highest diversity although no latitudinal pattern in species richness was discernible. Multivariate analysis identified three distinct communities of phytoplankton across the studied region even though many species were shared across stations. These corresponded to (i) waters of the Sub-Tropical Anticyclonic Gyre, (ii) the Agulhas and Sub-Tropical Fronts and (ii) waters south of the Sub-Tropical Front. Functional group dominance shifted from dinoflagellates to diatoms with increasing latitude. Temperature, nitrate and oxygen were the dominant environmental drivers of phytoplankton community composition. Although a general seamount effect in phytoplankton biomass or community composition was not found phytoplankton biomass appeared to be enhanced over the shallow summits of Coral Seamount and Melville Bank. Both these seamounts showed evidence of internal tides and vertical displacement of isopycnals, potentially enhancing the delivery of phytoplankton to the seamount summits (Read & Pollard, 2017). Strong vertical mixing at these seamounts may have enhanced delivery of nutrients from deeper water into the euphotic zone.

Djurhuus et al., (2017) is one of three papers in this volume that include data collected on a subsequent cruise on the Royal Research Ship *James Cook* (cruise JC136) in November-December, 2011. The paper examines patterns of distribution of particulate organic carbon (POC) and microbial plankton over four seamounts on the South West Indian Ridge, Coral Seamount, Melville Bank, Middle of What Seamount and Atlantis Bank. Patterns of temperature and concentrations of macronutrients were similar to those observed by Sonnekus et al. (2017). Generally, POC concentrations decreased with depth with the carbocline coinciding with the fluorescence maximum (f_{max}). Coral Seamount showed the highest f_{max} POC values and Atlantis Bank the lowest with Melville Bank and Middle of What Seamount showing intermediate values. Patterns were not so clear from water sampled at the base of the euphotic zone or near the seabed with Middle of What Seamount showing the highest values. This may reflect the strong currents measured over this seamount in 2011 (~66.0 cm s-1 at the surface). Atlantis Seamount actually showed an incline in POC values with depth possibly related to a deep chlorophyll maximum. Microbial abundance correlated with POC and thus was highest at Coral Seamount. Although analyses of variation across the seamounts was based on only five groups of microorganisms they demonstrated three distinct communities corresponding to the same regions as for the three phytoplankton communities identified by Sonnekus et al. (2017). Notable here, was the switch between dominance of *Prochlorococcus* in the north to *Synechococcus* in the south reflecting the environmental preferences of these taxa. Whilst this study was not amenable to detection of a “seamount effect” there was some evidence for depletion of POC around the summits of shallower seamounts perhaps reflecting the feeding of seamount-associated organisms.

Letessier et al (2017) report on the micronektonic crustaceans sampled during Fridtjof Nansen Cruise 2009-410. 31 species were captured the majority of which represented new records for the Indian Ocean reflecting the lack of study of the mesopelagic fauna outside of the Arabian Sea. PERMANOVA indicated significant differences in the species richness and assemblages observed across the different water masses in the South West Indian Ocean. Although the patterns were not as clear as for phytoplankton or microplankton studies clusters of species representing different communities were characteristic of the Sub-Tropical Anticyclonic Gyre, the zone around the Sub-Tropical and Sub-Antarctic Fronts and the zone associated with the Sub-Antarctic Front. Some species were ubiquitous in all areas and it is apparent the micronektonic crustaceans are highly mobile and populations of many species maintain high connectivity across the region. The most striking results of this study are that the species richness and abundance of these organisms is highest on seamount stations indicating an “oasis effect” (McClain, 2007). Several species of lophogastrids were caught uniquely on seamount stations and even ubiquitous species were more abundant over seamounts (e.g. *Sergestes armatus*). The likely reason for this effect is that the sampled seamounts provide additional habitats for these micronektonic crustaceans. These habitats may be pelagic or include benthic habitats as there is evidence of feeding on or near the seabed for some species or diurnal migration into this habitat (Vereschaka, 1995). Micronektonic crustaceans are prey for larger predatory fish providing one possible explanation for the concentration of species of interest to fisheries in the vicinity of seamounts.

Laptikhovsky et al. (2017) present evidence that the South West Indian Ocean is a remarkable hotspot of pelagic cephalopod diversity. 68 cephalopod species representing 10-11% of the known diversity of these animals and 25% of the known diversity of pelagic squids. The majority of species have a circumglobal distribution in the southern hemisphere with the majority being pelagic spawners and only two known to lay eggs on the seabed (both Sepiolida). Four distinct assemblages of cephalopods were identified, one located in the northern boundary of the Sub-Tropical Anticyclonic Gyre, the other three corresponding to the same water masses identified as comprising distinct assemblages for the phytoplankton and microbial plankton (Sonnekus et al., 2017; Djurhuus et al., 2017). The assemblage associated with the Sub-Tropical and Agulhas Fronts was the most diverse whilst that lying close to the Sub-Antarctic Front (Coral Seamount) included both Antarctic species and a number associated with benthic habitats. There was also a shift in life history with species reproducing in the epipelagic zone dominant in most of the sampled area but declining in importance moving south. Species reproducing in the mesopelagic and bathypelagic with juveniles ascending to shallower water increased in prevalence towards the south and were joined by species which lay their eggs on the seabed. Epipelagic spawners were absent from the area around the Sub-Antarctic Front. Again, the richness of cephalopod communities around seamounts may be related to increased habitat availability (e.g. seabed for bottom-spawning species) and is likely important in attracting predatory fish to these locations.

Boersch-Supan et al. (2017) analyse the backscatter strength of multifrequency acoustic data to gain important insights into changes in epipelagic and mesopelagic communities across the

South West Indian Ocean. Again they identify significant changes in the patterns of distribution of deep-scattering layers (DSL) at ~32ºS and 42ºS. These zones correspond to the boundary regions of the distinct communities identified for phytoplankton, microbial plankton and cephalopods (Sonnekus et al., 2017; Djurhuus et al., 2017; Laptikhovsky et al. 2017). The northern region, corresponding to the central / northern Sub-Tropical Anticyclonic Gyre and the region associated with seamounts close to the Sub-tropical and Agulhas Fronts is characterised by two DSLs. These are located in shallow and deep water although they differ in depth between the two regions. The zone associated with the Sub-Antarctic Front is characterised by several less-defined DSLs. Sea surface temperature was identified as the most significant environmental driver of backscatter strength along with time of day. Peaks of backscatter were identified at the Sub-Tropical Front and Sub-Antarctic Front. These findings indicate the role of these frontal zones as both significant biogeographic boundaries but also a focus of biological activity. Given the importance of this region in terms of global oceanic primary production the finding of enhanced micronekton biomass at these frontal zones may indicate a larger role of active transport of carbon into the ocean interior of wider significance.

Amon et al. (2017) describe the results of the deployment and retrieval of a mooring with packages of whale bones and wood on to Coral Seamount and Atlantis Bank at depths between 700-800m. The packages were colonised by communities of organic food-fall specialists (e.g. *Xylophaga* spp.; *Idas* spp.) and opportunist species. Communities at the packages were different with a higher diversity found at Coral Seamount than Atlantis Bank and only 11 species found in common. At least 15 of the species found associated with these food falls were undescribed. The differences in the faunal assemblages reflect the major biogeographic differences in the waters close to the Sub-Antarctic Front compared to those in the Sub-Tropical Anticyclonic Gyre. There were also differences in the rates of biological processes between the two sites with the wood deployments being almost completely destroyed by *Xylophaga* cf *indica* on Atlantis Bank but just burrowed by *Xylophaga murrayi* on Coral Seamount. These represent large range extensions for these two *Xylophaga* species which have been rarely observed since their description from elsewhere in the Indian Ocean. Overall the study points to major differences in benthic communities across the seamounts of the South West Indian Ocean and also the lack of connectivity between these populations.

Overall, the papers in this volume represent a step change in our understanding of the pelagic ecosystems and processes that occur in association with seamounts in the South West Indian Ocean. Water mass has a major effect in determination of community structure across this complex and dynamic region including in the bacterioplankton, phytoplankton, pelagic invertebrates, other micronekton (fish) and even predators such as seabirds (see *Fridtjof Nansen* 2009-410 Cruise Report). Processes that are likely to influence the distribution of both benthic and pelagic communities of megafauna, including species of fisheries interest were identified. These include oceanographic phenomena such as internal tides or waves and biological phenomena such as provision of additional habitat for prey species such as micronektonic crustaceans and cephalopods. The studies emphasise how even a limited sampling effort in this region can significantly change knowledge of the biodiversity and ecology of this remote part of the Indian Ocean and contribute to our understanding of seamount ecology at a global scale.

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