Author's Accepted Manuscript

Seamount influences on mid-water shrimps (Decapoda) and gnathophausiids (Lophogastridea) of the south-west Indian ridge

Tom B. Letessier, Sammy De Grave, Philipp H. Boersch-Supan, Kirsty M. Kemp, Andrew S. Brierley, Alex D. Rogers

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

Tom B. Letessier[1,2,†], Sammy De Grave[3], , Philipp H. Boersch-Supan[1,4], Kirsty M. Kemp[5], Andrew S. Brierley[1], Alex D. Rogers[4]

Corresponding author: Tom.Letessier@ZSL.org

[1]Pelagic Ecology Research Group, Scottish Oceans Institute, University of St Andrews, KY16 8LB, United Kingdom.

[2]Centre for Marine Futures, The UWA Oceans Institute, The University of Western Australia, UWA (M470), Stirling Highway, Crawley WA 6009 Australia

[†]Current address: Institute of Zoology, Zoological Society of London, Regent's Park, London NW1 4RY

[3]Oxford Natural History Museum, Parks Road, Oxford, OX1 3PW, United Kingdom

[4]University of Oxford, Department of Zoology, The Tinbergen Building, South Parks Road, Oxford, OX1 3PS, United Kingdom.

[5]Institute of Zoology, Zoological Society of London, Regent's Park, London NW1 4RY, United Kingdom

1 Abstract

Maintenance of often-observed elevated levels of pelagic diversity and biomass on seamounts, that are 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 are but there was no apparent latitude-related patterns in species richness or abundance. Species richness predicted by rarefraction 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 net 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.

Key words: Conservation, Indian Ocean, Decapod shrimp, Gnathophausia, deep sea.

2 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 >1000m 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 (Hirch and Christiansen, 2010; hereafter 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 predation 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., 2009). 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., 2009; Rowden et al., 2010).

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

4

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 (SWIR) by French vessels in the 1970s and 1980s, particularly 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 10,000t, 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

5

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.

3 Materials and methods

3.1 Sampling area

The SWIR (Fig. 1) extends from northeast to southwest in the west of the Indian Ocean basin, extending over 1,200 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 with its associated shelf and the Mascarene plateau, and the Madagascar Ridge including Walters' shoal, a productive fishing ground that has recently had a small area voluntarily closed by some of the fishing industry (bottom trawl) for conservation (Rogers et al., 2009).

The physical oceanography and environmental conditions of the study area are explored in detail in two dedicated studies in this volume (R. Pollard and Read, 2015; Read and D. A. Pollard, n.d.). The sampling stations occupied in this study spanned 10 degrees of latitude, and surface temperature ranged from 27° in the North to 8° in the South. Oceanographically, the SWIR is influenced by several fronts with the combined effect of the retroflection of the Aghulas Return Current and the Subantarctic Front creating one of the most productive areas in the global ocean (161 gC m-2 yr-1, Read et al., 2000). The SWIR is also characterised by two biomes deemed ecologically distinct in primary production pattern: the Indian South Subtropical Gyre Province (ISSG), and the

South Subtropical Convergence Province (Longhurst, 1998), see also Vierros et al. (2008). Kostianoy et al (2004) and Pollard (2015) defined oceanographic sub-regions further by deriving frontal features from satellite sea surface temperature and sea surface height patterns: the Tropical region (TR, ~25° to 40° S; 25° to 17° C), Subtropical convergence (STC, ~40° to 43° S; 17° to 13° C), sub-Antarctic convergence (SAC, ~43° to 46° S; 13 to 10 °C).

3.2 Net sampling

Pelagic sampling was conducted using scientific nets at 8 stations along the SWIR (Fig. 1) from the R/V *Fridtjof Nansen* Cruise 2009-410. Forty depth-targeted hauls were conducted on 5 seamounts along the ridge, a single seamount of Walter's Shoal, and on two 'off-seamount' sites considered as control stations (station 2 on the abyssal plains between the Reunion and Atlantis seamount, and station 7 in the sub-Antarctic convergence, see Table 1, Fig.1). The routine approach to trawl sampling at all stations generally consisted of two day-time hauls (400-600 m and 720-1100 m) and two night-time hauls, using a medium-sized pelagic fish trawl (a Norwegian 'Åkratrawl', vertical net opening 20-35 m, door spread 110 m, cod-end mesh size 4 mm stretched). On three occasions, a 'benthic' trawl rigged without rollers or bobbins was hauled at high speed as close to the seamount peak as possible, without touching the seabed, in order to catch larger benthopelagic species, usually shoals identified by ship-mounted echosounders (Boersch-Supan, this volume). In all cases the trawl was lowered rapidly to the minimum depth to be sampled, and then fished on a slowly lowered trajectory to the maximum target depth, after which the trawl was collapsed and heaved quickly to the surface in order to minimise net contamination from shallower waters.

Upon recovery of the cod-end on deck, the material was sorted to nearest taxa, and fixed in 4% buffered formaldehyde (Steedman, 1976). Subsamples (usually ~50 individuals) of dominant species were fixed in 96 % ethanol for molecular studies. The portion of the catch kept in formaldehyde was transferred to 70% ethanol, usually within 48 hours of fixation. After the cruise, all samples were identified to the lowest taxonomic level possible (to species for 98% of samples) in the Oxford Museum of Natural History.

3.3 Data analysis

3.3.1 Net catchability

Relative abundance of species/taxa (numerical count) and species richness (total number of species recorded) were determined for each station. Because of the poor catchability of large crustaceans by the 'benthic' trawl (the 'benthic' trawl was fished at high speed and the net bag mesh size was coarser than the Åkratrawl) crustacean densities were derived using the Åkratrawl catches only. The benthic trawl catches were only considered when deriving species richness. Because the Åkratrawl likely undersampled greatly the Catch per Unit Effort (CPUE), densities were derived by standardizing the catch by the horizontal distance trawled (m) rather than by the volume (equation [1]).

Equation [1] CPUE = ind 10^{-3} m^{-1}.

Previous studies have shown that the catchability of invertebrate micronekton by the Åkratrawl can be very taxon specific, probably because of taxonomic size differences, 'herding' effects of the trawl doors, and the large mesh size at the mouth of the trawl (de L Wenneck et al., 2008; Heino et al., 2011). While all sampling gear holds some inherent bias because of its design parameters, the data derived directly from the raw Åkratrawl catches are probably unfit for comparison of relative abundance between the mikronekton, or for assemblage analysis (of other than presence/absence data). As a

consequence the catch-selectivity of the Åkratrawl (Heino et al., 2011) was considered for further analysis. This was aimed at making the present study more usefully comparable to other macrozooplankton/micronekton studies which typically use smaller gear types (Cox et al., 2013; Letessier et al., 2012; 2011; Pakhomov et al., 1999). The selectivity of the Åkratrawl ('y') relative to the reference trawl ('x'; a Norwegian macrozooplankton trawl (de L Wenneck et al., 2008), can be expressed by equation [2]

Equation [2]: $C_y = \rho C_x$

where p is the relative catchability coefficient and C is the catch standardized by the trawled distance (CPUE here). The Norwegian macrozooplankton reference trawl is not assumed to convey 100% catchability, but it is probably more quantitative than the Åkratrawl for the fauna in the size-range targeted here (<100 m).

True catches (C_x) were derived by dividing the distance-standardised catches (C_y) by the taxon specific catchability coefficients ('ρ') using parameters from Heino et al. (2011; personal communication; equation [3]) and 'a_y' a taxon specific model parameter (see Table 2 for the selected model taxon and model parameter).

Equation [3]: $\rho = e^{a\_y}$

Previous studies have shown that in the context of multidimensional assemblage analysis, the transformation applied here to the relative abundance reduces the gear effect to a weakly significant grouping term, when analysed together with replicates from a standard macrozooplankton trawl (Sutton et al., 2008). This potential source of bias was deemed acceptable for our purposes here, and numerical abundance at the level of the individual species and the assemblage is therefore reported using our standardised

10

CPUE densities.

The coefficients from Heino et al. (2011) were calculated with respect to an Åkratrawl with a net bag mesh of 22 mm, and this is likely to infer some bias compared to the trawl used here (net bag mesh 4 mm). However, net bags typically get clogged rapidly during hauls, and the difference in mesh size in the net bags would probably not influence the results, especially as the majority of species considered where larger than 22 mm.

3.3.2 Species richness estimation

Species sampling efficiency was explored using the expression of Gotelli & Colwell (2001), which finds the species accumulation curve and its standard deviation from random permutations of the sample pool. Species accumulation curves and predicted species richness patterns at each seamount were explored using the vegan package (Oksanen, 2011) in the R statistical programming environment (Team, 2012). In the absence of a balanced sampling design (effort varied slightly between stations, see Table 1) we followed the recommendation of (Colwell and Coddington, 1994) in order to estimate the number of unseen species, using the frequency of new species arrival to generate a bootstrap-predicted species richness (hereafter species richness) value and standard error. Species richness per station was predicted using the slope of the species-area curve, or the exponent z of the Arrhenius model (Oksanen, 2011).

3.3.3 Univariate and multivariate analysis

To determine the effect of sampling location compared to seamounts (on or off), hydrographic region (Kostianoy et al., 2004), depth (0-500, 500-800, > 800 m), and time in diel cycle (Night, Day and Dawn; Table 1), and interactions there of, on species richness, standardised numerical abundance and species assemblage composition, we conducted non-parametric permutational analysis of variance (PERMANOVA, Anderson, 2001), with 9999 permutations (on a Bray-Curtis resemblance matrix for the assemblage, Bray and Curtis, 1957).

Multivariate species assemblage patterns were further explored with multivariate statistics and classification techniques using Primer software v6 (K. R. Clarke and Gorley, 2006), namely non-metric multidimensional scaling (NMDS), ordination and cluster analysis. Input data were root-transformed density data (ind. 10^{-3} m^{-1}) to reduce the influence of dominant species. Similarity between samples was evaluated using the Bray-Curtis similarity index (Bray and Curtis, 1957). Analysis of individual net samples was carried out, where each cod-end collected was considered a distinct sample. Each cod-end was characterised by its standardized species-specific abundances and sample depth (Table 2). The appropriate discrimination level for determining clusters was decided by running similarity profile permutation tests (SIMPROF, 1000 permutations, $p < 5\%$ to determine at which similarity % the clusters significantly differed in structure). Species contribution to similarity (SIMPER) was applied to determine the characteristic species composition to each significant cluster.

3.3.4 Isolation and 'island' effect hypothesis

To test for any potential 'island' effect of seamount, the degree of connectivity between seamounts was explored by plotting the Bray-Curtis index of similarity distance between samples. The relationship was explored using linear regression of distance-between-sites (modelled at the independent variable) and the Bray-Curtis index as the

response. We would expect a perfectly connected assemblage to have a slope of 0, as the similarity index would be unaffected by distance. The actual model slope was compared with a slope of 0 using a Wald-test based comparison (Fox and Weisberg, 2011).

4 Results

4.1 Crustacean micronekton abundance and diversity distribution patterns

We caught 4936 individual decapods and lophogastrids in the size range 15 mm to 60 mm, representing 31 species and 14 families (Table 2), in 40 net hauls. The species accumulation curve revealed a rapid increase of species richness from 0 to 10 trawls, reaching an asymptote after approximately 35 samples (Fig. 2). Mean numerical abundance per station ranged from 10 to 79 ind.10^{-3} m^{-1}. Highest numerical abundances were observed over seamounts (Fig. 3 A). Highest species richnesses were predicted over Coral seamount (21 species, station 8), Walter's Shoal (20 species, station 10), and Melville bank (20 species, station 9).

Several decapod species were caught at almost every station, and so appeared ubiquitous (*Oplophorus novaezelandiae, Systellaspis debilis, Funchalis villosa*, *Sergia prehensilis, Deosergestes corniculum*; Table 2) but *S. debilis* and *F. villosa* were absent in catches from most stations in the sub-Antarctic convergence. The most abundant species overall were *S. prehensilis* and *S. debilis.* Several species were caught uniquely in the vicinity of seamounts (all lophogastrids and *Gennadas* spp, *Acanthephyra sica, Eupasiphae gilesii, Funchalia danae, Acanthephyra quadrispinosa, Meningodora vesca, Notostomus auriculatus. Parapasiphae sulcatifrons, Pasiphaea barnardi, Pasiphae gelasinus*; Table 2). Several species were caught uniquely in the sub-Antarctic convergence (*Pasiphaea rathbunae, Pasiphaea barnardi, Eusergestes* cf. *antarcticus,*

Petalidium foliceum, Gennadas kempi). No species were caught uniquely on off-seamount stations, although *Sergestes armatus* was most abundant on off-seamount stations.

4.2 Univariate and multivariate assemblage patterns

There were significant differences in species richness between depths, on and off seamounts, and between hydrographic zones (Table 3), but not between diel cycle times. Species richness, and numerical abundance were both higher on seamounts (Table 3, Fig. 3). Species assemblage was significantly different on and off seamount, and between hydrographic zone (Table 3), but not between depth and diel cycle time.

Cluster analysis and SIMPROF identified 8 significant clusters (Fig. 4) at 54% similarity (π=5.4, p<0.1%). The two dimensional MDS ordination gave a stress index of 0.15, and was deemed sufficiently low to enable meaningful interpretations of ecological patterns (Fig. 5). Horizontal dispersion in multidimensional space appeared to be related to latitude, as samples towards the centre of the plot were mostly from TR and STC stations. The largest of these clusters (h) contained 17 samples from seamounts between 31.5° and 40°S, and all but two stations from the Subtropical Convergence region (STC) region (Table 1, Fig. 4 and 5). Cluster 'h' contained 65 % of seamounts stations overall and comprised mostly *Sergia prehensilis* and *Systellaspis debilis* (37 and 34 % respectively, see Fig. 6). The second largest (*n*=7), cluster 'c', consisted of three samples from the TR zone (station 2, 4), one from the STC zone (station 9), and two from the SAC zone (station 7 and 8) and comprised *S. debilis, Oplophorus novaezelandia, Sergestes corniculum* and *Oplophorus spinosus* (26, 21, 28, and 25 % respectively, Fig. 6). Cluster 'd' (*n*=3) was predominantly from the TR (station 2, 10), with a single station from the sub-Antarctic convergence zone (SAC). Cluster 'g'

consisted of two stations, one from the TR zone and one from the SAC zone (Fig. 4), and comprised mostly of *S. armatus* (80%, Fig. 6). Clusters 'a', 'b', and 'f' all consisted of either a single or two stations from the sub-Antarctic convergence (SAC) zone (station 7 or 8). Cluster 'e' comprised a single sample from the STC zone (station 6). Similarity (Bray-Curtis index) showed a very weak correlation with distance between samples and seamount (R^2 = 0.034, Fig. 7). The F statistics of the linear regression indicated that the slope was significantly different from 0 (p <0.001).

5 Discussion

Very little information exists on the deep-sea ecosystems of the Indian Ocean outside the Arabian Sea (Ingole and Koslow, 2005). Thus the majority of species caught in this study represent new records of occurrence. As the PERMANOVA results suggested that the numerical abundance, species richness, and species assemblage were all influenced by the properties of the water mass and the proximity to seamounts, this Discussion will be focussed around these two factors. The apparent low influence on clusters of depth strata and diel cycle position may be a result of the lack of opening/closing mechanisms utilised on the Åkratrawl on this cruise rather than true biological affects. Arguably, although the trawl was collapsed during deployments, there may still have been some fishing effect and hence some shallow water contamination. Typically, shallow-living species are more abundant than deeper living species (pelagic biomass decreases logarithmically with depth, Angel and Pugh, 2000), thus the Bray Curtis similarity measures could potentially be highly sensitive to biases imposed by this shortcoming. Nevertheless, previous studies that utilized opening/closing gears to consider effects of diel cycle on assemblage structure, have not detected diel cycle effects either (Letessier et al., 2011; Sutton et al., 2008). The studies of Letessier *et al.* (20011) and Sutton *et al.*

15

(2008) opted to analyse the effect of diel cycle and depth in their permutation test (ANOSIM) independently, and may therefore have failed to detect interactions between terms (for example, the effect of diel cycle on assemblages may be dependent upon depth). While we did not detect any interactions here, our analysis was conducted on different taxa, and on a smaller number of samples (n = 40, versus 115 and 167 for Sutton *et al.* and Letessier *et al.* respectively), so further study with larger sample sizes may be needed before the null hypothesis that diel cycle position does not influence assemblage structure across depth could be rejected.

5.1 Biogeography

High abundances of *Systellaspis debilis* and *Sergia prehensilis* were found throughout the survey area outside the sub-Antarctic convergence, and these species were dominant in the seamount cluster (e). This is not consistent with the findings of Vereshchaka (1995) who observed that both species showed decreased abundance with proximity to the seabed of seamounts and of the abyssal plains. While both species are pan-temperate (Poupin, 1998), *S. debilis* is reported to be less abundant over continental slopes than over seamounts (Vereshchaka, 1995). In the present study, *S. debilis* was caught in all the nets fished over the tropical abyssal plains (i.e. station 2), albeit in fewer numbers than over the seamounts. *S. debilis* has been shown to have a high benthic component to its diet compared to other shrimps (Rau et al., 1989), thus potentially explaining its affinity with seamounts.

Previously *Acanthephyra sica* has only been recorded from the sub-Antarctic front (Burukovsky and Romensky, 1982): the present study is the first to report this species north of 40º S (station 10, 32 ºS, north of Walter's Shoal). Several species were caught uniquely in the SA front, although they were not ubiquitous south of 40º S. Three species, were found uniquely on Coral seamount, *Pasiphae barnardi, Gennadas kempi,*

16

Funchalia danae but the SA front was not sampled sufficiently to distinguish whether these were associated solely with that seamount or - as seems more probable due to previous records in the SA front (Burukovsky and Romensky, 1982)- typical inhabitants of the SA front.

Observations of less similarity amongst samples south of 37ºS (of 8 significant clusters, 4 were restricted to > 37º S whereas no clusters were restricted to <37º, Fig. 6) suggest that this area is highly heterogeneous, typical for a frontal zone where there is substantial mesoscale eddy formation and mixing of water masses (Read et al., 2000): this dynamic physical-oceanographic regime is evident in observations of high sea surface height variance (Babu et al., 2011). Decapod abundance was highest in this area (~75 ind 10. ^{3} m^{-1}, station 5 and 6), which is consistent with previous findings (Pakhomov et al., 1999; 1994) and acoustic observations of watercolumn biomass made from the same cruise as net samples reported here were collected (P. Boersch-Supan, this volume). Southern stations (station 6 to 9) harboured several species typical of Antarctic waters and not observed in other areas in this study and thus indicating the influence of Antarctic faunas (Burukovsky and Romensky, 1982; A. Clarke and Holmes, 1987). It is likely that the difference in crustacean micronekton species distribution and assemblage across the SA front reflect major difference in mid-water biovolumes and production regimes, typical of difference observed across fronts elsewhere (e.g north Atlantic, see Cox et al., 2013).

5.2 Seamount effects

Following variability associated with hydrographic zones, the most important and consistent factor in determining species richness, numerical abundance, and species assemblage was proximity to seamount. The increased numerical abundance and species richness over seamounts is consistent with patterns observed on other micronekton taxa

17

(Wilson and Boehlert, 2004; sternopthychid fish, 1993) and of higher trophic levels such as marine mammals and commercially important species of fish (Genin, 2004; Haney et al., 1995; Morato et al., 2010; Pitcher and Bulman, 2007; Rogers, 1994), and supports the 'oasis' effect hypothesis of seamounts (McClain, 2007). We think it likely that our observations of this pattern are due to micronekton actively resisting advection away from seamounts (using their capacity for active locomotion). This is in contrast to biophysical mechanisms related to interactions between DVM behaviour and topographic trapping that influence the distribution of meso- and macrozooplankton such as euphausiids. Moreover, while observations of seabed foraging by euphausiids are not uncommon (Tarling and Johnson, 2006), evidence suggests that euphausiids are outcompeted or preyed upon in the vicinity of seamount and ridges (Letessier et al., 2011) probably by specialists nekton in the benthic boundary layer (Sutton et al., 2008), and that seabed foraging by euphausiids is favoured primarily during food-shortages or high predation pressure common in shallower waters (Schmidt et al., 2011). DVM trapping and other linkages between micronekton and seamounts through the diel cycle may be occurring, however, we were unable to detect such mechanism here.

A possible explanation for the observed increase in abundance and species richness is that the seamounts afford additional habitats (both pelagic and benthic) to the target taxa. Less than 200 of the world's ~4000 species of shrimps are considered truly pelagic (De grave et al., 2014), and SWIR seamounts could be acting as diversity sources from which species radiate out into the mid-water. Vereshchaka (1995) described mid-water communities caught only in the mid-water over seamounts at night, which were absent in daytime catches. He further suggested that organisms in these communities spent the daytime on or near the seabed, or in the sediments. Other organisms (such as the shrimp *S. debilis*) appeared to be seamount mid-water-specialist, that descend into the near-

bottom layer during the daytime. This behaviour ('habitat diversification') could theoretically be acting independently of DVM trapping behaviour, as no extra trophic input would be required, from advected zooplankton to sustain it. However, ubiquitous species that occupied both off-seamount and seamount locations were more abundant on seamounts (with the single exception of *Sergestes armatus*) suggesting that seamounts present favourable habitats for mid-water micronekton in general, in addition to being necessary habitat for seamount specialist (such as lophogastrids).

When quantifying possible bio-physical mechanisms responsible for the seamount 'oasis' effect our analysis did not enable differentiation between the relative importance of DVM trapping of meso-plankton prey or 'habitat diversification'. Other bio-physical mechanisms have been suggested as possibilities by which diversity/biomass on seamounts might be enhanced. These include localized upwelling (Uda and Ishino, 1958) leading to increased productivity (Samadi et al., 2006), and trapping by Taylor cones (Pitcher and Bulman, 2007). However, we suspect the influences of such processes to be relatively minor compared to the mechanism of DVM trapping and 'habitat diversification' mentioned above, because Taylor columns were not identified on the seamounts here, and primary control of circulation (and primary production) appeared to be eddy activity operating at the mesoscale (R. Pollard and Read, 2015).

Distinction of the relative important of DVM trapping of meso-plankton prey and 'habitat diversification' could potentially be elucidated by exploring deep seamounts (>1000 m) where DVM is less prevalent (the majority of DVM takes place in the meso-pelagic, see Angel and Pugh, 2000; Flock and Hopkins, 1992). If mid-water abundance and diversity of micronekton are primarily controlled by 'habitat diversification' we would expect the ubiquitous micronekton to be as- or less abundant on the seamount than they are in the mid-water. Although no paired on/off sampling of a deep seamount

was conducted in this study, our impression is that 'habitat diversification' is likely underestimated as a driver of mid-water abundance.

Similarity between samples appeared to be influenced only very weakly by distance (isolation) between samples. According to our model a distance of 1,000 km between two sites would cause a decrease in assemblage similarity of just 7.6%, suggesting that there is high connectivity at the level of the assemblage between seamounts. Moreover, only four species were reported at a single seamount location (*Pasiphaea ratbunae*, *Eusergestes cf antarcticus* and *Pasiphaea gelasinus, Gennadas brevirostris*), and these species have previously been recorded from non-seamount locations elsewhere (De grave et al., 2014). As 70% of the seamount samples clustered within a single cluster spanning almost 10° of latitude (with no apparent influence of diel cycle or depth strata) the statement of Gjerde and Breide (2003) 'Seamounts are areas of high endemic biodiversity with little overlap in community composition between seamount' may not pertain to the mid-water taxa explored here. Our observations can be interpreted in two ways:

1) Our results do not support the 'island' effect hypothesis of seamounts that states that seamounts are reproductively isolated, thus promoting endemism (see Koslow and Poore, 2000, and see McClain, 2007 for a review), a hypotheses that has gained support from other studies (de Forges et al., 2000; Gjerde and Breide, 2003; Samadi et al., 2006).

2) The taxa investigated in this study are poorly suited to explore the 'island' effect hypothesis because of their high capacity for swimming.

Investigation of reproductive connectivity between seamounts, using population genetics of ubiquitous species may further resolve this issue.

5.3 Conclusion

This study has revealed that the distribution and abundance of decapod shrimps and *lophogastrids* on high-sea fishing grounds in the SWIR is greatly influenced by the presence of seamounts, potentially through our proposed mechanism of 'habitat diversification'. Enhanced numerical abundance and species richness may be linked to either (a) active migration undertaken by individuals to maintain their proximity to the seabed on seamounts, which provides habitat, or (b) may be associated with biophysical mechanisms such as DVM trapping of mesozooplankton prey. The taxa considered in this study are an important component of demersal fish diet (Bergstad et al., 2010; Mauchline and Gordon, 2006), perhaps more so than diurnally migrating zooplankton, even on seamounts (Hirch and Christiansen, 2010). Elevated abundances of decapod shrimps and lophogastrids in the vicinity of seamounts may provide an important prey item, linking between pelagic and/or benthic ecosystems and the demersal/pelagic fish fauna (see Letessier et al., 2012; Reid et al., 2012). Ubiquitous mesopelagic crustaceans with a benthic component to their diet (such as *S. debilis*, and maybe some gnathophausiids) may hold a more important trophic position in seamount food webs than previously assumed, by making benthic energy sources available to higher and pelagic trophic levels, thus enforcing benthopelagic connectivity.

Conservation and holistic fishery management efforts on seamounts require good understanding of open ocean energy pathways and food webs, and should consider micronekton distribution and connectivity patterns from the micro- to mesoscale (1 to 100 km). The consideration of the influences of different seamount substrata on associated resident micronekton assemblage structure should be an important aspect of fishery management and conservation, particularly when mitigating anthropogenic activity such as bottom trawling and, in the future, potential mining operations that have

21

the capacity to impact water column processes because of suspension of sediments.

6 Acknowledgement

8 Reference

Anderson, M.J., 2001. A new method for non-parametric multivariate analysis of variance. Austral Ecology 26, 32–46.

Angel, M.V., Pugh, P.R., 2000. Quantification of diel vertical migration by micronektonic taxa in the northeast Atlantic. Hydrobiologia 440, 161–179–179. doi:10.1023/A:1004115010030

Babu, V.R., Somayajulu, Y.K., Anilkumar, N., Sudhakar, M., 2011. Geostrophic volume transport and eddies in the region of sub-tropical and sub-Antarctic waters south of Madagascar during austral summer (January-February) 2004. Current Science 100, 1044–1050.

Bensch, A., Gianni, M., Grébroval, D., Sanders, J.S., Hjort, A., 2008. Worldwide review of bottom fisheries in the high seas. FAO Fisheries and Aquaculture Technical Paper No. 522 Food and Agricultural Organisation of the UN, Rome, 145 pp.

Bergstad, O.A., Gjelsvik, G., Schander, C., Høines, A.S., 2010. Feeding ecology of Coryphaenoides rupestris from the Mid-Atlantic Ridge. PLoS ONE 5, e10453. doi:10.1371/journal.pone.0010453

Boehlert, G.W., 1988. Current-topography interactions at mid-ocean seamounts and the impact on pelagic ecosystems
. GeoJournal 16, 45–52.

Bray, J.R., Curtis, J.T., 1957. An Ordination of the Upland Forest Communities of Southern Wisconsin. Ecological Monographs 27, 326–349.

Burukovsky, R.N., Romensky, L., 1982. New findings of several species of shrimps and description of Pasiphaea natalensis. Zoologichesky Zhurnal 61, 1797–1801.

Clark, M.R., Vinnichenko, V.I., Gordon, J.D.M., Beck-Bulat, G.Z., Kukharev, N.N., Kakora, A.F., 2007. Large-scale distant-water trawl fisheries on seamounts, Seamounts: Ecology, Fisheries & Conservation. Blackwell Publishing, Oxford.

Clarke, A., Holmes, L.J., 1987. Notes on the Biology and Distribution of Pasiphae species from the Southern Ocean. British Antarctic Survey Bulletin 74, 17–30.

Clarke, K.R., Gorley, R.N., 2006. Primer v6: User Manual/Tutorial.

Collette, B.B., Paring, N.V., 1991. Shallow-water fishes of Walters Shoals, Madagascar Ridge. Bulletin of Marine Science 48, 1–22.

Colwell, R.K., Coddington, J.A., 1994. Estimating Terrestrial Biodiversity through Extrapolation. Philosophical Transactions of the Royal Society B: Biological Sciences.

Courchamp, F., Berec, L., Gascoigne, J., 2008. Allee effects in ecology and conservation. Environ Conserv.

Cox, M.J., Letessier, T.B., Brierley, A.S., 2013. Zooplankton and micronekton biovolume at the Mid-Atlantic Ridge and Charlie-Gibbs Fracture Zone estimated by multi-frequency acoustic survey. Deep Sea Research part II: Topical Studies in Oceanography 98, 269–278. doi:10.1016/j.dsr2.2013.07.020

de Forges, B.R., Koslow, J.A., Poore, G.C., 2000. Diversity and endemism of the benthic seamount fauna in the southwest Pacific. Nature 405, 944–947. doi:10.1038/35016066

De grave, S., Pentcheff, N.D., Ahyong, S.T., Chan, T.-Y., Crandall, K.A., Dworschak, P.C., Felder, D., Feldmann, R.M., Fransen, C.H.J.M., Lemaitre, R., Low, M.E.Y., Martin, J.W., Ng, P.K.L., Schweitzer, C.E., Tan, S.H., Tshudy, D., Wetzer, R., 2014. A Classification of living and fossil genera of decapod crustaceans. Raffles Bulletin of Zoology 21, 1–109.

de L Wenneck, T., Falkenhaug, T., Bergstad, O.A., 2008. Strategies, methods, and technologies adopted on the R.V. G.O. Sars MAR-ECO expedition to the Mid-Atlantic Ridge in 2004. Deep Sea Research part II: Topical Studies in Oceanography 55, 6–28. doi:10.1016/j.dsr2.2007.09.017

Dick, H., 1998. Indian Ocean's Atlantic Bank yields deep-Earth insight. Oceanus 41.

Flock, M., Hopkins, T.L., 1992. Species Composition, Vertical Distribution, and Food Habits of the Sergestid Shrimp Assemblage in the Eastern Gulf of Mexico. Journal of Crustacean Biology 12, 210–223.

Fox, J., Weisberg, S., 2011. An R Companion to Applied Regression. SAGE Publications.

Genin, A., 2004. Bio-physical coupling in the formation of zooplankton and fish aggregations over abrupt topographies. Journal of marine systems 50, 3–20. doi:10.1016/j.marsys.2003.10.008

Gjerde, K.M., Breide, C., 2003. Towards a strategy for high seas marine protected areas. Proceedings of the IUCN, WCPA, and WWF Experts' Workshop on High Seas Marine Protected Areas, 15 to 17 January 2003,Malga, Spain, IUCN, Gland, Switzerland.

Gotelli, N.J., Colwell, R.K., 2001. Quantifying biodiversity: procedures and pitfalls in the measurement and comparison of species richness. Ecology Letters 4, 379–391. doi:10.1046/j.1461-0248.2001.00230.x

Haney, J.C., Haury, L.R., Mullineaux, L.S., Fey, C.L., 1995. Sea-bird aggregation at a deep North Pacific seamount. Marine Biology 123, 1–9. doi:10.1007/BF00350317

Hargreaves, P.M., 1985. The Distribution of Mysidacea in the Open Ocean and near-

Bottom over Slope Regions in the Northern Northeast Atlantic-Ocean During 1979. Journal of Plankton Research 7, 241–261.

Heino, M., Porteiro, F.M., Sutton, T., Falkenhaug, T., Godo, O.R., Piatkowski, U., 2011. Catchability of pelagic trawls for sampling deep-living nekton in the mid-North Atlantic. ICES Journal of Marine Science 68, 377–389. doi:10.1093/icesjms/fsq089

Hirch, S., Christiansen, B., 2010. The trophic blockage hypothesis is not supported by the diets of fishes on Seine Seamount. Marine Ecology 31, 107–120. doi:10.1111/j.1439-0485.2010.00366.x

Horn, P.L., Forman, J., Dunn, M.R., 2010. Feeding habits of alfonsino Beryx splendens. Journal of Fish Biology 76, 2382–2400. doi:10.1111/j.1095-8649.2010.02630.x

Ingole, B., Koslow, J.A., 2005. Deep-sea ecosystems of the Indian Ocean. Indian Journal of Marine Sciences 34, 27–34.

Isaac, J.D., Schwarzlose, R.A., 1965. Migrant sound scatterers: Interaction with the seafloor. Science 150, 1810–1813.

Johannesson, K., 1988. The paradox of Rockall: why is a brooding gastropod (Littorina saxatilis) more widespread than one having a planktonic larval dispersal stage (L. littorea). Marine Biology 99, 507–513.

Kar, T.K., Ghosh, B., 2013. Sustainability and economic consequences of creating marine protected areas in multispecies multiactivity context. J. Theor. Biol. 318, 81–90. doi:10.1016/j.jtbi.2012.11.004

Koslow, J.A., Boehlert, G., Gordon, J., Lorance, P., Parin, N., 2000. Continental slope and deep-sea fisheries: implications for a fragile ecosystem. ICES Journal of Marine Science 57, 548–557.

Kostianoy, A., Ginzburg, A.I., Frankignoulle, M., Delille, B., 2004. Fronts in the Southern Indian Ocean as inferred from satellite sea surface temperature data. Journal of marine systems 45, 55–73. doi:10.1016/j.jmarsys.2003.09.004

Letessier, T.B., Falkenhaug, T., Debes, H., Bergstad, O.A., Brierley, A.S., 2011. Abundance patterns and species assemblages of euphausiids associated with the Mid-Atlantic Ridge, North Atlantic. Journal of Plankton Research 33, 1510–1525. doi:10.1093/plankt/fbr056

Letessier, T.B., Pond, D.W., McGill, R.A.R., Reid, W.D.K., Brierley, A.S., 2012. Trophic interaction of invertebrate zooplankton on either side of the Charlie Gibbs Fracture Zone / Subpolar Front of the Mid-Atlantic Ridge. Journal of marine systems 94, 174–184. doi:10.1016/j.jmarsys.2011.11.020

Longhurst, A.R., 1998. Ecological geography of the sea.

Mauchline, J., Gordon, J.D.M., 2006. Oceanic Pelagic Prey of Benthopelagic Fish in the Benthic Boundary-Layer of a Marginal Oceanic Region. Mar. Ecol. Prog. Ser. 74, 109–115.

McClain, C.R., 2007. Seamounts: identity crisis or split personality? J Biogeography 34, 2001–2008. doi:10.1111/j.1365-2699.2007.01783.x

Meland, K., Aas, P.O., 2013. A taxonomical review of the Gnathophausia (Crustacea, Lophogastrida), with new records from the northern mid-Atlantic ridge. Zootaxa 3664, 199–225. doi:10.11646/zootaxa.3664.2.5

Morato, T., Hoyle, S.D., Allain, V., Nicol, S.J., 2010. Seamounts are hotspots of pelagic biodiversity in the open ocean. Proc Natl Acad Sci U S A 107, 9707–9711. doi:10.1073/pnas.0910290107/-/DCSupplemental/pnas.200910290SI.pdf

Oksanen, J., 2011. Multivariate analysis of ecological communities in R: vegan tutorial. R package version.

Pakhomov, E.A., Perissinotto, R., Froneman, P.W., 1999. Predation impact of

carnivorous macrozooplankton and micronekton in the Atlantic sector of the Southern Ocean. Journal of marine systems 19, 47–64. doi:10.1016/S0924-7963(98)00023-2

Pakhomov, E.A., Perissinotto, R., McQuaid, C.D., 1994. Comparative structure of the macrozooplankton micronekton communities of the subtropical and Antartic Polar fronts. Mar. Ecol. Prog. Ser. 111, 155–169.

Pitcher, T.J., Bulman, C., 2007. Raiding the larder: a quantitative evaluation framework and trophic signature for seamount food webs, Seamounts: Ecology, Fisheries & Conservation.

Pollard, R., Read, J., 2015. Circulation, stratification and seamounts in the South West Indian Ocean. Deep Sea Research part II: Topical Studies in Oceanography 1–17. doi:10.1016/j.dsr2.2015.02.018

Poupin, J., 1998. Crustacea Decapoda and Stomatopoda of French Polynesia. Atoll Research Bulletin 451, 62.

Rau, G., Heyraud, M., Cherrry, R., 1989. 15N/14N and 13C/12C in mesopelagic shrimp from the northeast Atlantic Ocean: evidence for differences in diet. Deep-Sea Research Part a-Oceanographic Research Papers 36, 1103–1110. doi:10.1016/0198-0149(89)90080-0

Read, J.F., Lucas, M., Holley, S., Pollard, R., 2000. Phytoplankton, nutrients and hydrography in the frontal zone between the Southwest Indian Subtropical gyre and the Southern Ocean. Deep Sea Research Part I: Oceanographic Research Papers 47, 2341–2368.

Read, J.F., Pollard, D.A., n.d. An introduction to the physical oceanography of six seamounts in the Southwest Indian Ocean. Deep-Sea Research II: Topical studies in Oceanograph.

Reid, W., Wigham, B.D., McGill, R., Polunin, N., 2012. Elucidating trophic pathways in benthic deep-sea assemblages of the Mid-Atlantic Ridge north and south of the Charlie-Gibbs Fracture Zone. Mar. Ecol. Prog. Ser. 463, 89–103. doi:10.3354/meps09863

Rogers, A.D., 1994. The Biology of Seamounts. Advances in marine biology 30, 305–350.

Rogers, A.D., Alvheim, O., Bemanaja, E., Benivary, D., Boersch-Supan, P.H., Bornman, T., Cedras, R., Plessis, Du, N., Gotheil, S., Hoines, A.S., Kemp, K., Kristiansen, J., Letessier, T.B., Mangar, V., Mazungula, N., Mørk, T., Pinet, P., Read, J.F., Sonnekus, T., 2009. Cruise Report "Dr. Fritjof Nansen" Southern Indian Ocean Seamounts (IUCN/UNDP/ASCLME/NERC/EAF/Nansen Project 2009 Cruise 410) 12th November - 19 December, 2009. Institute of Marine Research, Reports on surveys with the R/V Dr Fritdjof Nansen 2009410.

Romanov, E.V., 2003. Summary and Review of Soviet and Ukrainian scientific and commercial fishing operations on the deepwater ridges of the Southern Indian Ocean. Fao Fisheries Circular 991, 84.

Samadi, S., Bottan, L., Macpherson, E., 2006. Seamount endemism questioned by the geographic distribution and population genetic structure of marine invertebrates. Marine Biology 149, 1463–1475.

Schmidt, K., Atkinson, A., Steigenberger, S., Fielding, S., Lindsay, M.C.M., Pond, D.W., Tarling, G.A., Klevjer, T.A., Allen, C.S., Nicol, S., Achterberg, E.P., 2011. Seabed foraging by Antarctic krill: Implications for stock assessment, bentho-pelagic coupling, and the vertical transfer of iron. Limnol. Oceangr. 56, 1411–1428. doi:10.4319/lo.2011.56.4.1411

Sestak, Z., 1974. Book review Zeitschel, B. (ed.): The biology of the Indian ocean.

Biologia Plantarum 16, 549.

Steedman, H.F., 1976. General and applied data on formaldehyde fixation and preservation of marine zooplankton, Zooplankton fixation and preservation.

Stephens, P.A., Sutherland, W.J., Freckleton, R.P., 1999. What Is the Allee Effect? Oikos 87, 185–190. doi:10.2307/3547011?ref=no-x-route:5ad96ff0b712dca93478d64db8ab7694

Stowasser, G., McAllen, R., Pierce, G.J., Collins, M.A., Moffat, C.F., Priede, I.G., Pond, D.W., 2009. Trophic position of deep-sea fish—Assessment through fatty acid and stable isotope analyses. Deep Sea Research Part I: Oceanographic Research Papers 56, 812–826. doi:10.1016/j.dsr.2008.12.016

Sutton, T., Porteiro, F.M., Heino, M., Byrkjedal, I., Langhelle, G., Anderson, C.I.H., Horne, J., Soiland, H., Falkenhaug, T., Godo, O.R., Bergstad, O.A., 2008. Vertical structure, biomass and topographic association of deep-pelagic fishes in relation to a mid-ocean ridge system. Deep Sea Research part II: Topical Studies in Oceanography 55, 161–184.

Sutton, T.T., 2013. Vertical ecology of the pelagic ocean: classical patterns and new perspectives. Journal of Fish Biology 83, 1508–1527. doi:10.1111/jfb.12263

Tao, C.J., Lin, S., Guo, Y.J., Chen, G.W.X., Han, C.R., German, D.R., Yoerger, J., Zhu, N., Zhou, X., Su, E.T., Baker, T., Party, A.D.-1.S., 2007. First discovery and investigation of a high-temperature hydrothermal vent field on the ultra-slow spreading Southwest Indian Ridge. EOS Trans AGU, Fall Meet Suppl, Abstract T52B-07.

Tarling, G.A., Johnson, M.L., 2006. Satiation gives krill that sinking feeling. Current Biology 16, R83–R84. doi:10.1016/j.cub.2006.01.044

Team, R.C., 2012. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. ISBN 3-900051-07-0, URL. … to R Notes on R: ….

Uda, M., Ishino, M., 1958. Enrichment pattern resulting from eddy systems in relation to fishing grounds. Journal of Tokyo University Fisheries 44, 105–120.

Vereshchaka, A.L., 1995. Macroplankton in the near-bottom layer of continental slopes and seamounts. Deep Sea Research Part I: Oceanographic Research Papers 42, 1639–1668. doi:10.1016/0967-0637(95)00065-E

Vierros, M., Cresswell, I., Escobar-Briones, E., Rice, J., Ardron, J., IOC, 2008. Global open oceans and deep seabed (GOODS): biogeographic classification; IOC. Technical series; Vol.:84; 2009. Oceans 1–96.

Wilson, C.D., Boehlert, G., 1993. Population biology of Gnathophausia longispina (mysidacea: Lophogastrida) from a central north pacific seamount. Marine Biology 115, 537–543. doi:10.1007/BF00349360

Wilson, C.D., Boehlert, G., 2004. Interaction of ocean currents and resident micronekton at a seamount in the central North Pacific. Journal of marine systems 50, 39–60. doi:10.1016/j.jmarsys.2003.09.013

Yesson, C., Clark, M.R., Taylor, M.L., Rogers, A.D., 2011. The global distribution of seamounts based on 30-second bathymetry data. Deep Sea Research Part I: Oceanographic Research Papers 58, 453–442. doi:10.1016/j.dsr.2011.02.004

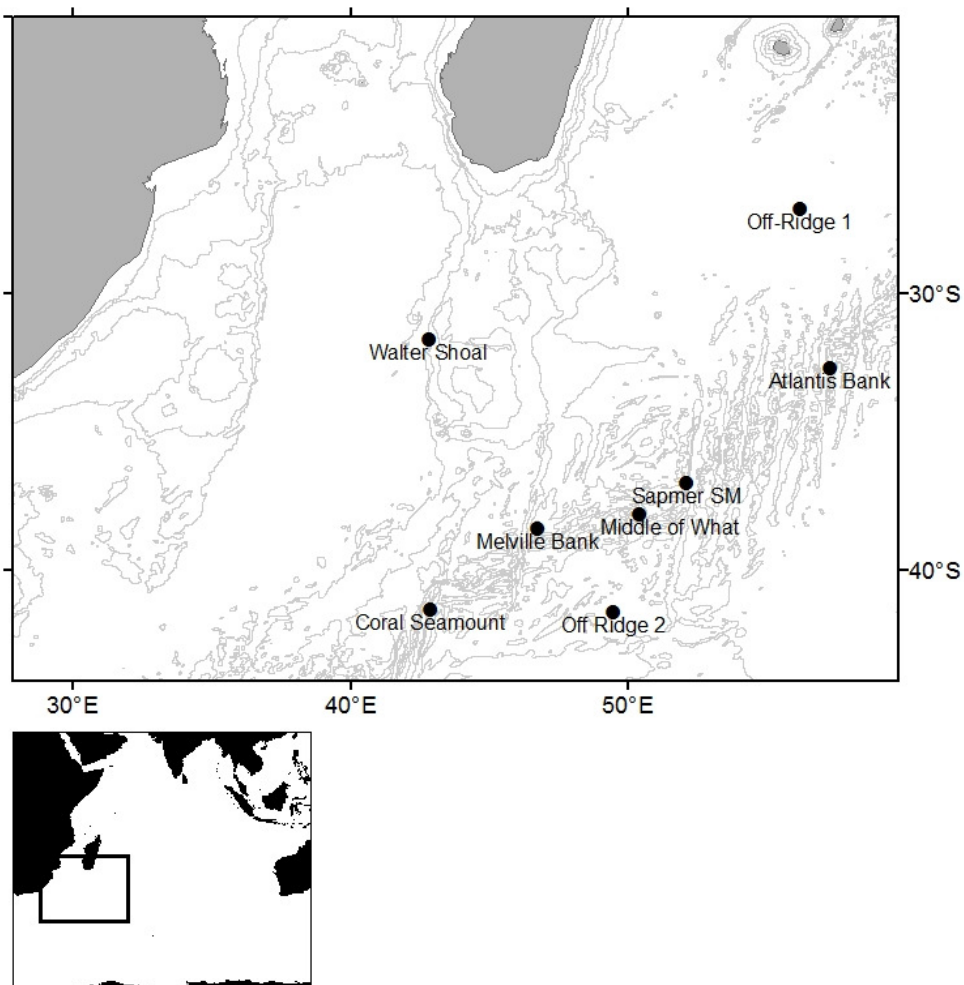Zeitzschel, B., 1973. The biology of the Indian Ocean. Ecological studies 3 549.

7 Figure

Fig.1 Map of survey area and stations. See Table 1 for station activity. The 500, 1000, 2000, 3000, 4000 m isobaths are shown.
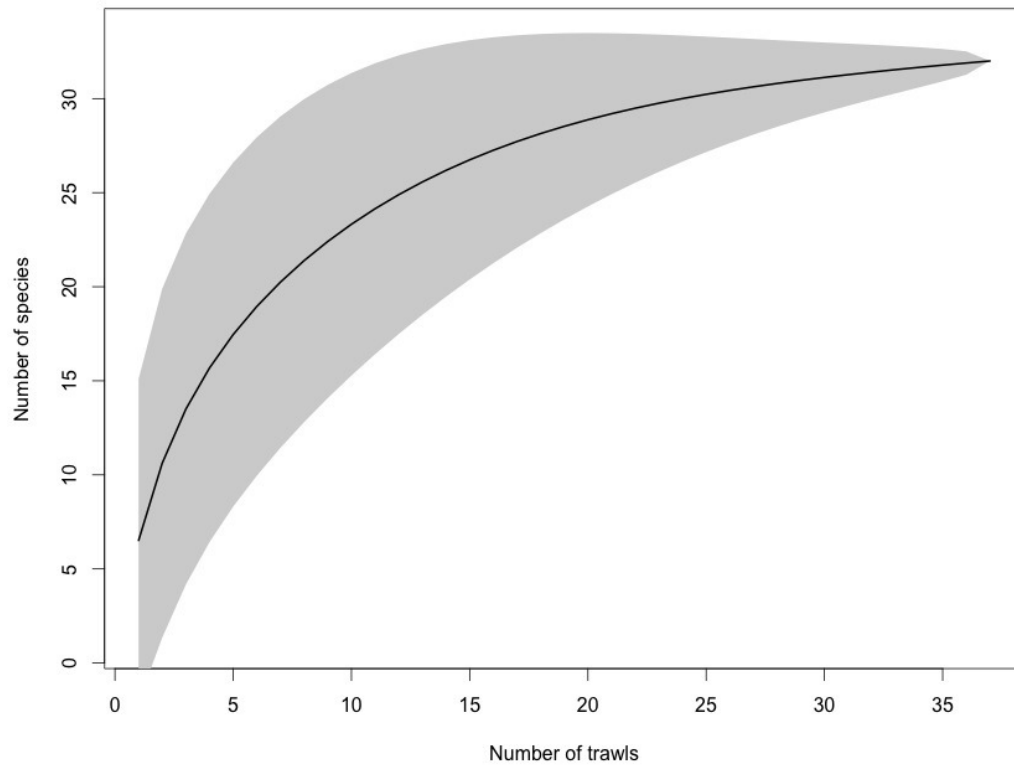
Fig 2 Species accumulation curve for the 37 Åkratrawls conducted at all locations. Shaded areas indicate the standard deviation.
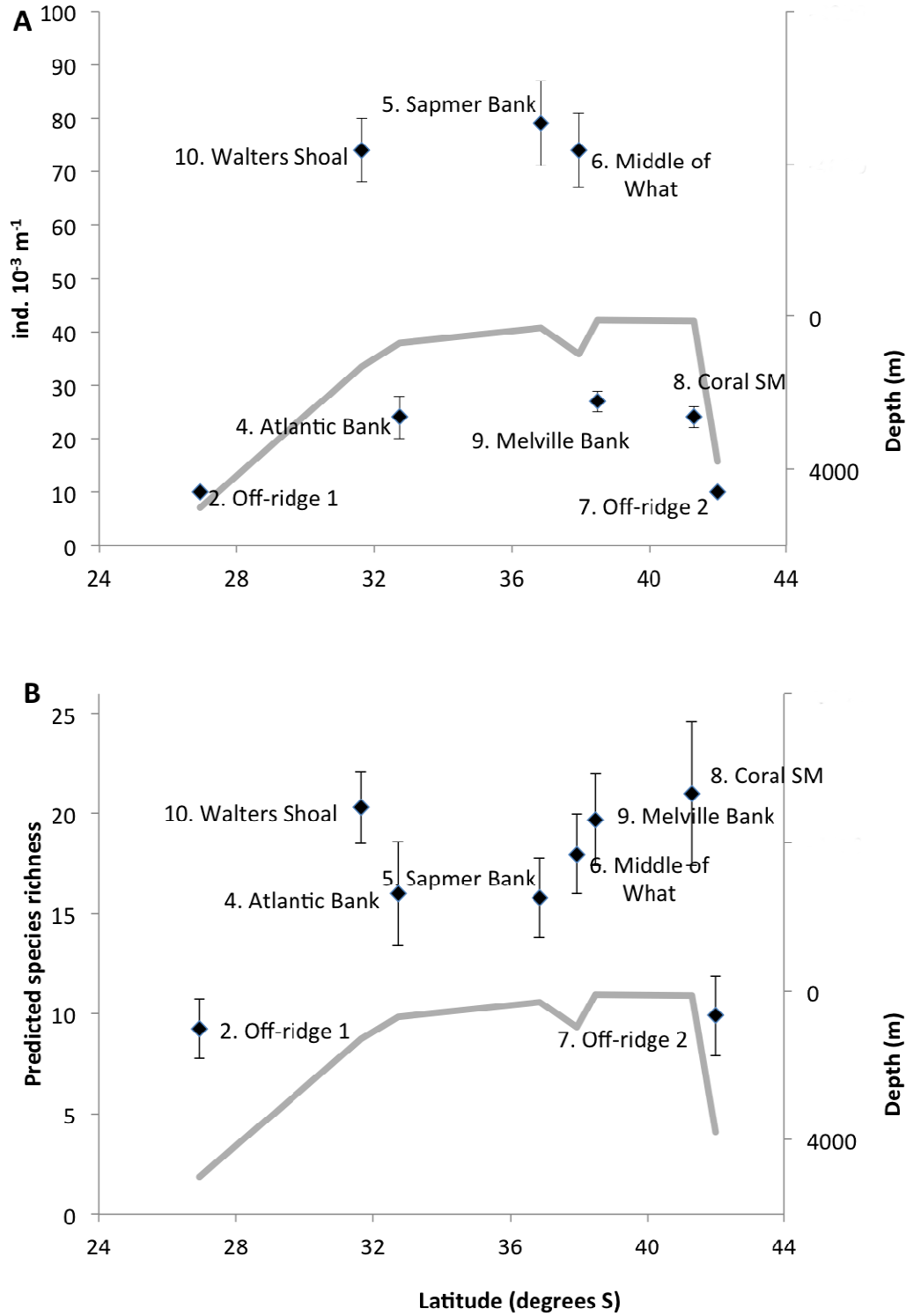
Fig. 3 Micronekton crustacean numerical abundance (A. mean ± SE ind.10^3 m^{-1}), predicted species richness (B. Bootstrapped values ±SE), and seamount summit depth (gray line, in m) per stations.
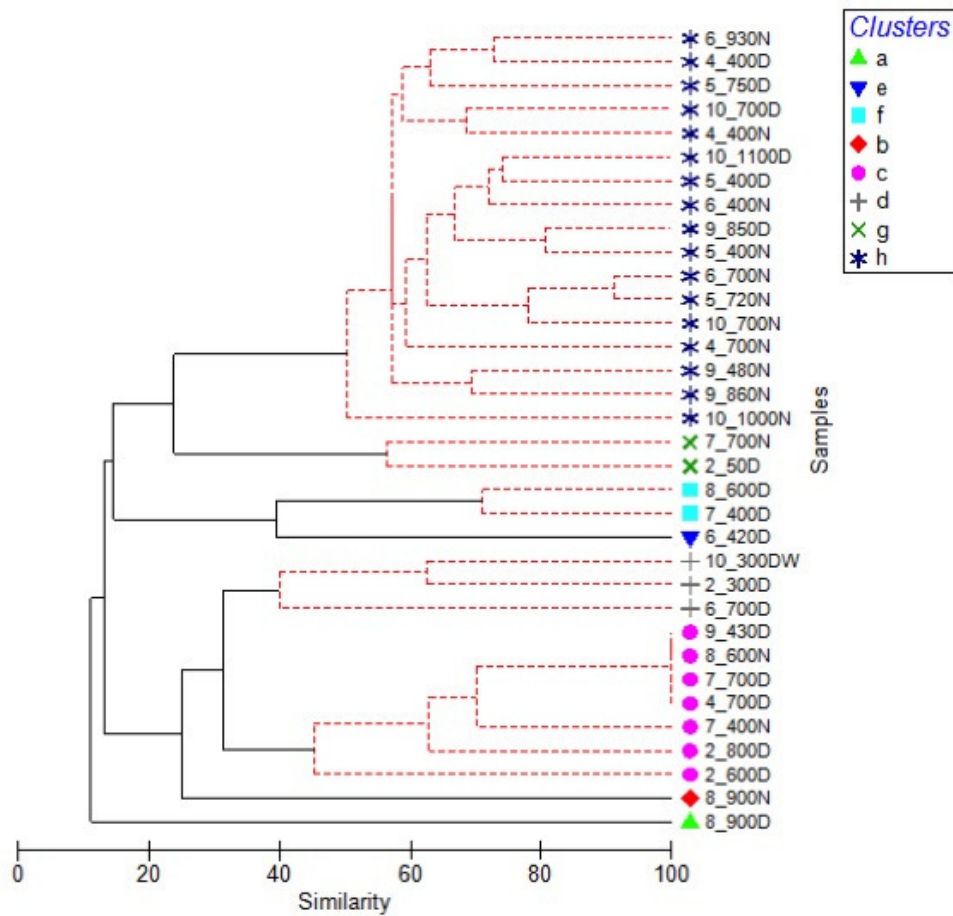
Fig. 4 Cluster analysis dendrogramme based on square root transformed species density data, and characteristics of samples in significant clusters (SIMPROF): depth (m), Diel cycle (D/N/DW).

Fig. 5 Non-metric multidimensional scaling ordination (MDS) of root transformed density estimates in individual net samples. Overlayed are significant clusters 'a-h' (A), resulting from the SIMPROF classification analysis (see text for explanation), hydrographic zone (B), and seamount presence (yes or no, C).

31

Fig. 6 Species assemblage composition (averaged amongst cod-ends; assemblage 'd',

'c', 'h') and latitudinal extend of assemblage.

Fig. 7 Relationship between Bray-Curtis index of similarity and distance between individual samples on seamounts.

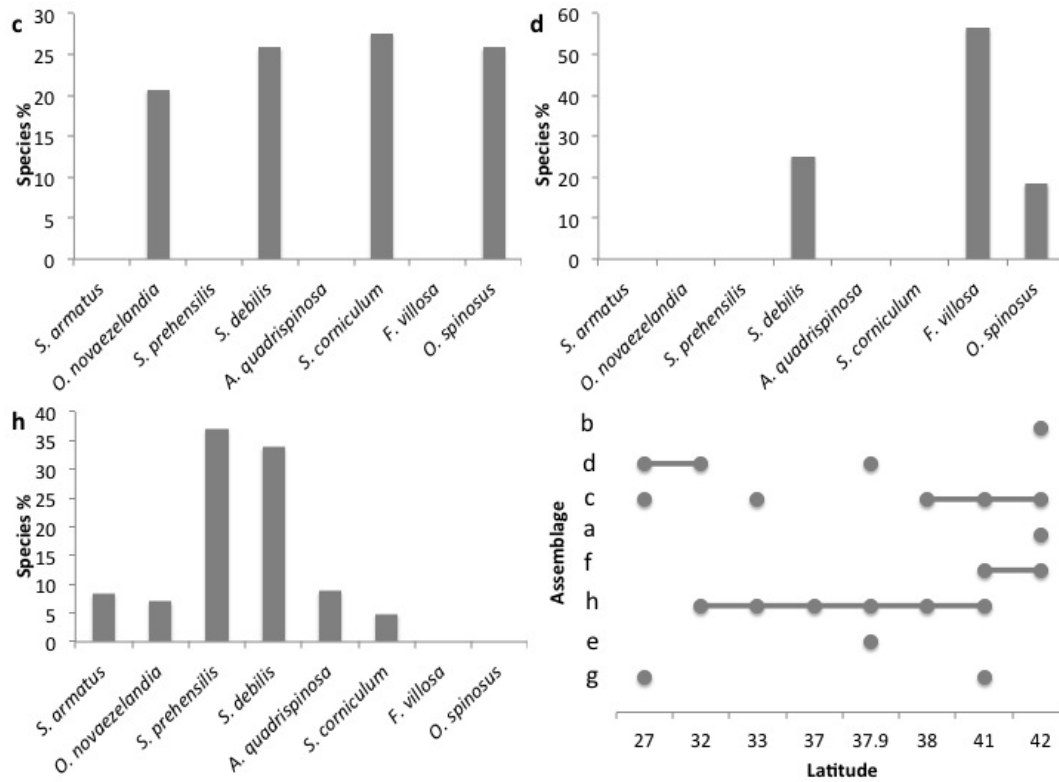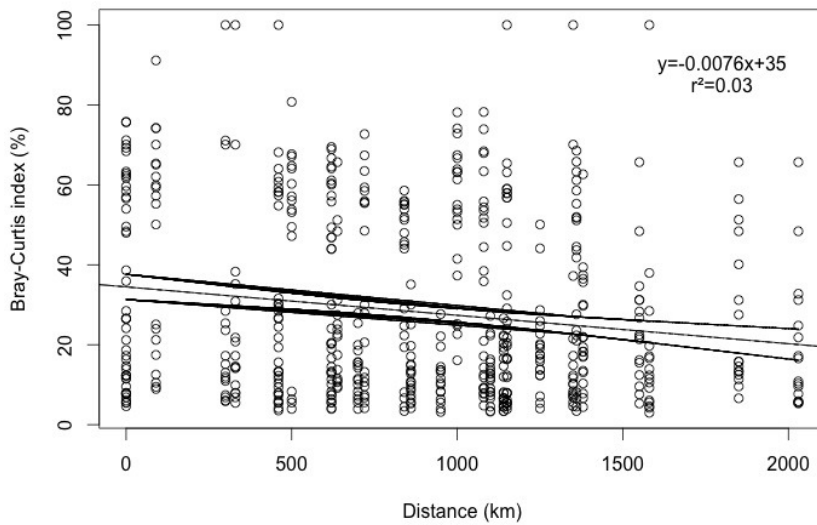Table 1 Trawl activity on the R/V *Fridtjof Nansen* Cruise 2009-410

Stations	Latitude (deg S)	Longitude	Depth (m), Day, Night, Dawn 5(D,N, DWN)	Hydrographic region (Kostianov, et al. 2004): Tropical (TR), Subtropical convergence (STC), sub-Antarctic front (SA)	Target loc
2	26.94	56.23	50D, 300D, 600D, 800D	TR	Off-Ridge
4	32.72	57.29	700D, 400D[+], 700N, 400N, 740DW*	TR	Atlantis B
5	36.86	52.05	750D, 400D, 720N, 400N, 500N*, 750DW*	STC	Sapmer B
6	37.95	50.37	700N, 400N, 930N, 700D, 420D	STC	Middle of
7	41.48	49.53	700N, 400N, 700D, 400D[+]	SA	Off-Ridge
8	41.42	42.9	900D, 600D, 900N, 600N, 270DW*	SA	Coral Sea
9	38.5	46.75	860N, 480N, 320DW*, 850D, 430D[+], 560D*	STC	Melville E
10	31.64	42.83	700N, 1100N, 300DW, 1100D, 700D	TR	Walters S

*Benthic trawl

[+]Negative trawls

Table 2 Micronektic crustacean species sampled in association with the South West Indian Ocean Ridge (26-42 °S). Station locations given in Table 1 and Fig. 1. Column headings need sorting

Species	Authority	Number of specimens collected (C_y)	e^{a-y} Closest taxon to which relative catchability coefficient	True catches (C_x)	Latitudinal range (deg S)	Longitudinal range (deg E)	Stations at which species was recorded

33

				exists (from Heino et al 2011)					
Sergia prehensilis	(Bate, 1881)	2092	0.90	*Sergia* sp	2306	27-38.5	57-42	2.800D, 4.400, 5.750D, 5.720N, 5.500N, 6.700N, 6.930N, 8.900D, 8.643N, 9.480N, 10.700N, 10.1100D,	4.700N, 4.740DW, 5.400D, 5.400N, 5.750DW, 6.400N, 6.700D, 8.600D, 9.860N, 9.850D, 10.1100N, 10.700D
Systellaspis debilis	(A. Milne-Edwards, 1881)	1392	0.75	*S. debilis*	1834	27-38.5	57-42	2.600D, 2.50D, 4.700N, 4.740DW, 5.400D, 5.400N, 5.750DW, 6.400N, 6.700N, 9.480N, 10.700N, 10.300N, 10.700D	2.300D, 2.800D, 4.400N, 5.750D, 5.720N, 5.500N, 6.700N, 6.930N, 9.860N, 9.850D, 10.1100N, 10.1100D,
Parasergest es armatus	(Krøyer, 1855)	96	0.20	*Sergestes* sp	457	27-38.5	57-42	2.600D, 5.400D, 5.750DW, 6.700D, 8.900N, 9.850D,10.700N	4.700D, 5.400N, 6.400N, 7.400N, 9.860N,
Acanthephy ra quadrispino sa	Kemp, 1939	118	0.57	*Acantheph yra* sp	205	32.8-41.5	57.3-42.8	4.700N, 5.400N, 5.750N, 6.700N, 8.600D, 10.700N,10.1100D	4.740DW, 5.500DW, 6.400N, 6.930DW,
Oplophorus novaezelan diae	(De Man, 1931)	208	1.60	*Oplophoru s* sp	129	27-38.5	57-42	2.300D, 4.400N, 6.700N, 6.930N, 6.420D, 7.700N, 9.860N, 9.850D	4.700N, 4.740DW, 6.400N, 6.700D, 7.700D, 8.900D, 9.480N,
Eusergestes cf antarctica	(Verescha ka, 2009)	25	0.20	*Sergestes* sp	119	41.5	43	8.600D	
Funchalia villosa	(Bouvier, 1905)	93	NA(1)	NA	93	27-38.5	57-42	2.800D, 4.400N, 4.700N, 6.700N,	2.50D, 4.400N, 4.740DW, 6.400N,

								6.420D, 9.480N, 10.700N, 10.300N, 10.1100D, 10.700D
Petalidium folicea	Bate, 1881	19	0.20	*Sergestes* sp	90	38-42	50-43	7.700N, 8.900D, 8.900N,9.860N
Acanthephyra sica	Bate, 1888	40	0.57	*Acantheph yra* sp	70	31-41	43-49	7.700N, 8.900D, 8.900N, 10.1100D
Gennadas gilchristi	Calman, 1925	43	0.75	*Gennadas* sp	57	31-42	50-43	6.700D, 8.900D, 8.900N, 9.860N, 9.850D, 10.700N
Deosergeste s corniculum	(Krøyer, 1855)	384	8.40	*S. corniculu m*	46	27-38.5	57-42	2.600D, 2.300D, 2.300D,4.700D, 4.740DW, 5.400D, 5.720N, 5.400N, 5.750DW, 6.700N, 6.400N, 6.930N, 6.700D, 7.700N, 8.900D, 9.860N, 9.480N, 9.850D,10.700N,10.1 100N, 10.1100D,10.700D
Pasiphaea diaphana	Burukovs ky & Romensk y, 1980	99	2.51	*Pasiphaea* sp	39	27-38.5	57-42	6.700N, 6.930N(c.f), 8.900N, 9.850D, 5.720D(c.f), 5.400N(c.f), 5.750DW(c.f) 9.480N(c.f), 10.700N (c.f), 4.700N (c.f), 6.700N, 9.860N, 10.300N, 10.1100D, 4.740DW, 5.750DW
Gnathopha usia ingens	(Dohrn, 1870)	39	NA(1)	NA	39	27-38.5	57-42	4.740DW, 5.750DW, 6.700N, 6.930N, 8.900D, 8.900N, 9.860N, 9.850D, 10.1100N, 10.300N, 10.1100D, 10.700N
Pasiphaea romenskyi	Burukovs ky, 1995	73	2.51	*Pasiphae* sp	29	33-42	58-50	7.700N(c.f), 4.400N, 5.400N, 4.700N, 4.400D
Oplophorus spinosus	(Brullé, 1839)	37	1.66	*O. spinosus*	22	27-38.5	57-42	2.50D, 2.300D, 2.800D, 4.700N, 4.400N, 4.740DW, 9.480N, 10.700N, 10.300N, 10.700D
Pasiphaea rathbunae	(Stebbing, 1914)	50	2.51	*Pasiphaea* sp	20	42	50-43	7.400N, 7.700N, 8.900D, 8.900N,
Gennadas kempi	Stebbing, 1914	11	0.75	*Gennadas* sp	14	41.5	43	8.900D, 8.900N
Sergia potens	(Burkenro ad, 1940)	12	0.90	*Sergia* sp	13	38-42	47.5-43	8.900D, 8.900N, 9.850D

Pasiphaea gelasinus	Hayashi & Yaldwyn, 1998	27	2.51	*Pasiphaea* sp	11	38.5	46.75	9.480N(c.f)
Gennadas propinquus	Rathbun, 1906	8	0.75	*Gennadas* sp	11	37-38.5	47-52	5.400N, 6.400N, 9.480N
Notostomus auriculatus	Barnard, 1950	7	0.66	*Notostomus* sp	11	38-41.5	50-43	6.700N, 6.930N, 8.900N, 9.850D
Eupasiphae gilesii	(Wood-Mason, 1892)	11	NA(1)	NA	11	31-42	50-43	6.930N, 10.700N, 8.900D, 8.900N, 10.1100D
Stylopandalus richardi	(Coutière, 1905)	9	NA	NA	9	27-37	57-43.5	5.400D, 5.400N, 2.300D, 10.700D, 4.700N
Pasiphaea barnardi	Yaldwyn, 1971	21	2.51	*Pasiphae* sp	8	41.5	43	8.900N, 8.643N
Meningodora vesca	(Smith, 1886)	4	0.52	*M. vesca*	8	38-32	50-43	6.700N, 6.930N, 10.1100N, 10.1100D
Parapasiphae sulcatifrons	Smith, 1884	6	0.89	*P. sulcatifrons*	7	38-41.5	50-43	6.930N(c.f), 8.900N(c.f), 10.1100N, 1100D
Funchalia danae	Burkenroad, 1940	4	NA(1)	NA	4	41.5	43	8.900D, 8.600D, 8.900N
Gennadas capensis	Calman, 1925	3	0.75	*Gennadas* sp	4	32-33	57.5-43	4.700N, 10.1100D
Gnathophausia zoea	Willemoes-Suhm, 1875	3	NA(1)	NA	3	32.8-41.5	57.3-42.8	4.700N, 8.900D, 8.900N
Gennadas brevirostris	Bouvier, 1905	1	0.75	*Gennadas* sp	1	37	52	5.400N
Gnathophausia gracilis	Willemoes-Suhm, 1875	1	NA(1)	NA	1	32	43	10.1100D

Table 3 PERMANOVA results for predicted total numerical abundance, species richness, and species assemblage composition on and off seamount, in different hydrographic regions, and at different times of day.

Source	d.f	Numerical abundance			Predicted species richness			Species assemblage		
		MS	Pseudo-F	P(perm)	MS	Pseudo-F	P(perm)	MS	Pseudo-F	P(perm)
Seamount (Yes/No)	1	0.80	3.66	0.017	0.44	2.73	0.019	1.29	4.38	0.0009
Hydrographic zone	2	0.28	1.27	0.093	1.32	4.08	0.0001	0.59	2.03	0.029
Diel	2	0.31	1.43	0.18	0.59	1.83	0.051	0.36	1.25	0.22
Depth	2	0.41	1.87	0.09	0.96	2.96	0.0027	0.46	1.59	0.089
Residual	29	0.21			0.16			0.29		
Total	36									