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Seamount influences on mid-water shrimps (Decapoda) and gnathophausiids (Lophogastridea) of the South-West Indian Ridge

Tom B. Letessier [a,b,*], Sammy De Grave [c], Philipp H. Boersch-Supan [a,d], Kirsty M. Kemp [e], Andrew S. Brierley [a], Alex D. Rogers [d]

[a] Pelagic Ecology Research Group, Scottish Oceans Institute, University of St Andrews, KY16 8LB United Kingdom
[b] Centre for Marine Futures, The UWA Oceans Institute, The University of Western Australia, UWA (M470), Stirling Highway, Crawley, WA 6009 Australia
[c] Oxford Natural History Museum, Parks Road, Oxford OX1 3PW, United Kingdom
[d] University of Oxford, Department of Zoology, The Tinbergen Building, South Parks Road, Oxford OX1 3PS, United Kingdom
[e] Institute of Zoology, Zoological Society of London, Regent's Park, London NW1 4RY, United Kingdom

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ABSTRACT

Maintenance of often-observed elevated levels of pelagic diversity and biomass on seamounts, of relevance to conservation and fishery management, involves complex interactions between physical and biological variables that remain poorly understood. To untangle these biophysical processes we explore factors influencing the distribution of epi- and meso-pelagic (0–1000 m) micronektonic crustaceans ($>$15 mm; order Lophogastridea, family Gnathophausiidea; and order Decapoda) on and off seamounts along the South West Indian Ridge (SWIR, 27° to 42°S) and on a seamount off the Madagascar Ridge (31.6°S, 42.8°E). Thirty-one species of micronektic crustaceans were caught using mid-water trawls within the study area but there was no apparent latitude-related patterns in species richness or abundance. Species richness predicted by rarefaction curves and numerical abundance was highest in the vicinity ($<$1 km) of seamounts (species richness: 15 to 21; abundance: 10 ± 2 to 20 ± 1 ind.10^{-3} m^{-1}) compared with over the abyssal plains and ridge slopes (species richness: 9.2–9.9; abundance: 24 ± 2 to 79 ± 8 ind.10^{-3} m^{-1}). Multivariate analysis of assemblage composition revealed significant groupings of individual trawl samples with respect to whether the sample was on or off a seamount and hydrographic region, but not with time of sampling relative to diel cycle (day/night or dawn) or depth of sampling (0–500, 500–800, $>$800 m). The dominant species assemblage comprised the shrimps *Systellaspis debilis* (37%) and *Sergia prehensilis* (34%), and was restricted to seamounts on the subtropical SWIR. Our observations suggest that the 'oasis effect' of seamounts conventionally associated with higher trophic levels is also applicable to pelagic micronektic crustaceans at lower trophic levels. We suggest that the enhanced biomass and species richness attributed is due to 'habitat enrichment', whereby seamounts provide favourable habitats for both pelagic and bentho-pelagic mid-water crustaceans.

1. Introduction

Seamounts are topographic elevations with a limited extent across the summit (Rogers, 1994). There are more than 33,000 seamounts in the World Ocean with an elevation $>$1000 m and a much larger number of smaller features (Yesson et al., 2011). The biomass of commercially important species of fishes (e.g orange roughy and billfish) and that of other large nekton is often enhanced around seamounts (Hirch and Christiansen, 2010; McClain, 2007; often referred to as the 'oasis' effect of seamounts, see Morato et al., 2010), through poorly understood ecological mechanisms. This enhanced biomass is thought to be sustained through trophic interactions between fish resident on seamounts and diurnally vertically migrating (DVM) layers of epi- (0–200 m) and mesopelagic (200–1000 m) zooplankton and micronekton that drift over the seamount summit and slopes at night (Rogers, 1994). At dawn, organisms comprising these layers would ordinarily descend, but become trapped in the shallower waters over the seamount and are consumed by predatory nekton. This mechanism is known as the sound-scattering layer interception hypothesis, or the DVM trapping/ topographic blockage hypothesis

* Corresponding author. Current address: Institute of Zoology, Zoological Society of London, Regent's Park, London NW1 4RY, UK..
E-mail address: Tom.Letessier@ZSL.org (T.B. Letessier).

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(Hirch and Christiansen, 2010; here after DVM trapping, Isaac and Schwarzlose, 1965). Taylor columns – quasi-stationary eddies – may also be present over the seamount (Boehlert, 1988), driving localised enhanced primary production and trapping of meso-zooplankton (0.2–2 mm), facilitating their capture by seamount predators, although evidence for this is weak. Seamounts has the potential to harbour reproductively isolated population, with little connectivity between mounts, as species and assemblages tend to specialised to the local conditions (de Forges et al. (2000); the 'island' effect, see Johannesson (1988)). However, recent work has suggested that this isolation, if it occurs at all, is likely to occur in species with life histories that confer a low probability of dispersal (Clark et al., 2012). The fauna of seamounts has been found to resemble that of the nearest shelf environments although community structure and biomass can be markedly different (McClain et al., 2007); (Priede et al., 2013).

In oceanic systems in general, interactions between meso-zooplankton and demersal fish populations are mediated by a trophic spectrum of micronekton (> 15 mm), which forms intermediate links in food chains (Sutton, 2013). This fraction forms the focus of this study. Decapod shrimps and gnathophausiids are an important component in the diet of demersal and benthopelagic fish on ridges (Bergstad et al., 2010; Horn et al., 2010), abyssal plains (Stowasser et al., 2009), and seamounts (Hirch and Christiansen, 2010). Although DVM has been observed in both shrimps and gnathophausiids, the behaviour is not universal within either taxa (Sergestes, see Flock and Hopkins (1992); Gnathophausia ingens, see Hargreaves (1985)). In a mechanism that is almost a corollary of DVM trapping outlined above, resident shrimps and Gnathophausiidae may actively resist advection away from the seamount (Wilson and Boehlert, 2004). The reasons for and mechanisms of this behaviour are poorly understood and its taxonomic prevalence unknown. Some species may be benthopelagic specialists, and thus require habitats in proximity to the seabed, which seamounts provide (Meland and Aas, 2013). How seamounts influence the distribution of shrimps and gnathophausiids and by what mechanism this influence is maintained is thus of relevance to the understanding of oceanic and seamount trophic food-web.

The seamounts of the southwestern Indian Ocean have been exploited from a fishery perspective for nearly 50 years. Exploratory fishing on the South West Indian Ocean Ridge (SWIR), the Mozambique Ridge and the Madagascar Ridge began in the 1970s by the Soviet fleet, and associated research institutions, with commercial trawling beginning in the early 1980s (Clark et al., 2007; Romanov, 2003). These fisheries targeted redbait (*Emmelichthys nitidus*) and rubyfish (*Plagiogeneion rubiginosus*) with catches peaking about 1980 and then decreasing to the mid-1980s. Fishing then switched to alfonsino (*Beryx splendens*) in the 1990s as new seamounts were exploited. Some exploratory trawling was also carried out on the Madagascar Ridge and South West Indian Ocean Ridge by French vessels in the 1970s and 1980s, targeting Walter's Shoals and Sapmer Bank (Collette and Paring, 1991). In the late 1990s, a new fishery developed on the SWIR with trawlers targeting deep-water species such as orange roughy (*Hoplostethus atlanticus*), black cardinal fish (*Epigonus telescopus*), southern boarfish (*Pseudopentaceros richardsoni*), oreo (Oreosomatidae) and alfonsino (Clark et al., 2007). These species are generally slow to reproduce and typically form breeding aggregation on seamounts, making them particularly susceptible to overexploitation (Koslow et al., 2000). This fishery rapidly expanded, with estimated catches of orange roughy being in the region of 10,000 t, but then rapidly collapsed. Fishing then shifted to the Madagascar Plateau, Mozambique Ridge and Mid-Indian Ocean Ridge, targeting alfonsino and rubyfish (Clark et al., 2007). Most of these areas have therefore been significantly impacted by deep-sea bottom fisheries and exploitation of these stocks, as well as new ones, such as the lobster fishery (*Palinurus barbarae*) on Walter's Shoal, continue (Bensch et al., 2008).

In spite of a series of concerted efforts in the 1960s (Zeitzschel, 1973), the basin scale biogeography and ecology of the Indian Ocean and the SWIR is poorly known, in part because of the ocean's remoteness to nations with large-scale historical, oceanographic research programmes. Most basin-scale studies arising from those intensive efforts were on epipelagic meso-zooplankton, and few baseline data exists for deeper depth horizons, or on specific energy pathways in oceanic food webs (Letessier et al., 2012; Sestak, 1974). Moreover, recent deep-sea studies on the SWIR are limited to a series of geological surveys of the Atlantis Bank (Dick, 1998), and to the hydrothermal vents in the vicinity of Melville Banks (Tao et al., 2007). Some previous work stemming from a series of Russian cruises in the 1990s provides baseline species records for zooplankton and micronekton from Walter's Shoal (Vereshchaka, 1995).

As a result of historical overfishing and subsequent collapse, some of the fish populations on the SWIR may be in a state of recovery, the rate of which will depends partly on energy input and prey accessibility (Kar and Ghosh, 2013). Moreover, population connectivity and the potential 'island' effect of seamount will have relevance for replenishment and for the capacity of population to resist any depensation (Courchamp et al., 2008) at low densities arising from the allee effect (Stephens et al., 1999). How seamounts influence mid-water micronekton distribution and the function of open ocean food-wed is therefore of relevance for management, whilst being of scientific interest for the broader understanding of open ocean food webs, and ecological processes. The faunal assemblage composition of seamount micronekton, their overlap with true pelagic communities, and their potential role in the DVM trapping are poorly understood, yet remain crucial for the management of the SWIR and associated fishing grounds.

Here we address this paucity in knowledge by presenting new records of epi- and mesopelagic crustaceans along the SWIR and on a seamount on the Madagascar Ridge, north of Walters' shoal. The aims of this study were threefold:

1) To describe epi- (0–200 m) and mesopelagic (200–1000 m) micronektic crustacean assemblage composition on and off seamounts of the SWIR.
2) To test the influence of seamounts and hydrographical regions on the abundance and species richness of micronekonic crustaceans, and to elucidate mechanisms driving species richness and abundance enhancement (such as a potential 'oasis' effect of seamounts).
3) Explore connectivity between seamounts by comparing assemblage similarity and isolation, in order to explore the hypothesis of 'island' of these seamounts.

Work was conducted as part of the UNDP/IUCN project, which aims to provide ecosystem-based management of fisheries of the South West Indian Ocean.

2. Materials and methods

2.1. Sampling area

The SWIR (Fig. 1) runs broadly from northeast to southwest in the west of the Indian Ocean basin, extending over 1200 miles and varying from 200 to 300 miles in width (Romanov, 2003). The result is an axial valley with ridge terraces on either side, with several areas rising from the abyssal plains to within < 1000 m of the surface. To the north of the SWIR lies the Island of Madagascar