

ORIGINAL ARTICLE

Squat lobster assemblages on seamounts differ from some, but not all, deep-sea habitats of comparable depth

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Keywords

Beta-diversity; community composition; deep-sea; seamounts; squat lobsters.

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Accepted: 2 April 2010

doi:10.1111/j.1439-0485.2010.00374.x

Abstract

This study was carried out to test the hypothesis that benthic communities on seamounts are distinct from those of other deep-sea habitats at comparable depths. Analysis of the squat lobster fauna of deep-sea habitats in the Southwestern Pacific revealed that the species composition of assemblages on seamounts was not statistically dissimilar from assemblages on slope and plateau habitat at comparable depths. However, compositional differences were observed between seamount and rise and ridge habitat. Differences in assemblage composition between seamount and ridge habitat were statistically significant for two of the four ridge systems examined. Assemblages on seamounts that were distinct from non-seamount ridge habitat were typically dominated by small-bodied species with an abbreviated larval stage. Various environmental variables were correlated with the observed assemblage patterns observed; depth-related variables may account for differences between seamount and rise assemblages, whilst differences in POC flux likely play a role in determining the assemblage compositional patterns between seamount and non-seamount ridge habitat. Extensive pre-analysis data treatment was required to ensure that multivariate analyses of assemblage data from seamount and non-seamount habitats were robust. Our results confirm the findings of recent studies that found no compositional differences in assemblages from seamount and slope habitats, and support the idea that dissimilarity between seamount assemblages on different ridge systems increases with geographic distance. Further research will be required before the generality of these findings can be confirmed.

Introduction

Not long after the first detailed geological descriptions of seamounts (Hess 1946), biologists began to speculate that the composition of biotic communities in such environments might differ from other deep-sea habitats (Hubbs 1959). Early investigations of benthic assemblages on seamounts suggested that levels of endemism were relatively

high (Wilson & Kaufman 1987), thereby establishing a generalization that benthic communities on seamounts are distinct. This assertion was strongly supported by Richer de Forges *et al.* (2000), who showed that fish and invertebrate communities of seamounts on adjacent ridges in the Southwestern Pacific differed markedly at scales of 1000 km. Since then, researchers have sought to determine whether benthic communities on seamounts are

also dissimilar from other habitats. More recent studies have examined the species richness, endemism and or genetic population structure components of communities, rather than overall compositional characteristics, and how they might differ (*i.e.* beta-diversity or species turnover) among seamounts and other habitats (*e.g.* Samadi *et al.* 2006; O'Hara 2007). A few notable exceptions exist. First, Hall-Spencer *et al.* (2007) found that, on average, the composition of coral assemblages on North Atlantic seamounts were dissimilar to assemblages on island and slope habitats, but that only the taxonomic distinctness of coral assemblages on isolated oceanic seamounts and islands was consistently different from the expected taxonomic distinctness of the regional species pool. Secondly, O'Hara *et al.* (2008) found that only ophiuroid assemblages associated with coral matrix on seamounts were dissimilar in composition from assemblages not associated with biogenic habitat on slope and other seamounts (which were similar to one another) in the Southwestern Pacific. Finally, McClain *et al.* (2009) noted that although the epifaunal community on an eastern Pacific seamount and a nearby canyon were generally similar in composition, there was a difference in the frequency of occurrence of the component species.

Although worthy contributions to our understanding of seamount ecology, these recent compositional studies are somewhat equivocal regarding the question of whether benthic communities on seamounts are distinct. What they do demonstrate is that great care is needed when making comparisons among seamounts, and between seamounts and other habitats. That is, comparative analyses need to take account of the confounding factors that can plague examinations of data collected from sites with different depth ranges, and the combination of data from multiple sources where the taxonomic consistency among datasets may be in doubt. Unfortunately, the conclusions of the early study of Richer de Forges *et al.* (2000) are somewhat confounded by depth (McClain 2007), and thus the question of whether seamounts on adjacent ridges have distinct benthic communities remains unresolved. Likewise, the difference in assemblage composition between seamount and surrounding ridge habitats remains completely unassessed.

Squat lobsters (decapod families Galatheidae and Chirostyliidae) are particularly well-suited for examining ecological patterns in the deep-sea. They are (i) relatively large (carapace lengths of 2–70 mm), (ii) easily sampled by gears such as dredges, sleds and trawls, (iii) ubiquitous and common from the continental shelf to the deep-sea (including seamounts), (iv) they display a variety of opportunistic feeding strategies (*e.g.* suspension- and deposit-feeding, scavenging and predation) (Aurioles-Gamboa & Pérez-Flores 1997; Hudson & Wigham 2003;

Romero *et al.* 2004), (v) some species associate closely with habitat-forming benthic species such as corals (Rice & Miller 1991; Kilgour & Shirley 2008), a biogenic habitat that is found on seamounts (Rogers *et al.* 2007), and (vi) are well-resolved taxonomically. In fact, the Census of Marine Life project COMARGE (Continental Margin Ecosystems) recently produced a world catalogue of species (Baba *et al.* 2008). Finally, in terms of dispersal, whereas galatheids generally have extended planktotrophic larval stages, most chirostyliids have an abbreviated larval stage, thereby offering a useful contrast in terms of larval dispersal (Guerao *et al.* 2006; Clark & Ng 2008).

Squat lobster data have recently been compiled for the Southwestern Pacific (Schnabel 2009a), covering and extending the region studied by Richer de Forges *et al.* (2000) and including data from their analyses (although species identifications have been updated). These records were used to examine the following questions: (i) Are squat lobster assemblages on seamounts different from other habitats at comparable depths? (ii) Do assemblages on different ridges systems (seamounts and ridge habitat) differ? (iii) Do dispersal strategy, body size and environmental factors modify spatial patterns in assemblage composition?

Material and Methods

Study area

The study area is located in the Southwestern Pacific between 5–60° S and 145° E–170° W, and includes the Solomon Islands, Vanuatu, Fiji and Tonga in the north, Southeastern Australia in the west, and New Zealand in the south (Fig. 1). This area covers a diverse range of undersea geomorphological features, including extensive shallow shelf, continental slope, oceanic ridges, rises, abyssal basins, troughs, plateaux and seamounts (isolated, in complexes, chains, volcanic arcs, or as elevated features on ridges), which provide habitat for benthic assemblages.

Data

Data for galatheid and chirostyliid squat lobsters were compiled from multiple sources: (i) Historical records for global expeditions undertaken by the *Challenger*, *Albatross* and *Galathea*, and reports on local collections between 1873 and 1952 (Haswell 1882; Henderson 1888; Faxon 1895; Thompson 1899; Baba 1988, 1994, 2005) (67 records). (ii) Collections from the tropical Southwest Pacific Ocean carried out by the Institut de Recherche pour le Développement (IRD) and Muséum national d'Histoire naturelle, Paris (MnHn), since 1976 (*e.g.* Saint Laurent de & Macpherson 1990; Macpherson 1994, 1996,

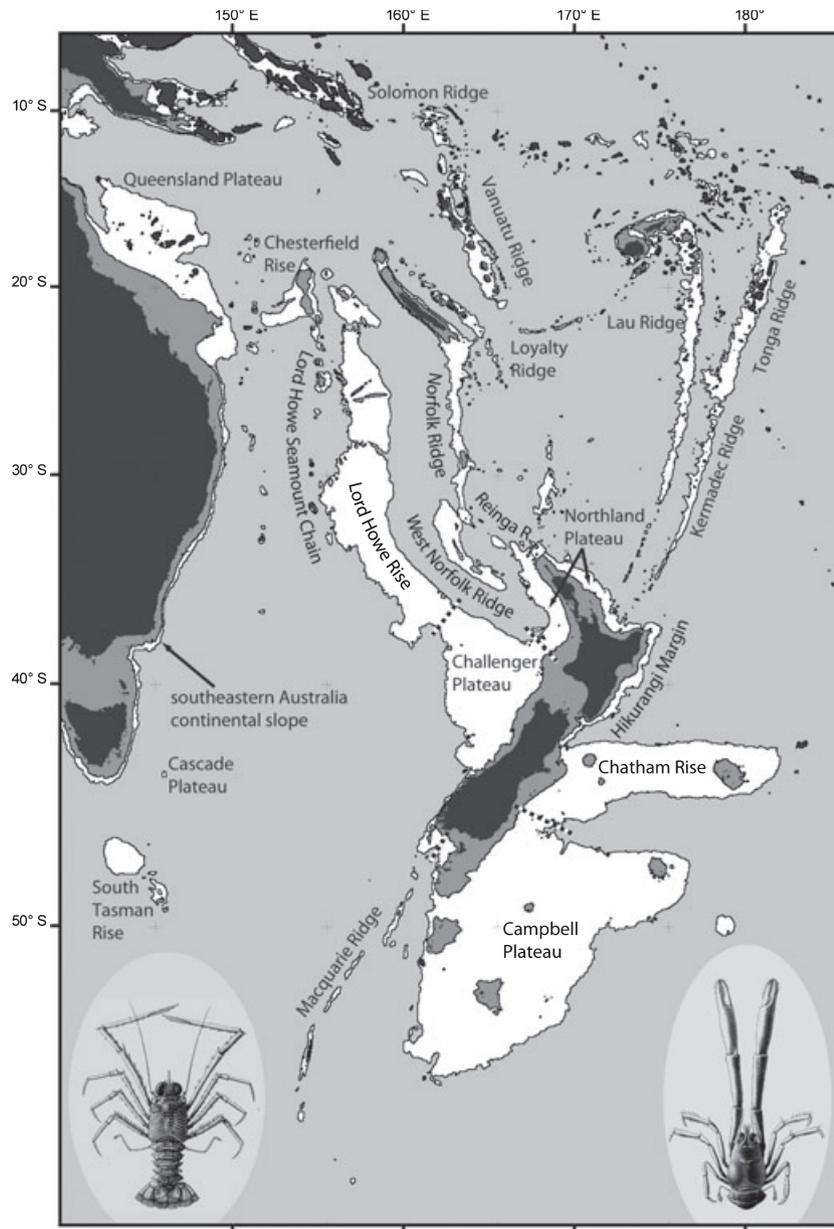


Fig. 1. Map showing the main geomorphic features in Southwestern Pacific Ocean from which squat lobster data were obtained for the study. Dotted lines indicate break between geomorphic features. Bathymetric contours for 200 and 1600 m are shown. Inset: galatheid *Munida obesa* (left) and chirostyliid *Uroptychus nitidus occidentalis* (right) [after Faxon 1895 and Henderson 1888, respectively].

1999, 2004; Saint Laurent de & Poupin 1996) (4253 records). (iii) Collections made by Australian scientific programs since 1948 by the Commonwealth Scientific and Industrial Research Organisation (CSIRO), South Australia Research and Development Institute (SARDI), New South Wales Fisheries, and the CIDARIS I, II and III expeditions between 1986 and 1992 (Baba 1994; Ah Yong & Poore 2004a,b) (436 records). (iv) Collections from the New Zealand region made primarily by the National Institute of Water and Atmospheric Research

(NIWA) and its predecessor the New Zealand Oceanographic Institute, plus miscellaneous collections in the Dominion Museum, now the National Museum Te Papa Tongarewa, made by Victoria University of Wellington, and the Portobello Marine Laboratory (University of Otago) since 1956 (e.g. Vereshchaka 2005; Schnabel & Bruce 2006; Schnabel 2009b) (1701 records). (v) Records from the 2003 NORFANZ voyage to the mid-Tasman Sea, a collaborative sea-floor survey between Australian and New Zealand institutions (National Oceans Office,

CSIRO Marine Research, Australia, New Zealand Ministry of Fisheries and NIWA (Ah Yong 2007) (33 records). The complete dataset comprised 6490 specimen records throughout the region and between 0 and 4520 m water depth.

The dataset contained 502 species of Galatheidae (24 genera, 302 species) and Chirostylidae (six genera, 200 species). Recent monographic treatments provide stable classifications within both families (e.g. Baba 2005; Macpherson 2007; Baba *et al.* 2008), allowing for taxonomic consistency across datasets and regions. Taxon names generally follow Baba *et al.* (2008); however, where species remained incompletely defined, the following conventions were followed: (i) *Agononida incerta* is represented by two unresolved species, type A and B, that co-occur along the eastern Australian margin. Not all, particularly historical, records can be referred to either of these types and all records were combined to a single species *A. incerta*. (ii) Approximately 100 undescribed taxa, primarily within the chirostylid genus *Uroptychus*, are currently being described. These undescribed species occur in the source records, and these have been reconciled by Keiji Baba (Kumamoto University, Japan) and K.S., based on drawings and unpublished descriptions.

Data treatment

To compare squat lobster assemblage composition among and within regions and major geomorphic habitat types (hereafter referred to simply as 'habitats'), the following series of treatments was applied to the compiled dataset:

Gear type

Only trawled gear (trawls, sleds, dredges, *etc.*) were included. Towed gear is efficient at sampling squat lobsters, and the different towed gears are likely to produce comparable data.

Habitat and region affiliation

The affiliation of each station was determined via a general geomorphic habitat classification (rise, ridge, plateau, continental slope) for the study area using ARCGIS 9.3.1 software. Stations were considered to be on a seamount when the sampling record made specific note of a seamount name, or when the station position was within 10 km of a seamount included in seamount databases for the Western Pacific and the New Zealand regions (Allain *et al.* 2008; Rowden *et al.* 2008). A 10-km radius approximates the average area of seamounts in the region (Rowden *et al.* 2005). Although this criterion will deem some station records to be associated with smaller features, the bias introduced is acceptably small. The regional affiliation (e.g. Tonga, Lord Howe, Southeastern Australia) of

stations within habitats was made with reference to a map of the study area that named each geomorphic habitat (Fig. 1).

Overall depth range

Graphical examination of the depth distribution of all seamount and non-seamount stations indicated that the majority of records for these two habitat groups spanned a depth range of 200–1600 m. Records outside this range were excluded.

Number of stations per 'feature'

This was used in the initial analysis to examine bias related to variable sample effort (see section below).

Spatial sampling scale

To account for a potential sampling area effect (see O'Hara 2007) it was necessary to standardize the area over which samples were taken on seamounts and non-seamount habitats. We used GIS software and tools (ARGIS 9.3.1) for our approach (some standard GIS terms are included in the following description). The geometric mean distance between sample stations was computed using the 'distance between points tool' in Hawth's Tools (Beyer 2004). The mean distance between seamount stations ranged from <100 m to approximately 100 km with an average distance of ~10 km. To attain a similar spatial scale of sampling density for seamount and non-seamount habitats, 'pseudo-features' were generated for non-seamount habitats that were of such a size that they contained sample stations at similar densities as occurred on individual seamounts (= features). This treatment was achieved by buffering sample stations on non-seamount pseudo-features by a radius which resulted in the mean distance between sample stations within the polygons being similar to that within seamounts. The individual buffers were dissolved based on the feature-type attribute for each station. Only pseudo-features that contained three or more sample stations were used in the mean distance calculations. A buffer radius of 7 km was found to produce similar densities between seamount features and non-seamount pseudo-features (hereafter both are referred to as simply 'features'), with average mean distances ranging from 9.2 (ridge) to 11.4 km (rise).

The net result of these five treatments was a dataset comprising 389 species from 1871 stations that were distributed among 201 features. There were one to 18 features within one region and habitat (Table 1). This dataset was further treated as follows:

Depth range per habitat/region

A graphical examination of the bathymetric distribution of stations for each habitat/region was used to select only

Table 1. Number of features (sample unit), and their depth range, per region and habitat (see text for full definition of these terms) for squat lobster data compiled for the study.

Region	Habitat	A – all features		B – selected features	
		No. of features	Depth range (m)	No. of features	Depth range (m)
Cascade	Plateau	1	843		
Challenger	Plateau	3	212–484		
Northland	Plateau	6	361–781	5	361–781
	Seamount	10	296–1373	7	296–998
Queensland	Plateau	3	606–1424		
Chatham	Rise	12	173–422	7	253–483
	Seamount	11	382–1081	3	382–699
Chesterfield	Rise	1	970		
	Seamount	2	401–622		
Hikurangi	Slope	5	478–806		
	Seamount	1	921		
SE Australia	Slope	11	397–1015	6	531–1015
	Seamount	6	828–1253	5	828–1253
Kermadec	Ridge	3	441–621	3	441–621
	Seamount	7	369–1387	4	369–659
Lau	Ridge	15	269–589		
	Seamount	1	492		
Loyalty	Ridge	4	409–700	4	425–700
	Seamount	5	323–722	5	323–722
Norfolk	Ridge	18	202–754	18	202–754
	Seamount	18	279–1207	17	279–778
Solomon	Ridge	12	327–1164		
Tonga	Ridge	10	323–585	10	323–585
	Seamount	10	401–1285	9	401–734
Vanuatu	Ridge	12	343–1392		
	Seamount	1	450		
Lord Howe	Seamount	7	309–763		
Macquarie	Seamount	1	1297		
Reinga	Seamount	1	653		
West Norfolk	Seamount	3	428–811		

Regions in bold indicate sufficiently large sample size for comparisons of assemblages between seamount and non-seamount habitats. A: all possible features between 200 and 1600 m. B: features selected for comparable depth, habitat and with ≥ 3 features per habitat.

data from a depth range that overlapped between the seamount and non-seamount group of stations. The resulting depth ranges varied from 300–700 m for the Chatham Rise to 200–1200 m for the Norfolk Ridge.

Number of species per feature

Features with fewer than three species were excluded, as exploratory analysis revealed that such features appeared as outliers in terms of their assemblage dissimilarity to other features.

Number of features per habitat/region

To ensure at least three features per seamount and non-seamount habitat in a region, data were excluded from

habitats with fewer than three features and from regions with only one habitat type.

These final treatment steps resulted in a dataset of 290 species distributed among 1202 stations on 109 features within four habitat types (plateau, rise, continental slope, ridge) over seven regions (Chatham, Kermadec, Loyalty, Norfolk, Northland, Southeastern Australia and Tonga) (Fig. 2). This dataset allowed for four regional seamount-ridge comparisons and single comparisons between seamount and rise, plateau and continental slope habitats (Table 1).

Environmental data

To identify important factors that may influence the composition of squat lobster assemblages, a dataset of environmental variables for each station was compiled from a number of sources: (i) Mean depth per station was calculated from start- and end-depth for each tow from published and unpublished station records. In the absence of an end-depth, the start-depth alone was used. (ii) Sea-floor temperature ($^{\circ}\text{C}$), salinity (ppm) and oxygen (mL^{-1}) data were derived from the CARS2006 dataset, which contains mean values and seasonal coefficients (annual/semi-annual sine/cosine values) created by averaging/interpolating available oceanographic cast data across the southern hemisphere and equatorial regions for 79 depth layers at a resolution of 0.5° latitude/longitude (Dunn & Ridgway 2002; Ridgway *et al.* 2002; <http://www.marine.csiro.au/~dunn/cars2006/>). (iii) Estimates of particulate organic carbon (POC) were derived from a global NPZD (nutrient-phytoplankton-zooplankton-detritus) model (R. Matear, CSIRO unpublished data), of resolution 1.875° longitude, 0.9375° latitude, and 31 depth layers, by converting the detritus data ($\text{mmol N}\cdot\text{m}^{-3}$) to carbon ($\mu\text{g C}\cdot\text{m}^{-3}$) using the 106:16 N:C ratio of seawater multiplied by the molar weight of carbon ($12.01\text{ g}\cdot\text{mol}^{-1}$). All data were horizontally interpolated (and extrapolated across coastlines) for each depth layer to 0.02° by using the inverse distance weighted algorithm in the Spatial Analyst module of ARCMAP v. 9.0 (ESRI 2004). Values for each station (on the sea floor) were then calculated by trilinear interpolation between these fine-scale depth layers, scaled by the actual latitude/longitude/depth recorded for each station. (iv) Additionally, POC flux ($\text{mol}\cdot\text{m}^{-2}\cdot\text{day}^{-1}$) values were obtained from the sea-floor model of these variables by Yool *et al.* (2009). (v) Data for scleractinian or stony coral habitat suitability (%), as a proxy for the availability of such coral as a habitat for squat lobsters, was obtained from Tittensor *et al.* (2009).

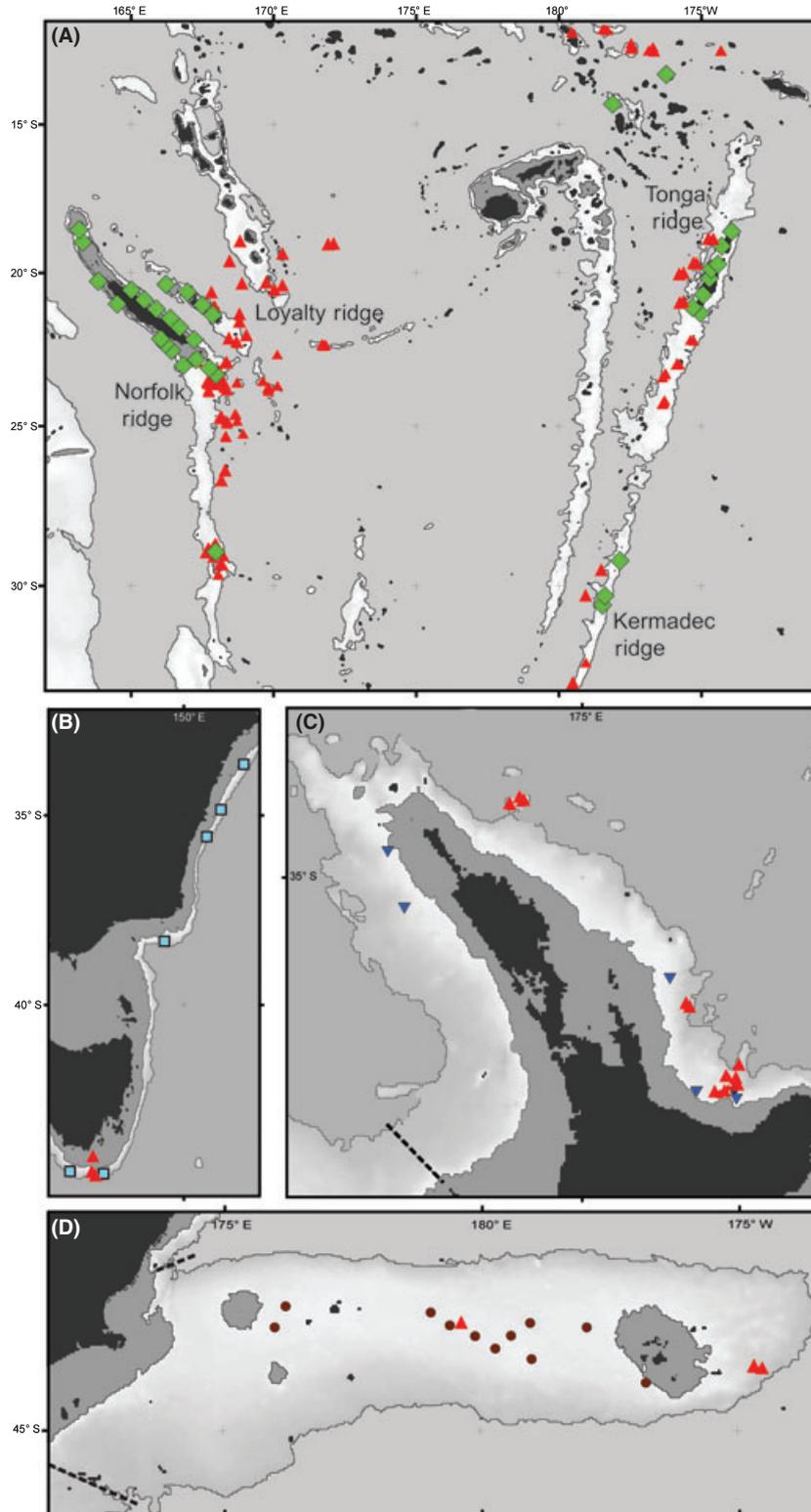


Fig. 2. Maps showing the location of 'features' (see text for definition) from which squat lobster data were analysed from different regions and habitats: (A) Norfolk, Loyalty, Kermadec and Tonga Ridges, (B) Southeastern Australia continental slope, (C) Northland Plateau and (D) Chatham Rise. Symbols indicate sampled features, with red triangles representing seamount habitat, diamonds inverted triangles (plateau), squares (slope) and circles (rise) representing non-seamount habitat. Bathymetric contours for 200 and 1600 m are shown.

Ancillary biological data

Factors implying either an abbreviated (short) or complete (long) larval duration were assigned to each species using information from the literature to examine possible effects for the assemblage patterns observed. For example, most chirostyliid larvae (observed in genera *Chirostylius*, *Uroptychus* and *Gastroptychus*, but not *Eumunida*) appear to hatch at an advanced zoeal stage equivalent to the fourth or fifth stage zoea of galatheids (with the exception of the galatheid genus *Munidopsis*) (Pike & Wear 1969; Samuelsen 1972; Guerao *et al.* 2006; Clark & Ng 2008). Secondly, maximum body size (measured as the postorbital carapace length in mm) was established for each species, based on examinations of specimens and literature.

Data analysis

Data were analysed using the PRIMER v. 6 software package (Clarke & Gorley 2006; and references in Clarke & Warwick 2001). Species data were first averaged for the selected features (so that feature rather than station became the 'sample unit' of comparison), then presence-absence transformed. The Bray-Curtis coefficient was used to measure assemblage similarity between all features.

Assessment of sampling effort bias

To address the possibility of a bias imposed by the difference in sampling effort per feature (*i.e.* number of stations per feature ranged from three to 97, with a mean of 9.1 ± 12.7 SD), a series of Spearman's rank correlation coefficients (ρ) were computed using the RELATE routine in PRIMER to test for significant deviations between the similarity matrices for features containing all and a maximum of 20, 10 and five stations. Stations were chosen at random for features with stations exceeding the chosen number of stations and a similarity matrix was constructed for the averaged station data by feature. In all cases the Spearman rank correlations indicated that there were no significant differences between fully (all stations) and partially (20, 10, 5 randomly sampled stations) sampled features ($\rho > 0.96$ in all cases). Thus, all subsequent analyses included data from all stations for each seamount and non-seamount feature.

Assemblage composition

Non-metric multi-dimensional scaling (NMDS) ordination plots were used to visualize the similarity among squat lobster assemblages of different features among habitats/regions. Differences in assemblage composition

between seamount and non-seamount habitats were tested with analysis of similarities (ANOSIM). For features from the habitat rise, plateau and slope, only one-way comparisons with seamount habitat were possible for the Chatham, Northland and Southeastern Australia regions, respectively. For features of the ridge habitat, a two-way crossed test was examined using the habitat (seamount or non-seamount) and region (Norfolk, Kermadec, Loyalty and Tonga) as the factors.

Species contributing the most to the average similarity within a habitat/region and the average dissimilarity between habitat/region were identified using the similarities percentage (SIMPER) routine. SIMPER was conducted using the same design as used for the ANOSIM test. Characterizing and discriminating species were ranked by their average contribution (%) to the within- and between-group similarity and dissimilarity and the ratio of similarity/dissimilarity and standard deviation (SD), respectively. Species are considered a good characterizing/discriminating species if the ratio of the mean to the standard deviation of the contribution of each species to the overall similarity/dissimilarity between groups is ≥ 1.3 (page 7-3, Clarke & Warwick 2001).

The body size of characterizing/discriminating species, whether the species belonged to the families Galatheididae or Chirostyliidae, or had a complete (long) or abbreviated (short) larval stage was recorded to assess qualitatively whether there were any notable differences in these biological attributes for squat lobster assemblages from seamount and non-seamount habitats.

Relationship with environmental variables

Relationships between environmental data and overall squat lobster assemblage composition pattern were assessed using the BIOENV Spearman rank correlation routine for each of the subsets of seamount and non-seamount habitat assemblage data. BIOENV searches for the smallest possible subset of variables which, in combination, describe most of the pattern in the full dataset. Before running the analyses, draftsman's plots of pairwise combination of variables were examined visually for collinearity. A variable would be excluded if its correlation with another variable(s) exceeded 0.90. Environmental variables in the final analysis were normalized, and included mean station depth, mean temperature, temperature range, mean salinity, mean oxygen, POC concentration, POC flux, and stony coral habitat suitability. 'Bubble plots', where the values for the BIOENV identified environmental variable(s) are overlaid as proportional circles on the NMDS plots for assemblage data, were used to visually explore how environmental

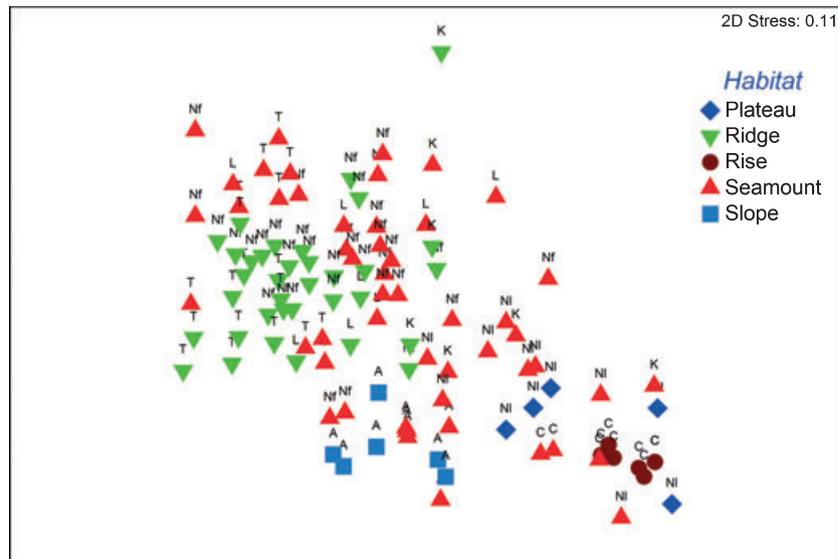


Fig. 3. NMDS ordination plot of presence/absence squat lobster data for all features coded by habitat (see key) and labelled by region. Norfolk (Nf), Loyalty (L), Tonga (T) and Kermadec (K) ridges, Northland Plateau (Ni), southeastern Australia continental slope (A), Chatham Rise (C).

variability is related to differences in assemblage composition by habitat/region.

Results

Differences in assemblage composition

The overall NMDS ordination (Fig. 3) revealed a regional separation of squat lobster assemblages on features that is apparently unrelated to habitat type; with a generally south–north gradient from the southern assemblages of the Chatham Rise and the Southeastern Australian continental margin (bottom right and bottom of plot), to those of the northern ridges of Norfolk, Loyalty and Tonga (top left of plot), with assemblages of the Northland Plateau and the Kermadec Ridge in between (roughly in the centre of plot). Within regions, differences in assemblage composition between habitat types were less obvious. However, for ridge habitat, which is not predominantly restricted to a single region, assemblages of features from this habitat mostly cluster separately from those of seamount habitat (Fig. 3). Examination of separate NMDS plots for each habitat/region (Fig. 4) within which an assemblage composition comparison can be made between seamount habitat and another habitat, allowed for a better appreciation of differences that were indicated by the formal ANOSIM tests.

One-way ANOSIM tests (Table 2) revealed that the composition of squat lobster assemblages on seamount habitat was significantly different from that on rise habi-

tat (Chatham Rise region), but not plateau (Northland region) or slope (southeastern Australia region) habitat. The two-way ANOSIM test (Table 2) indicated a relatively small yet significant difference in assemblage composition across regions, and between seamount and non-seamount habitats for the four ridge regions examined. Pair-wise tests revealed that differences in assemblage composition between seamount and non-seamount ridge habitat were significant for the Norfolk and Tonga ridge regions, but not the Kermadec and Loyalty ridge regions.

Assemblage composition

SIMPER analyses provided a list of the species that contribute to 90% of the similarity/dissimilarity observed for/between squat lobster assemblages of seamount and non-seamount habitats for the Southeastern Australia slope, Chatham Rise and Northland Plateau (Table 3), and for the Kermadec, Loyalty, Norfolk and Tonga Ridges (Table 4). The taxonomic group, body size and larval duration of these contributing species is also noted in these tables.

As indicated by the proportional contribution to the total similarity, most of the assemblages were dominated by galatheid taxa, primarily of the genera *Munida*, *Phylladiorhynchus* and *Agononida*. In particular, two species, *Munida gracilis* and *Munida isos*, not only were dominant in the slope, rise and plateau habitats but were also consistently identified as characterizing species. However,

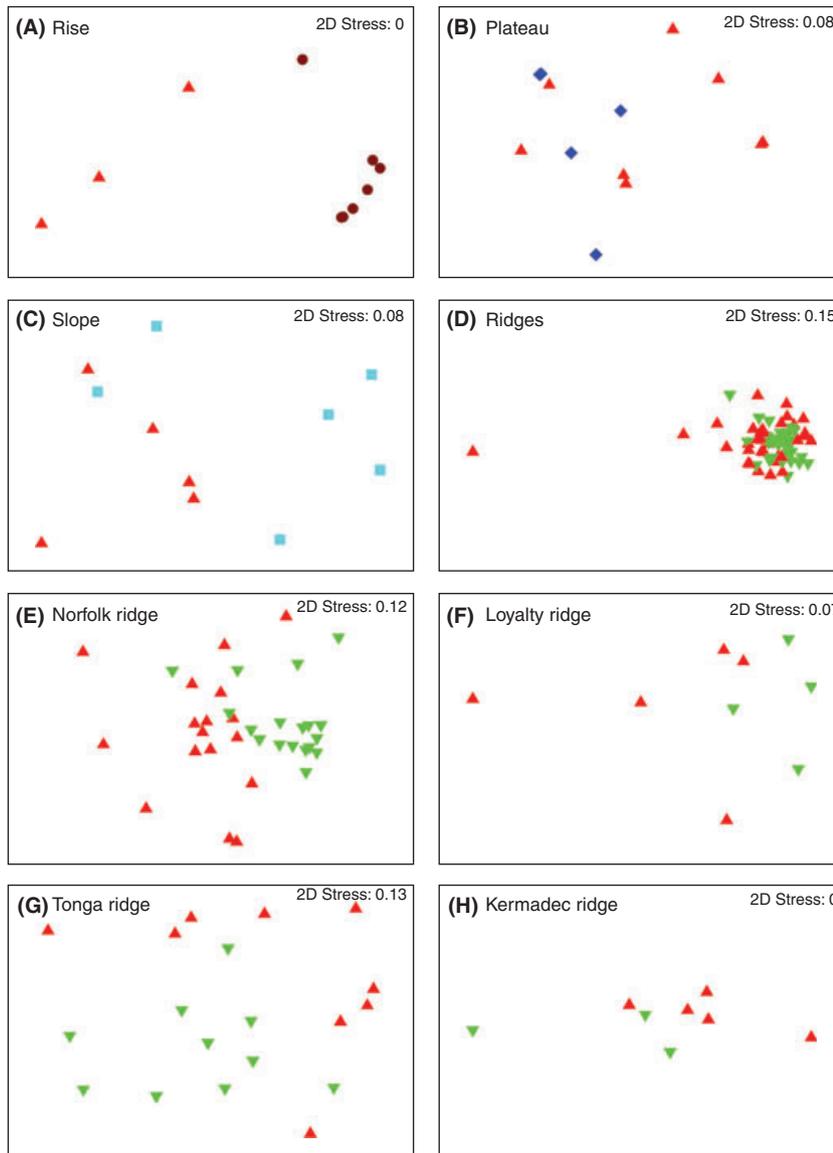


Fig. 4. NMDS ordination plots of presence/absence of squat lobster assemblage composition data for seamount and non-seamount habitats: (A) rise, (B) plateau, (C) continental slope, (D) ridges (all regions); and for seamount and ridge habitat within a region: (E) Norfolk Ridge, (F) Loyalty Ridge, (G) Tonga Ridge, (H) Kermadec Ridge. Seamounts are shown by red triangles in all cases.

with the exception of *M. isos* on the Chatham Rise, these species tend to occur in both seamount and non-seamount habitats. The latter species, along with *Munidopsis ceres*, are the galatheids that discriminate between assemblages of seamount habitat (where they occur more frequently) and the non-seamount habitat on the rise (which were identified by the ANOSIM as being significantly different in composition).

Chirostyliids were represented primarily by the genus *Uroptychus* in both seamount and non-seamount habitats (with the exception of the plateau habitat). *Uroptychus gracilimanus* and *Gastroptychus novaezelandiae* were the

characterizing species for non-seamount habitats of the slope and rise, whilst two undescribed species of *Uroptychus* characterized the assemblage of the seamount habitat on the Chatham Rise. An undescribed species (*U. sp. P*) and *G. novaezelandiae* were the most important discriminating species for assemblages from the seamount and non-seamount habitats on the rise, with the former occurring more often on seamount habitat and the latter more often sampled on the non-seamount habitat on the rise.

For assemblages associated with different ridge structures, only one species (*Munida leagora*) was deemed a

Table 2. Results of the ANOSIM analysis (R values) for tests of squat lobster assemblage composition dissimilarity between habitat and region.

	Rise	Plateau	Slope	
One-way				
Seamount versus non-seamount habitat	0.956	0.105	0.179	
Two-way crossed				
Across regions	0.292			
Seamount versus Ridge habitat	0.264			
Pair-wise for each region (ridge system)	Norfolk	Kermadec	Loyalty	Tonga
Seamount versus Ridge habitat	0.310	0.148	0.047	0.263

Bold indicates results with significance levels of $P < 0.05$.

characterizing species (for non-seamount habitat on Loyalty Ridge). Three different *Munida* species were identified as discriminating species from seamounts and non-seamount ridge habitats for Kermadec, Loyalty and Tonga Ridges. *Munida runcinata*, which occurred more often on non-seamount ridge habitat, was the discriminating species for one (Tonga) of two pair-wise, inter-ridge comparisons of assemblage composition identified by ANOSIM as being statistically significant (the other being the Norfolk Ridge).

No chirostylid species were identified as discriminating species for the dissimilarity observed between seamount and non-seamount habitat on the Tonga and Norfolk Ridges. However, this taxonomic group dominated the list of species that contributed to the similarity for the assemblage of the seamount habitat on Norfolk Ridge, and representative species were also found among those that defined the similarity of the seamount assemblage on the Tonga Ridge.

Species characteristics

The average body size of species that contributed to 90% of the similarity observed for squat lobster assemblages of seamount and non-seamount habitats was larger for non-seamount rise and plateau habitat (19 mm) than for seamount habitat (13/14.5 mm) (Table 4). The size of the individual discriminating species for the Chatham Rise comparison of seamount and non-seamount assemblages reflected the aforementioned differences in average size between habitats. No obvious difference in average size was observed for assemblages of slope habitats. For assemblages of the different ridge structures, average body

size was somewhat larger for non-seamount ridge habitat (18.6/16 mm) than for seamount habitat on Norfolk and Tonga Ridges (13.8/14.9 mm). The size of the single discriminating species for the Tonga Ridge comparison of seamount and non-seamount assemblages did not reflect the aforementioned differences in average size between habitats. No obvious difference in average size was observed for assemblages of habitats on the Loyalty and Kermadec Ridges.

Examination of the list of species that contributed most to the dissimilarity observed in assemblage composition between habitats on the rise and plateau indicated that species that occur more frequently on seamount habitat have a short larval duration. A similar pattern was observed for the ridge structure, where an examination of the list of species that contributed most to the dissimilarity observed in assemblage composition between habitats on the Tonga and Norfolk Ridges (those assemblages that indicated significant differences between seamount and non-seamount assemblages) indicated that typically, species that occur more frequently on non-seamount ridge habitat have a long larval duration.

Environmental drivers

Results of the BIOENV analysis reveal that different environmental drivers, or combinations of variables, appear to provide the highest explanatory power for different assemblage groupings (Table 5). The overall assemblage pattern (which, as already noted, appeared to at least partly reflect a geographic pattern) was most highly correlated with the predicted average flux of POC to the sea floor. Examination of the bubble plot (not shown) for the overall assemblage data indicates that POC flux to be relatively high on the Chatham Rise (where it was particularly high), Northland Plateau, and Southeastern Australian continental slope for both seamount and non-seamount habitats.

For assemblage data that ANOSIM revealed to be different between seamounts and other habitats, *i.e.* rise and some ridges, median depth was indicated as being correlated with the assemblage pattern observed. Bubble plots indicated that seamounts on the Chatham Rise were generally deeper than non-seamount features on this rise. No obvious depth-habitat pattern was suggested by the bubble plots for the overall ridge assemblage data. However, in addition to depth, the predicted average flux of POC was also included as an explanatory environmental variable for the seamount-ridge assemblage pattern. Examination of the bubble plot suggests that the overall ridge assemblage pattern is partly driven by a decreasing south-north gradient in POC flux.

Table 3. Results of the SIMPER analysis for one-way comparisons between seamount and non-seamount habitats (slope, rise, plateau) within a region, listing squat lobster species that contributed the most to assemblage similarity/dissimilarity observed.

	Seamount						Non-seamount						Seamount versus non-seamount							
	Family	Taxon	Contrib %	Sim /SD	Body size	Larval dev	Family	Taxon	Contrib %	Sim /SD	Body size	Larval dev	Family	Taxon	Abund SMT	Abund nSMT	Contrib %	Diss /SD	Body size	Larval dev
Slope	G	<i>Munida isos</i>	57.67	7.75	14	I	C	<i>Uroptychus gracilimanus</i>	32.14	1.29	8	s	C	<i>Uroptychus gracilimanus</i>	0	0.83	11.54	1.93	8	s
	G	<i>Munida endeavourae</i>	16.37	0.62	18	I	C	<i>Uroptychus australis</i>	21.36	0.77	11	s	G	<i>Munida isos</i>	1	0.5	7.95	0.96	14	I
	C	<i>Uroptychus australis</i>	16.37	0.62	11	s	C	<i>Uroptychus babai</i>	10.54	0.47	13	s	C	<i>Uroptychus babai</i>	0	0.5	7.37	0.94	13	s
							C	<i>Gastroptychus rogeri</i>	9.52	0.47	30	s	G	<i>Munida endeavourae</i>	0.6	0.5	7.17	0.94	18	I
						G	<i>Munida endeavourae</i>	9.52	0.47	18	I	C	<i>Gastroptychus rogeri</i>	0.2	0.5	6.98	0.94	30	s	
						G	<i>Munida isos</i>	8.25	0.48	14	I	C	<i>Uroptychus australis</i>	0.6	0.67	6.66	0.88	11	s	
			Average body size										C	<i>Uroptychus enpheres</i>	0.4	0.33	6.43	0.89	12	s
										Average body size	15.7		C	<i>Uroptychus litosus</i>	0.4	0.33	6.43	0.89	15	s
											14.3		G	<i>Munidopsis kensleyi</i>	0	0.33	4.30	0.68	19	s
											1/2		G	<i>Munidopsis cf. serricornis</i>	0.2	0.17	4.26	0.63	12	s
Rise	G	<i>Munida gracilis</i>	20.71	4.64	25	I	G	<i>Munida gracilis</i>	35.9	5.36	25	I	C	<i>Uroptychus sp. P</i>	1	0	17.46	4.20	9	s
	G	<i>Phylladorhynchus sp. 1</i>	20.71	4.64	12	I	G	<i>Phylladorhynchus sp. 1</i>	35.9	5.36	12	I	C	<i>Gastroptychus novaezelandiae</i>	0	0.82	14.24	1.82	20	s
	C	<i>Uroptychus sp. A</i>	20.71	4.64	7	s	C	<i>Gastroptychus novaezelandiae</i>	23.3	1.29	20	s	C	<i>Uroptychus sp. A</i>	1	0.36	11.82	1.22	7	s
	C	<i>Uroptychus sp. P</i>	20.71	4.64	9	s	G	<i>Munida isos</i>	0.67	0	10.18	1.33	14	I						
G	<i>Munida isos</i>	5.710	0.58	14	I	G	<i>Munidopsis ceres</i>	0.67	0	10.18	1.33	11	s							
G	<i>Munidopsis ceres</i>	5.710	0.58	11	s	C	<i>Uroptychus sp. T</i>	0.67	0.18	1.18	10	s								
													G	<i>Phylladorhynchus pusillus</i>	0.33	0.27	8.07	0.81	4	I
													G	<i>Munidopsis papanui</i>	0.33	0	4.28	0.69	7	s
			Average body size								13		G	<i>Munidopsis cf. serricornis</i>	0.33	0	4.28	0.69	12	s
											3/3		G							
													G							

Table 4. Results of the SIMPER analysis for the pairwise (from two-way crossed) comparisons between seamount and ridge habitat for four regions (ridge systems), listing squat lobster species that contributed the most to assemblage similarity/dissimilarity observed.

	Seamount						Non-seamount					
	Family	Taxon	Contrib %	Sim /SD	Body size dev	Larval dev	Family	Taxon	Contrib %	Sim /SD	Body size dev	Larval dev
Kermadec	G	<i>Munida kapala</i>	63.64	0.88	8	I	G	<i>Paramunida antipodes</i>	100	0.58	12	I
	G	<i>Agononida nielbrucei</i>	18.18	0.41	18	I	G	<i>Paramunida antipodes</i>	100	0.58	12	I
	G	<i>Leogalatheae laevirostris</i>	18.18	0.41	8	I	G	<i>Paramunida antipodes</i>	100	0.58	12	I
Loyalty	C	<i>Uroptychus alcocki</i>	19.30	0.62	7	S	G	<i>Munida leagora</i>	24.19	2.01	15	I
	G	<i>Crosnierita uzuae</i>	9.69	0.32	11	I	G	<i>Munida notata</i>	9.01	0.83	13	I
	C	<i>Uroptychus cf. brucei</i>	9.69	0.32	13	S	G	<i>Munida runcinata</i>	9.01	0.83	11	I
	C	<i>Uroptychodes spinimarginatus</i>	7.62	0.32	7	S	G	<i>Onconida alaini</i>	9.01	0.83	7	I
	G	<i>Agononida sphaecia</i>	6.88	0.32	24	I	C	<i>Uroptychus scambus</i>	7.42	0.41	7	S
	G	<i>Munida acantha</i>	6.88	0.32	13	I	G	<i>Paramunida granulata</i>	4.33	0.41	13	I
	G	<i>Munida guttata</i>	6.88	0.32	17	I	G	<i>Agononida eminens</i>	2.73	0.41	23	I
	G	<i>Munida mollae</i>	6.88	0.32	21	I	G	<i>Munida rosula</i>	2.73	0.41	18	I
	G	<i>Munida notata</i>	6.88	0.32	13	I	C	<i>Uroptychus alcocki</i>	2.73	0.41	7	S
	C	<i>Uroptychus sp. F</i>	6.88	0.32	9	S	G	<i>Heteronida aspinirostris</i>	2.51	0.41	5	I
		(total: 11 spp)					(total: 18 spp)					
		Average body size			11.3		Average body size			12		
		Proportion of s/I			3/0		Proportion of s/I			1/0		
		Contrib %					Contrib %					
		Sim /SD					Sim /SD					
		Body size dev					Body size dev					
		Larval dev					Larval dev					
		Family					Family					
		Taxon					Taxon					
		Abund SMT					Abund SMT					
		nSMT					nSMT					
		Contrib %					Contrib %					
		Diss /SD					Diss /SD					
		Body size					Body size					
		Larval dev					Larval dev					
		Family					Family					
		Taxon					Taxon					
		Abund SMT					Abund SMT					
		nSMT					nSMT					
		Contrib %					Contrib %					
		Diss /SD					Diss /SD					
		Body size					Body size					
		Larval dev					Larval dev					
		Family					Family					
		Taxon					Taxon					
		Abund SMT					Abund SMT					
		nSMT					nSMT					
		Contrib %					Contrib %					
		Diss /SD					Diss /SD					
		Body size					Body size					
		Larval dev					Larval dev					
		Family					Family					
		Taxon					Taxon					
		Abund SMT					Abund SMT					
		nSMT					nSMT					
		Contrib %					Contrib %					
		Diss /SD					Diss /SD					
		Body size					Body size					
		Larval dev					Larval dev					
		Family					Family					
		Taxon					Taxon					
		Abund SMT					Abund SMT					
		nSMT					nSMT					
		Contrib %					Contrib %					
		Diss /SD					Diss /SD					
		Body size					Body size					
		Larval dev					Larval dev					
		Family					Family					
		Taxon					Taxon					
		Abund SMT					Abund SMT					
		nSMT					nSMT					
		Contrib %					Contrib %					
		Diss /SD					Diss /SD					
		Body size					Body size					
		Larval dev					Larval dev					
		Family					Family					
		Taxon					Taxon					
		Abund SMT					Abund SMT					
		nSMT					nSMT					
		Contrib %					Contrib %					
		Diss /SD					Diss /SD					
		Body size					Body size					
		Larval dev					Larval dev					
		Family					Family					
		Taxon					Taxon					
		Abund SMT					Abund SMT					
		nSMT					nSMT					
		Contrib %					Contrib %					
		Diss /SD					Diss /SD					
		Body size					Body size					
		Larval dev					Larval dev					
		Family					Family					
		Taxon					Taxon					
		Abund SMT					Abund SMT					
		nSMT					nSMT					
		Contrib %					Contrib %					
		Diss /SD					Diss /SD					
		Body size					Body size					
		Larval dev					Larval dev					
		Family					Family					
		Taxon					Taxon					
		Abund SMT					Abund SMT					
		nSMT					nSMT					
		Contrib %					Contrib %					
		Diss /SD					Diss /SD					
		Body size					Body size					
		Larval dev					Larval dev					
		Family					Family					
		Taxon					Taxon					
		Abund SMT					Abund SMT					
		nSMT					nSMT					
		Contrib %					Contrib %					
		Diss /SD					Diss /SD					
		Body size					Body size					
		Larval dev					Larval dev					
		Family					Family					
		Taxon					Taxon					
		Abund SMT					Abund SMT					
		nSMT					nSMT					
		Contrib %					Contrib %					
		Diss /SD					Diss /SD					
		Body size					Body size					
		Larval dev					Larval dev					
		Family					Family					
		Taxon					Taxon					
		Abund SMT					Abund SMT					
		nSMT					nSMT					
		Contrib %					Contrib %					
		Diss /SD					Diss /SD					
		Body size					Body size					
		Larval dev					Larval dev					
		Family					Family					
		Taxon					Taxon					
		Abund SMT					Abund SMT					
		nSMT					nSMT					
		Contrib %					Contrib %					
		Diss /SD					Diss /SD					
		Body size					Body size					
		Larval dev					Larval dev					
		Family					Family					
		Taxon					Taxon					
		Abund SMT					Abund SMT					
		nSMT					nSMT					
		Contrib %					Contrib %					
		Diss /SD					Diss /SD					
		Body size					Body size					
		Larval dev					Larval dev					
		Family					Family					
		Taxon					Taxon					
		Abund SMT					Abund SMT					
		nSMT					nSMT					
		Contrib %					Contrib %					
		Diss /SD					Diss /SD					
		Body size					Body size					
		Larval dev					Larval dev					
		Family					Family					
		Taxon					Taxon					
		Abund SMT					Abund SMT					
		nSMT					nSMT					
		Contrib %					Contrib %					
		Diss /SD					Diss /SD					
		Body size										

Table 4. (Continued)

Seamount		Non-seamount						Seamount versus Non-seamount											
Family	Taxon	Contrib %	Sim/SD	Body size	Larval dev	Family	Taxon	Contrib %	Sim/SD	Body size	Larval dev	Family	Taxon	Abund SMT	Abund nSMT	Contrib %	Diss /SD	Larval size	Larval dev
Norfolk	<i>Uroptychus longior</i>	10.93	0.40	6	s	G	<i>Agononida incerta</i>	12.63	1.14	36	I	G	<i>Agononida incerta</i>	0.17	0.83	2.57	1.02	36	I
	<i>Uroptychus</i> sp. D	7.42	0.42	8	s	G	<i>Agononida squamosa</i>	9.80	1.04	24	I	G	<i>Agononida squamosa</i>	0	0.78	2.38	1.24	24	I
	<i>Uroptychus</i> sp. F	7.29	0.42	9	s	G	<i>Munida rhodonia</i>	8.95	0.91	14	I	G	<i>Munida rhodonia</i>	0.22	0.72	2.11	0.99	14	I
	<i>Uroptychus alcocki</i>	6.92	0.35	7	s	G	<i>Enriquea leviantennata</i>	7.36	0.79	17	I	G	<i>Enriquea leviantennata</i>	0	0.67	2.08	1.05	17	I
	<i>Agononida laurentae</i>	4.18	0.39	32	I	G	<i>Agononida callirrhoe</i>	6.44	0.79	18	I	G	<i>Munida notata</i>	0.11	0.61	1.98	0.73	13	I
	<i>Munida zebra</i>	3.95	0.39	19	I	G	<i>Munida notata</i>	5.92	0.63	13	I	G	<i>Agononida callirrhoe</i>	0	0.67	1.89	1.08	18	I
	<i>Uroptychus levicrustus</i>	3.27	0.23	5	s	G	<i>Paramunida longior</i>	5.27	0.60	11	I	G	<i>Paramunida longior</i>	0	0.56	1.79	0.88	11	I
	<i>Uroptychus nanophyes</i>	2.95	0.32	12	s	G	<i>Paramunida setigera</i>	5.05	0.61	12	I	G	<i>Paramunida setigera</i>	0	0.56	1.72	0.93	12	I
	<i>Agononida sphaeia</i>	2.91	0.32	24	I	G	<i>Munida rosula</i>	3.43	0.52	18	I	C	<i>Uroptychus alcocki</i>	0.39	0.39	1.63	0.68	7	s
	<i>Munida armilla</i>	2.82	0.32	16	I	G	<i>Agononida eminens</i>	2.54	0.36	23	I	C	<i>Uroptychus longior</i>	0.5	0.11	1.55	0.68	6	s
(total: 44 spp)		Average body size		13.8				Average body size		18.6									
		Proportion of s/I		6/4				Proportion of s/I		0/10									
Tonga	<i>Munida tuberculata</i>	20.50	0.6	5	I	G	<i>Munida runcinata</i>	16.4	1.07	11	I	G	<i>Munida runcinata</i>	0	0.8	4.03	1.41	11	I
	<i>Agononida normani</i>	12.51	0.43	15	I	G	<i>Munida notata</i>	13.0	0.85	13	I	G	<i>Munida notata</i>	0.33	0.7	2.94	0.98	13	I
	<i>Agononida incerta</i>	11.33	0.44	36	I	G	<i>Paramunida labis</i>	5.36	0.51	8	I	G	<i>Munida tuberculata</i>	0.56	0.3	2.79	0.92	5	I
	<i>Munida notata</i>	6.55	0.29	13	I	G	<i>Munida leptitis</i>	4.91	0.51	7	I	G	<i>Agononida incerta</i>	0.44	0.4	2.50	0.87	36	I
	<i>Paramunida stichas</i>	5.41	0.29	11	I	G	<i>Agononida squamosa</i>	4.80	0.52	24	I	G	<i>Paramunida labis</i>	0.22	0.5	2.46	0.89	8	I
	<i>Munida psamathe</i>	4.92	0.29	7	I	G	<i>Paramunida stichas</i>	4.80	0.52	11	I	G	<i>Paramunida stichas</i>	0.33	0.5	2.45	0.90	11	I
	<i>Munida militaris</i>	4.74	0.30	21	I	G	<i>Paramunida granulata</i>	4.69	0.52	13	I	G	<i>Agononida normani</i>	0.44	0.1	2.44	0.81	15	I
	<i>Agononida eminens</i>	4.58	0.30	23	I	G	<i>Munida militaris</i>	3.63	0.37	21	I	G	<i>Munida militaris</i>	0.33	0.4	2.39	0.84	21	I
	<i>Uroptychus australis</i>	4.43	0.30	11	s	G	<i>Paramunida longior</i>	3.16	0.37	11	I	G	<i>Munida leptitis</i>	0.22	0.5	2.34	0.91	7	I
	<i>Uroptychus scambus</i>	4.43	0.30	7	s	G	<i>Onconida tropis</i>	3.14	0.38	7	I	G	<i>Paramunida granulata</i>	0.11	0.5	2.19	0.93	13	I
(total: 15 spp)		Average body size		14.9				Average body size		16									
		Proportion of s/I		2/8				Proportion of s/I		0/10									

Galathea (G) and Chirostyliidae (C); average percentage contribution (Contrib %) to similarity (Sim) or dissimilarity (Diss) within or between habitat assemblages; characterizing and discriminating species are those with a ratio of Sim/SD and Diss/SD of ≥ 1.3 (in bold); average abundance (Abund) for seamount (SMT) and non-seamount (nSMT) species (average abundance with presence/absence data equates to frequency of occurrence); body size is indicated in mm; larval development (larval dev) s either short (s) or long (l).

Table 5. Results of the BIOENV analysis for squat lobster assemblages from seamount and non-seamount habitats. Highest Spearman rank correlation (ρ) for best combination of factors indicates the highest correlation with observed patterns of species assemblage composition.

	ρ	No. of variables	Environmental variables selected	Environmental variables
All features	0.399	1	3	
Plateau	0.528	6	1, 2, 3, 5, 7, 8	1. Coral habitat suitability
Rise	0.687	1	8	2. POC flux
Slope	0.664	1	5	3. POC concentration
Ridge (averaged across regions)	0.440	2	2, 8	4. O ₂ concentration
Norfolk Ridge	0.518	3	2, 3, 4	5. Salinity
Kermadec Ridge	0.266	2	7, 8	6. Temperature
Loyalty Ridge	0.509	1	4	7. Temperature range
Tonga Ridge	0.520	3	2, 3, 5	8. Depth

For ridge systems with different assemblage compositions for seamount and non-seamount ridge habitats, *i.e.* Norfolk and Tonga Ridges, a combination of the predicted average POC flux to the sea floor and the average amount of POC at the sea floor, together with average oxygen concentration (Norfolk) and average salinity of bottom water (Tonga), were the environmental variables with the highest correlation. Examination of the bubble plots (not shown) for the Norfolk Ridge indicates that POC flux and oxygen concentration are higher for seamount habitat than for non-seamount ridge habitat, whilst the relationship between the amount of POC reaching the sea floor and assemblage composition reflects to some extent a geographic gradient (particularly high values for some of the more southern features). Bubble plots (not shown) for the Tonga Ridge are less revealing of obvious habitat or geographic pattern, although POC flux was generally higher on seamounts than on non-seamount ridge habitat.

Discussion

The results help to further our understanding of how benthic communities on seamounts differ from those found on other habitats at comparable depths. Our analyses confirmed the findings of some previous seamount studies, while also providing new insights. The findings are discussed below with reference to the three questions posed at the outset of the study.

Do squat lobster assemblages on seamounts differ from those on other habitats at comparable depths?

The overall pattern of squat lobster assemblage composition has a geographic component across the study area.

This reflects recent biogeographic patterns for squat lobsters in the region (Macpherson *et al.* 2010) and emphasizes the need to account for regional differences in analyses of differences in assemblage composition by habitat type (*e.g.* O'Hara 2007). Where data were unavailable for seamount and particular non-seamount habitats across regions, our within-region analyses revealed that assemblage composition was not different between seamount and slope, and plateau habitats. These results are similar to those of O'Hara *et al.* (2008), who found no difference between ophiuroid assemblages of seamount and slope habitats. McClain *et al.* (2009) also found that assemblages on a seamount and a canyon (incised in a nearby slope) were similar in terms of species composition.

In contrast, squat lobster assemblage composition was dissimilar between seamount and rise habitats. The galatheid species that discriminated the seamount assemblage from the assemblage of non-seamount habitat were *Munida isos* and *Munidopsis ceres*, which occurred more frequently on seamounts. These species have a relatively small body size, a characteristic that could explain their being typical of the assemblages of seamount habitat (see 'Do dispersal strategy, body size and environmental factors modify spatial patterns in assemblage composition?' below for more discussion). For the less dominant chirostylid component of the squat lobster assemblage, *Uroptychus* sp. P and *Gastroptychus novaezelandiae* discriminated between assemblages of the different habitats on the rise (the former occurring more often on seamounts, the latter on the rise). *Gastroptychus novaezelandiae* Baba 1974 was originally described from muddy and sandy substrate on the Chatham Rise and has been found in association with the pennatulacean *Balticina willemoesii* (Kölliker), which resides in soft substrata. The new species of *Uroptychus* was collected with coral matrix sampled on seamounts (K.E. Schnabel personal observation). This difference in assemblage composition is therefore perhaps not surprising, considering the stark difference in substratum type between these two habitats on the Chatham Rise (the rise is predominantly composed of soft sediments such as mud, sand and gravels; Norris 1964). However, our environmental analysis results (see 'Do dispersal strategy, body size and environmental factors modify spatial patterns in assemblage composition?' below) suggest that the observed difference in assemblage composition between seamount and rise may be depth-confounded, despite our best efforts to account for sampling effects, and should thus be treated with caution.

Differences in assemblage composition between seamount and non-seamount habitat have been observed previously for coral assemblages, where corals of slope and island habitats were dissimilar to those on seamounts

(Hall-Spencer *et al.* 2007). However, it is not possible to determine whether this comparison was confounded by environmental factors such as water depth.

Do assemblages on different ridges systems (seamounts and ridge habitat) differ?

Our across-region analysis shows an overall dissimilarity in the squat lobster assemblages of seamount and ridge habitat, but that this difference also had a regional (different ridge system) component. Before considering the within-ridge and between-ridge differences in more detail, it is worth noting that the overall dissimilarities observed, though statistically significant, were not particularly large.

Results of pair-wise tests to determine dissimilarity in assemblage composition between seamount and non-seamount habitats on different ridge systems indicated that differences between these habitats were only significant for the Tonga and Norfolk Ridges. In general, chirostyliids were more typical of the squat lobster assemblages

on seamount habitat for these two ridges. However, it was differences in the frequency of occurrence of galatheid *Munida* species that best discriminated between the assemblages of the different habitat types on the ridges. *Munida runcinata*, which occurred more often on non-seamount habitat, was the discriminating species for Tonga Ridge assemblages. The reason why chirostyliid rather than galatheid species such as *Munida* spp. were more often found on seamount habitat probably relates to their presumed association with live corals, which are often found on seamounts in the region (see Do dispersal strategy, body size and environmental factors modify spatial patterns in assemblage composition? below for more discussion).

Pair-wise tests failed to reveal a difference in the assemblage composition between seamount and ridge habitats for the Kermadec and Loyalty Ridges. This finding may relate to the particular geomorphological/environmental conditions of these ridges. That is, conditions could be homogeneous enough to prevent significant dissimilarities from emerging between assemblages at seamount and

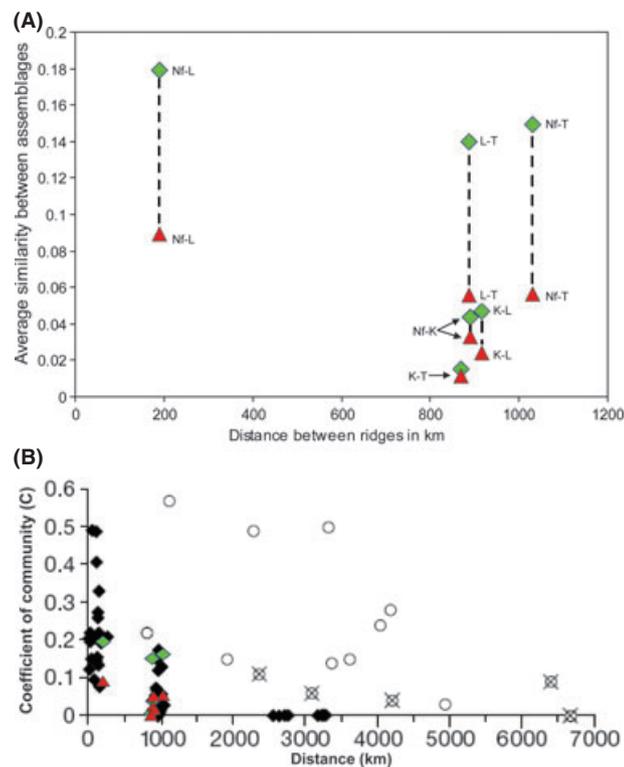


Fig. 5. (A) Relationship between average Bray–Curtis similarity of squat lobster assemblage composition for seamount/non-seamount habitat and geographic distance between ridges. Seamount habitats are represented by triangles and non-seamount ridge habitats by diamonds, and the identity of the ridges is indicated by a letter: Kermadec (K), Loyalty (L), Norfolk (Nf) and Tonga (T). (B) Same data as for (A) (green and red symbols) overlaid onto macrofauna assemblage data presented in Fig. 3 of Richer de Forges *et al.* (2000), where axes labels of original figure are retained. The coefficient of community (C) (equivalent to average Bray–Curtis similarity) is shown in relation to geographic distance between sites of different habitat. Seamount habitat (inverted solid diamonds), hydrothermal vent sites from the East Pacific Rise in the North and South Pacific and Galapagos Rift (open circles), and vent sites from disjunct ridges in the northeast Pacific at 41–49°N (crossed circles).

non-seamount habitats on these ridges. However, the prospect remains that some unaccounted for sampling artifact could prevent the detection of the sort of differences in assemblage composition that were observed for the Tonga and Norfolk Ridges.

Richer de Forges *et al.* (2000) previously observed differences between seamount macrofauna assemblages across different ridges in the Southwestern Pacific and found that assemblages on ridges systems separated by ~1000 km were dissimilar in composition, and that dissimilarity increased with geographic distance. Our results, when plotted as average levels of assemblage similarity for habitats *versus* geographic distance, suggest a similar decreasing trend in similarity with distance between ridge systems (Fig. 5A). Interestingly, this plot indicates that assemblages of non-seamount ridge habitat are more similar than are assemblages of seamount habitat between ridges, and that this pattern is consistent across different ridge systems [*i.e.* red triangles (seamount habitat) are always below green diamonds (non-seamount ridge habitat) on the plot]. This lends support to the suggestion that benthic communities on seamounts are likely to be more dissimilar to one another because of their 'island'-like nature than are communities at different locations in the surrounding habitat. However, it is worth noting that differences in the average assemblage similarity between the seamount and non-seamount habitat were greater for some between-ridge comparisons than for others. The small difference between levels of average similarity for the Kermadec–Tonga Ridges comparison is probably related to the semi-continuous nature of these two ridges, and arguably represents an along- rather than a between-ridge pattern.

Overlaying our data on the original Fig. 3 of Richer de Forges *et al.* (2000) reveals a reasonable congruence (Fig. 5B), despite the original data covering all macrofauna and sharing only a very limited amount of data (from Norfolk Ridge) with the present dataset. Thus, the present study supports the original finding of seamount assemblage dissimilarity between ridges, which increases with increasing geographic distance. Richer de Forges *et al.* (2000) argued that relatively closed circulation patterns at seamounts (*e.g.* Taylor columns and eddies) and rectification of currents along ridges were responsible for the differences in assemblage composition they observed, particularly between ridge systems. Larger scale oceanographic features such as fronts (Sokolov & Rintoul 2000; Schiller *et al.* 2008) could also affect dispersal of benthic fauna between ridge systems. A key finding of our study is that of consistent differences in levels of assemblage similarity for seamount and non-seamount habitats, nested within inter-ridge system patterns.

Do dispersal strategy, body size and environmental factors modify spatial patterns in assemblage composition?

For differences in assemblage composition between ridges that were significantly different, squat lobster species of seamount assemblages were relatively small and had short larval duration, compared to the larger species with long larval duration that dominated the assemblages of non-seamount ridge habitat. This observation supports a previous study that indicated seamount fauna are characterized by species with short larval durations and limited dispersal ability (Parker & Tunnicliffe 1994). It has been suggested that tidally rectified circulation of currents around seamounts serves to preferentially retain larvae with limited planktonic duration (Mullineaux & Mills 1997). Species with a smaller body size are generally more likely to brood or have abbreviated development than are those with a larger body size, which tend to have long-lived larvae that disperse more widely in the plankton (Stratham and Strathman 1982). Although this has not been demonstrated specifically for squat lobsters, our observations on body size and larval duration of squat lobsters on seamounts (on ridges) support the generalizations concerning the life history characteristics of species that are thought typical of island-like habitats (Whittaker & Fernandez-Palacios 2007).

In terms of environmental drivers, the overall pattern in assemblage composition across the study area (irrespective of habitat type) was related to the gradient in amount of POC reaching the sea floor. Whilst the amount of potential food arriving at the sea floor could influence overall compositional pattern, it is more likely that this general south–north gradient reflects the difference in the overall water mass characteristics (oligotrophic waters in the north moving towards more productive waters in the south of the area), as well as the related water circulation patterns (Sokolov & Rintoul 2000; Schiller *et al.* 2008). That is, as already mentioned (in 'Do squat lobster assemblages on seamounts differ from those on other habitats at comparable depths?' above) the overall assemblage pattern reflects the biogeographic pattern observed for squat lobsters in the Southwestern Pacific Ocean (Macpherson *et al.* 2010).

The environmental factor that was most strongly related to the assemblage composition for seamount and non-seamount habitats on Chatham Rise was water depth. However, seamount habitat was generally deeper than non-seamount habitat, which, despite our efforts to minimize the known influence of water depth, suggests that the assemblage dissimilarity observed between seamount and rise habitat is potentially depth-confounded. Future research will be required to determine whether a difference in assemblage composition

actually exists or whether (as for the plateau and slope) no difference is apparent between seamount and rise habitat at comparable water depths.

For assemblages on seamount and non-seamount habitats across all ridges there was a relationship with the indications of a geographic cline in POC flux. Like the amount of POC at this large spatial scale, this cline is thought to be related to differences in water mass/current circulation patterns and to influence biogeographic patterns (see above for overall assemblage pattern). Ideally, our environmental correlation analysis would have included variables that describe, or act as proxies for, the types of current flow proposed to explain between-ridge differences in the composition of assemblages on seamounts (e.g. Richer de Forges *et al.* 2000). Unfortunately, data (speed and direction) from regional circulation models are not yet available at the appropriate vertical (depth) spatial resolution.

Within regions (ridge system) where differences in assemblage composition were found between seamount and non-seamount ridge habitats (Tonga and Norfolk Ridges) the observed assemblage patterns were related to the POC flux, which was higher on seamounts. A difference in POC fluxes on and off seamounts (higher on seamounts) has been predicted to occur as a result of tidally forced circulation, accelerated current flow and turbulent mixing (White *et al.* 2007), and to have an influence on the faunal composition of seamounts; that is, seamount communities dominated by suspension feeding groups that could exploit the elevations in the delivery of a particulate food resource (e.g. corals, sponges, crinoids Samadi *et al.* 2007). It is possible that differences in POC flux are responsible for between-habitat compositional patterns within a group such as squat lobsters that exhibit a range of feeding strategies. Feeding strategies for chirostylids are unknown but they are assumed to be suspension feeders (e.g. Kilgour & Shirley 2008) and are associated with suspension feeding taxa such as corals, which could explain their dominance in seamount assemblages. Feeding studies and *in situ* observation have so far only been carried out for galatheids of genus *Munida*, and indicate that they are opportunistic feeders with a strong seasonal variation between predatory and deposit feeding (e.g. Romero *et al.* 2004). The flexible use of these feeding strategies by galatheids may explain their dominance in non-seamount habitat that receives a lower POC flux.

Dissolved oxygen concentration, which was higher on seamounts, was also related to differences in the assemblage composition between habitats on the Norfolk Ridge. The overall difference in oxygen concentration between the habitats was not large, nor was it across the oxygen minimum threshold. Thus, it is difficult to envisage how

this variable may be influencing assemblage composition in a way that has been observed previously for a single seamount in an oxygen minimum zone in the Northern Pacific Ocean (Wishner *et al.* 1990).

Stony coral habitat suitability was not identified as being correlated with any of the observed patterns. This finding was somewhat surprising because some squat lobsters, particularly chirostylids, use corals as a habitat from which to feed and gain shelter from predation (Kilgour & Shirley 2008). It was therefore expected that, as in a previous study on ophiuroids (O'Hara *et al.* 2008), there should be some form of pattern that reflected the relationship between assemblage composition and the presence of coral habitat. However, whereas the aforementioned study included data from samples known to have been taken from coral habitat, our study used output from a coral habitat suitability model. The uncertainty associated with this model and its spatial resolution may account for the lack of a relationship between squat lobster assemblage composition (particularly on seamounts) and presence of the biogenic habitat.

The present study lends further support to conclusions derived from recent studies that suggest benthic communities of seamounts are not distinct, in terms of species composition (rather than abundance or biomass), from those found at other habitats at comparable depth such as slope and canyons. However, our study provided evidence to suggest that the benthic communities of seamounts on ridges can be distinct from those found elsewhere on ridges. Our results also extend a previous finding that differences in seamount communities between ridges increase with geographic distance, by finding the same pattern for assemblages of non-seamount ridge habitat. Clearly, further study will be required to determine the generality of these findings (including a re-assessment of the case for rise habitat) can be fully realized. In addition, future analyses (with similarly robust datasets as used in the present study) should include a greater array of environmental data at appropriate spatial resolution, in order to gain a better understanding about the natural forces that drive any peculiarity in the composition of seamount communities.

Acknowledgements

The authors wish to acknowledge the squat lobster taxonomy and biogeography initiative of the Census of Marine Life (CoML) project COMARGE, which made possible the compilation of a dataset with consistent species identifications. Particular thanks are owed to the participants of a workshop run by the Data Analysis Working Group (DAWG) of the CoML project CenSeam, whose advice and support served to advance the analysis reported upon

here. In addition to their support at the DAWG workshop, Tim O'Hara (Victoria Museum, Australia) and Derek Tittensor (Dalhousie University, Canada) are thanked for their provision of environmental data. Kevin McKay (NIWA) provided a great deal of valuable GIS assistance during the data treatment phase of the study. Funding (for A.R. and K.S.) was provided by the New Zealand Foundation for Research, Science and Technology (FRST) for NIWA's research programme 'Seamounts: their importance to fisheries and marine ecosystems' (CO1X0508) and its 'Marine Biodiversity and Biosecurity Outcome Based Investment' (project CO1X0502).

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