Benthic community structure and water column characteristics at two sites in the Kermadec Islands Marine Reserve, New Zealand

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Abstract   The Kermadec Islands Marine Reserve (KIMR), which is located at 30°S, is New Zealand's largest marine reserve at 748 000 ha, and its biota is composed of a mix of warm temperate, subtropical, and tropical species. A depth-stratified ecological survey was conducted of the abundance and percentage cover of macrobenthic species and of the water column at two sites (Meyer Island and West Chanter Island) 2 km apart. Significant differences in benthic community structure and in water column turbidity and chlorophyll concentrations were observed between the two sites despite their proximity and physical similarity. Compared with other "snapshot" surveys of benthic community structure at sites within the KIMR there was a high degree of similarity among the species observed, but often a low degree of similarity in species abundance or percentage cover as a function of depth. We suggest that despite its isolation and the degree of difficulty of working at this location, a full-scale ecological survey of the coastal marine biota of the KIMR is warranted to better understand New Zealand's subtropical marine biota and its affinities with other marine biotas of the South Pacific.

INTRODUCTION

The Kermadec Islands are composed of 11 subtropical volcanic islands located in the far northeast of New Zealand's exclusive economic zone (Fig. 1). The islands are remote and inaccessible, being located 750 km from the mainland, and comprise three main groups: the most southerly (31°21′S, 178°48′W) includes L'Esperance Rock and Havre Rock, the middle group includes Cheeseman Island and Curtis Island to the south (30°32′S, 178°33′W), and Macaulay Island and Haszard Island to the north (30°14′S, 178°25′W). The most northerly group (29°15′S, 177°55′ W) includes Raoul, Meyer, North Chanter, South Chanter, West Chanter, Napier, and Nugent Islands. These Kermadec Ridge islands are volcanic in origin (Raoul, the largest island in the group, last erupted in 1964), and form part of the active Tonga-Kermadec Arc (Lloyd & Nathan 1981).

The Kermadec Islands are of ecological interest because of their isolation, relative youth (based on potassium-argon dating, the oldest parts of Raoul Island date back to 0.6–1.4 M ybp: Gabites, appendix 2 in Lloyd & Nathan 1981), and their subtropical location between temperate New Zealand and the tropical Tonga Islands (Brook 1998). The species composition of the Kermadec Islands reflects these factors, with a marine biota which is a mix of tropical, subtropical and temperate species, characterised by high rates of faunal turn-over and high rates of allopatric speciation (Brook 1998, 1999). To ensure the long-term preservation of the biota of these islands, in 1990 the New Zealand Department of Conservation gave Marine Reserve status (full no-take preservation) to all islands in the group (http://www.doc.govt.nz/Conservation/Marine-and-Coastal/Marine-Reserves/040~Kermadec/index.
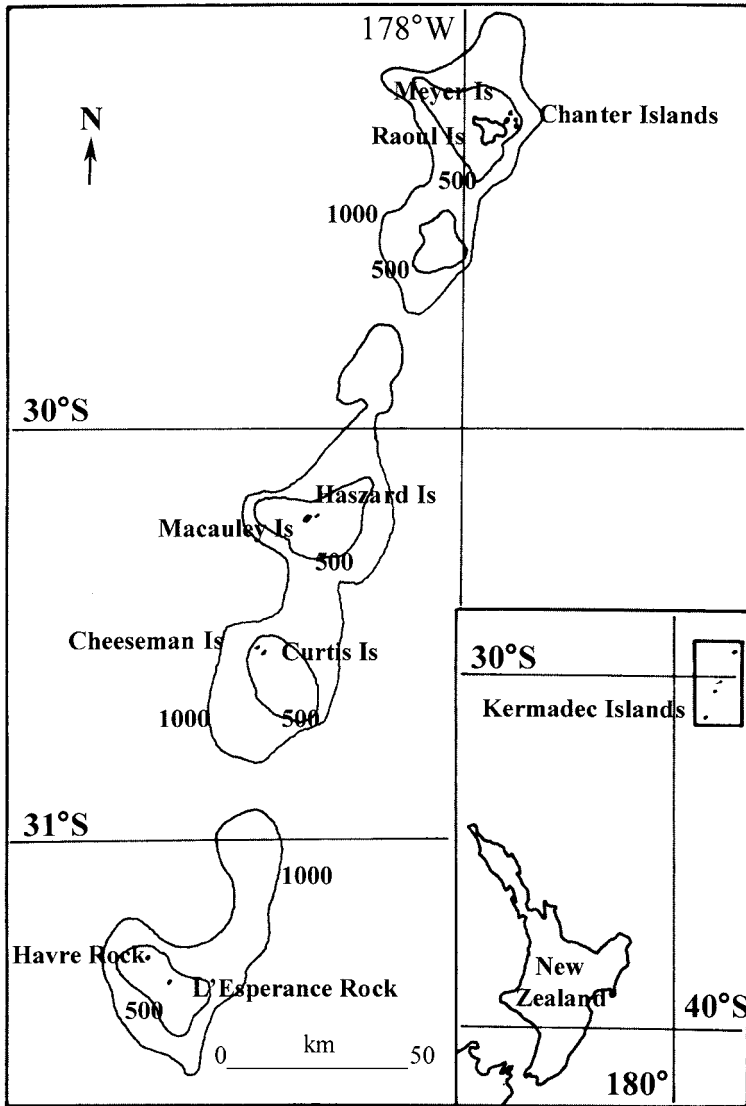
Fig. 1 Geographic location of the Kermadec Islands Marine Reserve (modified from Francis et al. 1987 with permission of the authors). The 500 m and 1000 m depth contours are shown around the islands. Scale bar is 50 km.

asp [accessed 25 November 2005]). The Kermadec Islands Marine Reserve (KIMR) is presently New Zealand's largest and third oldest marine reserve (http://www.doc.govt.nz/Conservation/Marine-and-Coastal/Marine-Reserves/040~Kermadec/index.asp [accessed 25 November 2005]). The reserve covers 748 000 ha and extends 22 km out to the limits of the territorial sea around each of the three island groups (Fig. 1).

In a wider perspective the Kermadec Islands are of considerable ecological and biogeographical interest because they form the southwest corner of a triangle which loosely delineates the marine Polynesian region, the other corners being Hawaii in the north and Easter Island in the east. The currents in this part of the Pacific Ocean are poorly understood, but the main flow into the region is thought to be eastward, from New South Wales towards Norfolk Island (1370 km to the west of the Kermadecs), before reaching northern New Zealand (North Cape and The Three Kings Islands, 830 km to the southwest) and then the Kermadec Island

group (Marshall 1979; Schiel et al. 1986). Flow from the northwest, most notably from the vicinity of New Caledonia (1590 km to the northwest) and from Fiji flowing past the Minerva Reefs which are southwest of Tonga (590 km to the north) may also be important, suggesting that the biogeographic affinities of the Kermadec group lie to the north and in particular to the west, rather than with other regions of the South Pacific.

Previous ecological work at the Kermadec Islands is limited, largely because of the inaccessibility and remoteness of the islands, but also because of the difficult sea conditions which characterise small, steep-sided volcanic islands located in open oceanic waters (Schiel et al. 1986; Brook 1999). For the Kermadec group, McKnight (1968), Marshall (1979, 1981), Foster (1981), Nelson & Adams (1984), Schiel et al. (1986), Francis et al. (1987), Creese et al. (1990), Cole et al. (1992), Francis (1993), Brook (1998, 1999), and Cole (2001) have all provided either species lists or descriptions of new species, or have described various aspects of the ecology of macroalgae, echinoderms, molluscs, cirripedes, scleractinian corals, and fish. However, work on subtidal benthic community structure is limited to only three studies. First, Schiel et al. (1986) surveyed subtidal communities at Boat Cove (Raoul Island) in March 1984 from the high intertidal to 20 m depth. They reported that inshore communities represented a mixture of temperate and tropical forms, and noted the absence of both coral reefs and stands of large brown algae. Second, Cole et al. (1992) surveyed mobile benthic invertebrates and pelagic fish at four sites, and benthic fish at six sites in September 1988. They concluded that their data were consistent with previously published accounts of zonation at the Kermadec Islands, and that the abundances of herbivores were insufficient to account for the lack of macroalgae at the islands. Third, Brook (1999) surveyed the coral fauna from the intertidal zone to 45 m depth based on material collected over a 10–year period (October 1985 to May 1995). He noted an attenuation from north to south in the number of coral species, that the biogeographic affinities of the coral fauna lie with other subtropical southwestern Pacific islands rather than with New Zealand, and that the majority of hermatypic species are restricted to <30 m depth and have an encrusting growth form.

The purpose of the present paper is to describe shallow subtidal community structure and water column characteristics at two Kermadec Island locations. In the 5 days available to us at KIMR we surveyed two sites using a depth-stratified approach. Our intention was to complement the previous benthic survey work carried out at KIMR, to investigate water column characteristics at these sites, and thereby to add to the meagre existing marine ecological knowledge of these islands.

MATERIALS AND METHODS

Site selection

Two sites were surveyed by SCUBA diving during the period 7–11 July 2002 (Fig. 2). The first location was a series of pinnacle rocks at the northeast corner of West Chanter Island (hereafter West Chanter), within c. 500 m of the site on North Chanter Island surveyed by Cole et al. (1992). The second location was a vertical, southeast facing rock wall on the northwest side of Meyer Island (hereafter Meyer), within c. 500 m of the site surveyed by Cole et al. (1992) and located very close to site 4 of Brook (1999). Both sites are west facing and have similar topography to allow comparison to be made between them. A preliminary dive survey conducted on 6 July 2002 indicated that the most widely occurring shallow subtidal community in the northern Kermadec Island group is composed of extensive cover of encrusting red coralline algae and fine filamentous red and green algae. A number of conspicuous macroinvertebrates (mostly echinoderms, molluscs, hard and soft corals) also define this community, which is mostly found on large boulders, pinnacle rocks, and vertical rock walls from approximately low water to a depth of c. 15 m. We selected our survey locations because they were accessible given the prevailing wind and sea conditions, extended to >15 m depth, and had well developed communities of the type described above.

Benthic macroinvertebrate abundance and percentage cover estimates

At West Chanter and at Meyer surveys were carried out at four depth strata, 3–6 m, 6–9 m, 9–12 m, and 12–15 m, consistent with previous surveys (Schiel et al. 1986; Cole et al. 1992; Brook 1999). Macro-invertebrate abundance data at each stratum were collected by counting all individuals in 19 groups (see Table 1) within 16 haphazardly located quadrats of 50×50 cm (total area sampled = 4 m^2 per stratum). At the same time, one diver in each pair of divers made a visual estimate of the percentage cover of sessile organisms of nine major groups, including coral rubble/sand, from each quadrat (see Table 1).
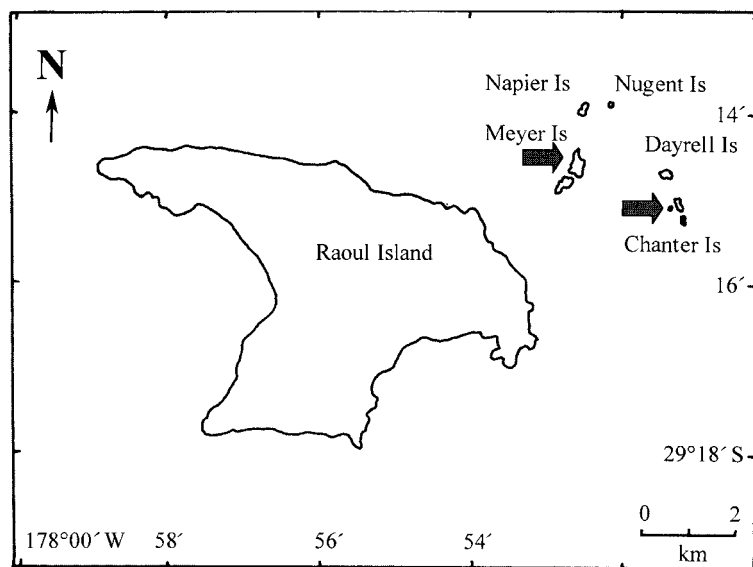
Fig. 2 Geographic locations of survey sites at Meyer Island and West Chanter Island (as indicated by arrows) within the Kermadec Islands Marine Reserve, New Zealand.

The groups whose abundance or percentage cover were estimated often represented numerous species/genera which were pooled for the surveys. For example, the "hard corals" included *Cyphastrea* sp., *Goniastrea* spp., *Montastrea curta*, *Montipora* spp., and *Pocillopora* sp.; the encrusting red algae included *Lithothamnion* sp., and *Apophloea* sp.; and the foliose and filamentous algae included such genera as *Caulerpa*, *Codium*, *Corallina*, *Enteromorpha*, *Galaxaura*, *Gelidium*, *Polysiphonia*, and *Pterocladia*. Photographs were taken of representative species and video recordings were made of the general environment.

Species identifications were obtained by reference to appropriate literature (e.g., McKnight 1968; Marshall 1979, 1981; Foster 1981; Nelson & Adams 1984; Schiel et al. 1986; Creese et al. 1990; Cole et al. 1992; Brook 1998, 1999) or were provided by individual authorities, either directly from inspection of specimens, or indirectly from photographs or video recordings.

Testing for diver error in estimating percentage cover

We tested the two divers who had visually estimated the percentage cover data to determine the accuracy of their estimates. Both divers were independently asked to provide estimates of percentage cover of different numbers of randomly sized and located test areas within each of 16 different test quadrats. Subsequently, images of the 16 test quadrats were scanned into a PC and the percentage cover of the areas within each test quadrat was determined by an independent researcher using SigmaScan Pro software (version 4.0, Jandel Scientific). We tested the data from divers' estimates and the actual values of percentage cover for normality (Kolmogorov-Smirnov test: Sokal & Rohlf 1995) and homogeneity of variances (Levene's test: Manly 2005) before carrying out a one-way analysis of variance (ANOVA: Sokal & Rohlf 1995) to test for significant differences among the two divers' estimates of percentage cover and the actual percentage cover values. A correlation analysis of percentage cover estimates as a function of actual percentage cover values was also carried out for each diver. For all analyses the significance level was set at $\alpha = 0.05$.

Water column characteristics

At both sites (Fig. 2) on sandy substrate in c. 15 m of water and within 20 m of the survey locations, two CTD units (Richard Brancker Research Ltd XR 420) custom fitted with fluorometers and turbidimeters were deployed at 3 m and 8 m below Mean Low Water. The four CTDs were deployed on 7 July 2002 and were retrieved 5 days later. The CTD data loggers recorded temperature (°C), pressure (deciBars), conductivity (mS cm^{-1}), chlorophyll concentration (μg litre^{-1}), and turbidity (FTU) at 1-min intervals for the duration of their deployment.

Data analysis

All statistical data analyses were conducted using the software packages Statistica version 6.0 (StatSoft

2001) or PRIMER version 5.2.4 (Clarke & Gorley 2001; Clarke & Warwick 2001). Where appropriate, data were tested for normality (Kolmogorov-Smirnov test: Sokal & Rohlf 1995) and homogeneity of variances (Levene's test: Manly 2005) and, if possible, data were transformed to achieve normality. When this was not possible, non-parametric analyses were used. For all analyses the significance level was set at $\alpha = 0.05$.

Analyses involved comparisons of abundance data from 19 different species or groups of species, percentage cover data for eight groups of species and coral rubble/sand. Hereafter, use of the term "group" refers to this combined abundance and percentage cover data derived from these 28 different categories (Table 1). Our intention was to investigate macro-benthic invertebrate community structure in the predominant community of the marine reserve: abundance and percentage data were therefore pooled whenever possible.

Mean ($\pm$ SD) estimates of the number of different groups were calculated across the 16 quadrat samples

Table 1 Major groupings for which abundance and percentage cover data were obtained at two sites (Meyer Island and West Chanter Island) and four depth-strata (3–6, 6–9, 9–12, and 12–15 m) in the Kermadec Islands Marine Reserve, New Zealand.

Phylum/Group	Genus and species	Common name
Major groupings assessed for abundance		
Echinodermata		
Asteroidea	*Ophidiaster kermadecensis*	Yellow 5-arm starfish
Asteroidea	Unknown	Orange 5-arm starfish
Asteroidea	*Astrostole rodolphi*	Black 7-arm starfish
Asteroidea	*Acanthaster planci*	Crown of thorns starfish
Echinoidea	*Centrostephanus rodgersii*	Purple sea urchin
Echinoidea	*Echinometra mathaei*	White spined urchin
Echinoidea	*Tripneustes gratilla*	Black urchin/white spines
Echinoidea	*Heliocidaris tuberculata*	Brown urchin
Crinoidea	*Tropiometra afra*	Sea lily
Mollusca		
Bivalvia	*Spondylus raoulensis*	Spiny oyster
Gastropoda	*Tectus royanus*	Top shell
Gastropoda	*Morula smittii*	Whelk
Gastropoda	Conidae	Cone shells
Gastropoda	Unknown	Nudibranch
Polyplacophora	*Leptochiton mestayerae*	Chiton
Arthropoda		
Cirripedia	*Tesseropora* sp.	Barnacles
Decapoda	*Calcinus* spp.	Hermit crabs
Decapoda	Unknown	Shrimp
Annelida		
Polychaeta	Unknown	Tube-dwelling worm

Group	Contents of group	
Major groupings assessed for percentage cover		
Filamentous algae	various genera of green and red algae including *Caulerpa*, *Codium*, *Corallina*, *Enteromorpha*, *Galaxaura*, *Gelidium*, *Polysiphonia* and *Pterocladia*	
Encrusting red algae	mostly restricted to *Apophloea* and *Lithothamnion*	
Hard corals	various genera including *Cyphastrea*, *Goniastrea*, *Montastrea*, *Montipora* and *Pocillopora*	
Soft corals	mostly *Efflatounaria* spp.	
Anemones	various genera	
Sponges	various genera	
Ascidians	various genera	
Bryozoans	various genera	
Coral rubble/sand	coral rubble and sand	

for each stratum. Two-way ANOVA (Sokal & Rohlf 1995) was used to test for differences in mean group abundance as a function of depth and site. A *t* test (Sokal & Rohlf 1995) was used to compare the mean number of groups observed at Meyer and at West Chanter without reference to depth-stratification (i.e., pooling across all depth strata within either site). For all analyses the significance level was set at $\alpha = 0.05$.

Based on the eight depth stratum-specific mean values derived from the combined raw abundance and percentage cover data, the software package PRIMER was used to compare community structure across sites and depths. Following a square root transformation (the least severe transformation available), similarity was estimated using the normalised Euclidean distance option because this permits the use of data with different units, which here involved absolute numbers and percentage cover (Clarke & Gorley 2001; Clarke & Warwick 2001). The CLUSTER procedure was used to generate a dendrogram of similarity (units in Euclidean distance) among all eight strata, and the MDS procedure was used to generate a non-metric multi-dimensional scaling ordination of the eight strata. These two techniques permit a visual examination of the relationships (similarity) among the depth strata, but do not permit hypothesis testing of differences in community structure. Finally, we used the analysis of similarities (one-way ANOSIM) procedure to test for differences in community structure among the eight depth strata. Analysis was carried out on the raw quadrat-specific data following the generation of a similarity matrix based on normalised Euclidean distances and using the square root transformation (for reasons as outlined above).

Mean values (± SD) of conductivity, temperature, chlorophyll concentration, and turbidity were calculated from the CTD data, and bi-variate plots were examined visually to determine the nature of the relationships between pairs of variables at each of the four depth strata. Because none of the CTD data were normally distributed, the non-parametric Kruskal-Wallis two-tailed multiple comparison test (Sokal & Rohlf 1995) was used to test for differences in each of the four variables among the four depth strata. *Gamma*, a non-parametric correlation coefficient (StatSoft 2001), was used to test for correlations between ranked data for turbidity and chlorophyll at each depth stratum. *Gamma* was used because it is preferable to Spearman's *R* and to Kendall's *tau* when the data contain many tied observations, as in our very large data sets (Clarke & Gorley 2001; StatSoft 2001).

RESULTS

Testing for diver error in estimating percentage cover

Both divers' estimates of percentage cover, and the actual percentage values, from the 16 test quadrats were normally distributed (diver A: Kolmogorov-Smirnov $D = 0.2011$, $P > 0.2$; diver B: Kolmogorov-Smirnov $D = 0.1966$, $P > 0.2$; actual values: Kolmogorov-Smirnov $D = 0.222$, $P > 0.2$), with homogeneous variances (Levene's $F = 0.253$, $P = 0.778$). One-way ANOVA indicated that there were no significant differences among the three groups (diver A versus diver B versus SigmaScan) in the percentage cover values ($F_{(2, 45)} = 0.379$, $P = 0.687$). Consistent with this result, the correlation analyses indicated that there were very good agreements of percentage cover estimates for both divers with the SigmaScan values (diver A: $r^2 = 0.9835$, d.f. = 14, $P < 0.0001$; diver B: $r^2 = 0.9758$, d.f. = 14, $P < 0.0001$). We therefore concluded that the percentage cover estimates obtained from both divers were of sufficient accuracy to use for our present purposes.

Table 2 Two-way ANOVA testing for differences in number of group as a function of Site (Meyer Island and West Chanter Island) and Depth (3–6, 6–9, 9–12, and 12–15 m) in the Kermadec Islands Marine Reserve, New Zealand.

Effect	Sum of squares	Mean d.f.	Significance square	F	(P)
Intercept	2574.03	1	2574.03	1581.99	<0.001
Site	26.28	1	26.28	16.15	<0.001
Depth	13.53	3	4.51	2.77	0.045
Site × Depth	16.91	3	5.64	3.46	0.019

Benthic macroinvertebrate abundance and percentage cover estimates

Site explained greater variation in the number of groups ($P < 0.001$) than did depth ($P = 0.0445$), but there was also a significant interaction term (site × depth, $P = 0.0185$) indicating that the mean number of groups differed between the sites as a function of depth (Table 2). Comparing the mean number of groups for each depth stratum between Meyer and West Chanter, the mean number of groups was greater at West Chanter than at Meyer at 3–6 m, but at 6–9, 9–12, and 12–15 m the opposite was true, with the greatest difference at 6–9 m, and the least difference at 12–15 m (Table 3). Overall, there was a higher mean number of groups observed at Meyer (mean = 4.92, SD = 1.36, $n = 64$) than at West Chanter (mean = 4.03, SD = 1.32, $n = 64$). This difference was statistically significant ($t = 3.830$, d.f. = 126, $P = 0.0002$).

Mean (±SD) estimates of abundance and percentage cover for each group reveal more about between-site differences than they do about within-site depth related differences (Table 4). Certain groups, such as the crown of thorns starfish *Acanthaster planci*, the black and white urchin *Tripneustes gratilla*, the orange 5-arm starfish (unknown species), the endemic spiny oyster *Spondylus raoulensis*, the hermit crabs of the genus *Calcinus*, the Conidae (cone shells), a chiton (probably *Leptochiton mestayerae*), and a nudibranch were only observed at Meyer, whereas other groups such as the yellow 5-arm starfish *Ophidiaster kermadecensis*, the pale-spined urchin *Echinometra mathaei*, the brown urchin *Heliocidaris tuberculata*, barnacles of the genus *Tesseropora*, ascidians, tube-dwelling serpulid worms, and the shrimp were only observed at West Chanter. Groups such as the predatory whelk *Morula smittii*, the hard corals, the soft corals, and coral rubble/sand were more abundant at Meyer, whereas the purple urchin *Centrostephanus rodgersii*, the top shell *Tectus royanus*, the encrusting red algae, bryozoans, and anemones were more abundant at West Chanter (Table 4).

The dendrogram of depth stratum similarity based on normalised Euclidean distance (Fig. 3) revealed two main clusters. Within the first were located the 3–6 m and the 6–9 m depth strata of West Chanter; the other two West Chanter depth strata and all four depth strata of Meyer formed another grouping. Thus, the two deeper depth strata at West Chanter showed greater similarity to all four depth strata at Meyer than they did to the two shallower depth strata at West Chanter. The MDS ordination (Fig. 4) shows that the Meyer depth strata group together, indicating a degree of among-stratum similarity, whereas the four West Chanter depth strata are more spread out, indicating lower similarity among depth strata. The West Chanter 9–12 m and 12–15 m depth strata are in closer proximity to the 3–6 m and 12–15 m Meyer depth strata than they are to the other West Chanter depth strata.

Analysis of similarities (ANOSIM) revealed significant differences in community structure among the eight depth strata (Global $R = 0.079$, $P < 0.001$). Of the 28 pair-wise comparisons between depth strata, 23 were significant at the $\alpha = 0.05$ level, and included all between-site comparisons (Table 5). Non-significant differences in community structure ($P > 0.05$) were observed only for pair-wise comparisons of depth strata from the same site, with three of six comparisons of Meyer depth strata and two of six comparisons of West Chanter depth strata being non-significantly different.

Table 3 Mean ± SD of number of groups per site (Meyer Island and West Chanter Island) as a function of depth (3–6, 6–9, 9–12, and 12–15 m) in the Kermadec Islands Marine Reserve, New Zealand.

Site	Depth (m)	Mean	SD	*n*
Meyer Island	3–6	5.00	0.89	16
	6–9	5.25	2.05	16
	9–12	4.81	0.98	16
	12–15	4.69	1.25	16
West Chanter Island	3–6	5.06	1.24	16
	6–9	3.38	0.81	16
	9–12	3.56	1.26	16
	12–15	4.13	1.31	16

Table 4 Mean (± SD) values of abundance and percentage cover standardised to 1 m² for each group as a function of depth (3–6, 6–9, 9–12, and 12–15 m) at two sites (Meyer Island and West Chanter Island) in the Kermadec Islands Marine Reserve, New Zealand.

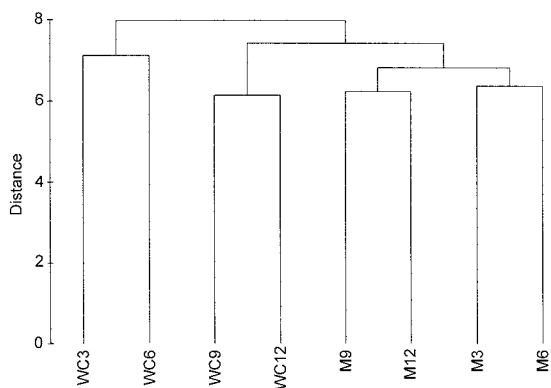| Group	Meyer Island				West Chanter Island			
	3–6 m	6–9 m	9–12 m	12–15 m	3–6 m	6–9 m	9–12 m	12–15 m
Acanthaster planci	0 (–)	0.25 (0.25)	0 (–)	0 (–)	0 (–)	0 (–)	0 (–)	0 (–)
Astrostole rodolphi	0 (–)	0.25 (0.25)	0 (–)	0 (–)	0 (–)	0.25 (0.25)	0 (–)	0 (–)
Ophidiaster kermadecensis	0 (–)	0 (–)	0 (–)	0 (–)	0 (–)	0 (–)	0.50 (0.34)	0 (–)
Orange 5-arm starfish	0 (–)	0 (–)	0.50 (0.34)	0 (–)	0 (–)	0 (–)	0 (–)	0 (–)
Centrostephanus rodgersii	1.25 (0.60)	0 (–)	0 (–)	0 (–)	4.25 (0.85)	1.50 (0.81)	2.00 (0.73)	0.25 (0.25)
Echinometra mathaei	0 (–)	0 (–)	0 (–)	0 (–)	0 (–)	0 (–)	0.25 (0.25)	0.25 (0.25)
Heliocidaris tuberculata	0 (–)	0 (–)	0 (–)	0 (–)	0.25 (0.25)	0.50 (0.34)	0 (–)	0 (–)
Tripneustes gratilla	0 (–)	0.75 (0.40)	0 (–)	0 (–)	0 (–)	0 (–)	0 (–)	0 (–)
Tropiometra afra	1.25 (0.60)	1.25 (0.79)	0.75 (0.54)	0.50 (0.50)	1.75 (1.26)	0 (–)	2.00 (1.51)	5.75 (2.28)
Spondylus raoulensis	0.25 (0.25)	0 (–)	0 (–)	0 (–)	0 (–)	0 (–)	0 (–)	0 (–)
Morula smittii	3.00 (1.06)	2.00 (0.82)	1.00 (0.58)	0.25 (0.25)	1.75 (1.09)	0 (–)	0.75 (0.40)	0.75 (0.54)
Tectus royanus	0.25 (0.25)	0.75 (0.40)	0 (–)	1.00 (0.58)	0.50 (0.34)	0.50 (0.50)	0 (–)	0.25 (0.25)
Cone shells	0 (–)	0.25 (0.25)	0 (–)	0 (–)	0 (–)	0 (–)	0 (–)	0 (–)
Nudibranch	0 (–)	0 (–)	0.25 (0.25)	0 (–)	0 (–)	0 (–)	0 (–)	0 (–)
Leptochiton mestayerae	0 (–)	0 (–)	0.25 (0.25)	0 (–)	0 (–)	0 (–)	0 (–)	0 (–)
Tesseropora sp.	0 (–)	0 (–)	0 (–)	0 (–)	0 (–)	2.50 (2.50)	0 (–)	0 (–)
Calcinus spp.	0 (–)	0.50 (0.34)	0.25 (0.25)	0.25 (0.25)	0 (–)	0 (–)	0 (–)	0 (–)
Shrimp	0 (–)	0 (–)	0 (–)	0 (–)	0 (–)	0 (–)	0 (–)	0.25 (0.25)
Polychaete	0 (–)	0 (–)	0 (–)	0 (–)	0 (–)	0 (–)	0.25 (0.25)	0.50 (0.34)
Filamentous algae (%)	45.31 (25.59)	40.31 (34.33)	39.06 (19.60)	29.69 (22.47)	15.62 (13.65)	53.75 (42.99)	21.63 (30.27)	53.13 (33.87)
Encrusting red algae (%)	27.50 (18.89)	24.06 (18.90)	32.50 (14.38)	40.31 (20.93)	51.25 (24.12)	46.75 (25.48)	45.50 (39.56)	28.38 (30.00)
Hard coral (%)	15.63 (17.31)	10.31 (12.67)	5.38 (6.49)	6.50 (8.70)	15.81 (26.28)	1.38 (2.85)	2.50 (5.48)	1.13 (2.70)
Soft coral (%)	13.06 (20.82)	16.38 (18.26)	12.81 (16.54)	16.63 (15.54)	0 (–)	0.63 (1.71)	1.88 (4.03)	5.31 (21.25)
Sponge (%)	3.19 (6.19)	3.75 (6.02)	1.50 (2.00)	0.94 (1.81)	3.94 (6.56)	2.50 (4.08)	3.56 (8.82)	1.13 (2.96)
Ascidian (%)	0 (–)	0 (–)	0 (–)	0 (–)	4.06 (8.00)	1.81 (3.47)	0.44 (1.21)	0 (–)
Bryozoan (%)	0 (–)	0 (–)	0 (–)	0.06 (0.25)	2.00 (4.00)	0.63 (2.50)	0.88 (2.55)	0.44 (0.51)
Anemone (%)	0 (–)	0 (–)	0 (–)	0.06 (0.25)	6.94 (15.34)	0.06 (0.25)	0 (–)	0 (–)
Coral rubble/sand (%)	1.06 (3.75)	2.50 (4.08)	0.63 (1.71)	9.38 (11.53)	3.13 (12.50)	0 (–)	0 (–)	2.81 (5.98)

Fig. 3 Dendrogram of community structure similarity (units in Euclidean distance) among the eight depth strata generated from a between-depth stratum similarity matrix of square-root transformed data. (M3, Meyer Island 3–6 m; M6, Meyer Island 6–9 m; M9,Meyer Island 9–12 m; M12, Meyer Island 12–15 m; W3, West Chanter Island 3–6 m; W6, West Chanter Island 6–9 m; W9, West Chanter Island 9–12 m; W12, West Chanter Island 12–15 m.)
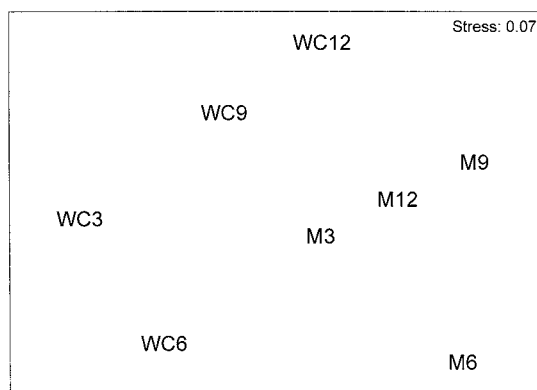

Fig. 4 Non-metric multidimensional scaling ordination of community structure similarity among the eight depth strata generated from a between-depth stratum similarity matrix of square-root transformed data. (M3, Meyer Island 3–6 m; M6, Meyer Island 6–9 m; M9,Meyer Island 9–12 m; M12, Meyer Island 12–15 m; W3, West Chanter Island 3–6 m; W6, West Chanter Island 6–9 m; W9, West Chanter Island 9–12 m; W12, West Chanter Island 12–15 m.)

Water column characteristics

At the Meyer Island site, the two CTD units moved on their mooring after c. 3 days, with the result that the 3-m unit dropped in the water column to a depth of 4.6 m and the 8-m unit dropped to a depth of 10.0 m. It is unknown why this shift occurred, but may have been brought about by the strong currents in the region (this may explain the differential decrease in height in the water column of the two CTD units). The shift in the water column resulted in an increase in the chlorophyll values at the 3 m (now 4.6 m) depth, but no such change was observed at the 8 m (now 10.0 m) depth. We ignored this increase in chlorophyll values recorded at the shallower Meyer depth stratum because it had no significant effect on the data, even though it did generate a bimodal distribution of values. All other variables were unaffected by the shifts in the depth of the two units.

Conductivity and temperature data at all four depth strata were generally constant over time, with the exception of conductivity at the Meyer 3 m depth stratum which cycled irregularly between a low of 27.5 and a high of 48 mS cm^{-1}, resulting in a bimodal distribution for this variable at this depth stratum. At both 3 m depth strata, temporal variation in turbidity and chlorophyll was small, with both depth strata exhibiting small and infrequent pulses in either variable. At West Chanter 8 m, the chlorophyll values were constant while the turbidity was very variable, whereas at Meyer 8 m the chlorophyll values were very variable while the turbidity was reasonably constant. Kruskall-Wallis tests revealed that the differences in mean values among the comparisons for each of the four variables were highly significant in all instances (Table 6), although there was no obvious pattern of variation in all four water column characteristics among the sites and depth strata (Table 7). Although statistically significant, the among-stratum variation in conductivity and temperature was small whereas the variation in turbidity and chlorophyll was more substantial, with the West Chanter depth strata typically having higher turbidity and lower chlorophyll mean values than the Meyer depth strata. *Gamma* values for the association between chlorophyll and turbidity were negative and significant at the Meyer 8 m (*gamma* = –0.252, *P* < 0.001) and West Chanter 3 m (*gamma* = –0.047, *P* < 0.001) depth strata, positive and significant (*gamma* = 0.102, *P* < 0.001) at the Meyer 3 m depth stratum, and not statistically significant (*gamma* = 0.015, *P* > 0.05) at the West Chanter 8 m depth stratum.

DISCUSSION

The Kermadec Islands Marine Reserve was established because the special status and unique value of the island group was widely recognised. The marine environment of the Kermadec Islands was, and is, largely unthreatened by extractive use or pollution, and can be viewed as being just about as pristine a marine environment as it is currently possible to find (http://www.doc.govt.nz/ Conservation/Marine-and-Coastal/Marine-Reserves/ 040~Kermadec/index.asp [accessed 15 November 2005]). No formal baseline marine ecological survey was conducted before the establishment in 1990 of the KIMR. Schiel et al. (1986) visited in March 1984, working at Boat Cove on Raoul Island (the major

Table 5 Analysis of similarities (ANOSIM) pair-wise comparison of community structure among all depth strata. Analyses based on a similarity matrix calculated from square-root transformed data. Statistically significant results ($P < 0.05$) in bold.

General comparison	Pair-wise depth stratum comparison	R statistic	Significance (P)
Within Meyer Is	Meyer 3–6 m versus Meyer 6–9 m	0.077	**0.007**
	Meyer 3–6 m versus Meyer 9–12 m	0.013	0.239
	Meyer 3–6 m versus Meyer 12–15 m	0.126	**0.002**
	Meyer 6–9 m versus Meyer 9–12 m	0.024	0.127
	Meyer 6–9 m versus Meyer 12–15 m	0.092	**0.003**
	Meyer 9–12 m versus Meyer 12–15 m	0.039	0.073
Within West Chanter Is	West Chanter 3–6 m versus West Chanter 6–9 m	0.062	**0.027**
	West Chanter 3–6 m versus West Chanter 9–12 m	0.065	**0.011**
	West Chanter 3–6 m versus West Chanter 12–15 m	0.149	**0.001**
	West Chanter 6–9 m versus West Chanter 9–12 m	0.017	0.190
	West Chanter 6–9 m versus West Chanter 12–15 m	0.042	**0.043**
	West Chanter 9–12 m versus West Chanter 12–15 m	0.022	0.164
Between Meyer Is and West Chanter Is	Meyer 3–6 m versus West Chanter 3–6 m	0.180	**0.001**
	Meyer 3–6 m versus West Chanter 6–9 m	0.099	**0.005**
	Meyer 3–6 m versus West Chanter 9–12 m	0.083	**0.007**
	Meyer 3–6 m versus West Chanter 12–15 m	0.095	**0.004**
	Meyer 6–9 m versus West Chanter 3–6 m	0.179	**0.001**
	Meyer 6–9 m versus West Chanter 6–9 m	0.091	**0.003**
	Meyer 6–9 m versus West Chanter 9–12 m	0.077	**0.002**
	Meyer 6–9 m versus West Chanter 12–15 m	0.059	**0.011**
	Meyer 9–12 m versus West Chanter 3–6 m	0.117	**0.002**
	Meyer 9–12 m versus West Chanter 6–9 m	0.045	**0.040**
	Meyer 9–12 m versus West Chanter 9–12 m	0.040	**0.042**
	Meyer 9–12 m versus West Chanter 12–15 m	0.046	**0.040**
	Meyer 12–15 m versus West Chanter 3–6 m	0.240	**0.001**
	Meyer 12–15 m versus West Chanter 6–9 m	0.121	**0.001**
	Meyer 12–15 m versus West Chanter 9–12 m	0.116	**0.001**
	Meyer 12–15 m versus West Chanter 12–15 m	0.112	**0.002**

Table 6 Kruskal-Wallis multiple comparisons of water column variables as a function of depth (3 m or 8 m) at two sites (Meyer Island and West Chanter Island) in the Kermadec Islands Marine Reserve, New Zealand. (Significance level of the Kruskal-Wallis statistic is calculated against H (3, $n = 22233$).)

Variable	Kruskal-Wallis statistic	Significance level (P)	Location of difference[*]
Conductivity (mS cm^{-1})	20564.44	< 0.0001	M8 > M3 > WC8 > WC3
Temperature (°C)	2410.99	< 0.0001	WC8 > M3 > WC3 > M8
Turbidity (FTU)	14942.09	< 0.0001	WC8 > WC3 > M3 > M8
Chlorophyll (μg litre^{-1})	11677.18	< 0.0001	M8 = WC8 > M3 > WC3

[*]M3, Meyer Island 3 m; M8, Meyer Island 8 m; WC3, West Chanter 3 m; WC8, West Chanter 8 m.

Table 7 Descriptive statistics of water column variables as a function of depth (3 m or 8 m) at two sites (Meyer Island and West Chanter Island) in the Kermadec Islands Marine Reserve, New Zealand. Sample size (n) = 3635 for Meyer Island 3 m, 5760 for Meyer Island 8 m, 5834 for West Chanter Island 3 m, and 7004 for West Chanter 8 m.

Site	Depth (m)		Conductivity (mS cm^{-1})	Temperature (°C)	Pressure (deciBars)	Turbidity (FTU)	Chlorophyll (μg litre^{-1})
Meyer Is	3	Mean	42.27	19.66	13.52	1.89	0.26
		SD	8.86	0.17	0.89	0.17	0.21
		Minimum	27.53	19.38	12.07	1.68	0.09
		Maximum	48.04	20.12	17.38	5.95	0.87
Meyer Is	8	Mean	48.07	19.61	19.33	0.68	0.36
		SD	0.14	0.15	0.99	0.20	0.11
		Minimum	47.77	19.32	15.80	0.49	0.11
		Maximum	48.52	20.09	22.62	12.02	1.27
West Chanter Is	3	Mean	48.61	19.68	13.30	2.91	0.10
		SD	0.09	0.07	0.27	1.05	0.20
		Minimum	48.32	19.51	12.77	0.83	0.00
		Maximum	48.93	19.96	15.05	10.34	5.01
West Chanter Is	8	Mean	50.87	19.72	18.11	2.92	0.28
		SD	0.20	0.11	0.54	1.02	0.02
		Minimum	49.74	19.51	17.30	0.84	0.27
		Maximum	51.41	20.15	20.52	15.45	0.90

island of the northern group), and Cole et al. (1992) visited the islands in September 1988, conducting survey work of mobile benthic invertebrates at four sites in the group, including the more southerly island groups. Brook's paper of 1999 is based on data collected during the period October 1985 to May 1995, and therefore spans by ± 5 years the establishment of the KIMR. Data from these three studies therefore represent the pre-reserve ecological situation, but unlike many other studies of marine reserves or marine protected areas, there is no *a priori* expectation of change in species abundance or size around the islands as a consequence of the establishment of the marine reserve.

The macroalgal flora of the KIMR is diverse, even if its biomass is not as great as in other parts of New Zealand, or in other subtropical localities (Nelson & Adams 1984). Schiel et al. (1986) reported percentage cover values of 25–60% for foliose and filamentous algae, there being no real evidence of depth-related zonation for this group. However, the same authors observed very high values of percentage cover for encrusting red algae (70%) from 2 m to 5 m depth, which declined dramatically to values of <10% by 10 m depth. In contrast to this, in the depth range of 1–20 m, Brook (1999) observed percentage cover values of 50–60% for filamentous and frondose algae, and values of 10–20% for crustose coralline algae. In the present study, percentage cover estimates for filamentous algae ranged from 15.6 to 53.8% (mean

= 37.4% for eight depth strata), and for encrusting red algae ranged from 24.1 to 51.3% (mean = 37.1% for all eight depth strata). The consistently high values of percentage cover for both filamentous and encrusting algae reported by all studies indicate the ecological importance of algae in general down to c. 20 m in the KIMR.

The conspicuous macrofauna of the KIMR principally includes echinoderms, molluscs, and corals (hard and soft). Schiel et al. (1986) and Cole et al. (1992) reported six species of echinoids and five species of asteroids at KIMR. We observed the echinoids *C. rodgersii*, *E. mathaei*, *H. tuberculata*, and *T. gratilla* in our survey, and we also observed *Phyllacanthus parvispinus* outside the surveyed areas, but we did not observe *Diadema* sp. at all. Of the asteroids, we observed in our survey and beyond it *A. planci*, *Astrostole rodolphi*, and *O. kermadecensis*, but we did not observe either *Pectria imperialis* or *Petricia vernicina*. We also observed an unidentified orange 5-arm starfish in and outside the survey area, as well as yellow and black varieties of the crinoid *Tropiometra afra*. Most of these echinoderms were not particularly abundant, making it difficult to describe ecologically meaningful changes in depth-related distributions. However, Schiel et al. (1986) observed a peak of abundance of *H. tuberculata* at 5 m, with very few individuals observed beyond 10 m depth. Cole et al. (1992) observed that *H. tuberculata* was most

abundant from 3 to 9 m depth, and that between 12 and 18 m depth *C. rodgersii* was most abundant. Other echinoderms were reported by both sets of authors as present in only low numbers. We did not observe the dominance of *H. tuberculata* in shallower regions at our two sites; this species was only observed at West Chanter 3–6 m and 6–9 m in our survey. The most abundant echinoderm in our survey was the echinoid *C. rodgersii*, which was observed at both sites, and was particularly abundant at West Chanter, where it decreased from 4.25 individuals m^{-2} at 3–6 m, to 0.25 individuals m^{-2} at 12–15 m depth. The only other echinoderm in our survey to occur at any notable abundance was the crinoid *T. afra* which exhibited a negative association between abundance and depth at Meyer Island (decreasing from 1.25 to 0.50 individuals m^{-2}), and a positive association at West Chanter (increasing from 1.75 to 5.75 individuals m^{-2}). Neither Schiel et al. (1986) nor Cole et al. (1992) made note of this species because their studies were focused on herbivorous grazers and predatory species, rather than on the abundance and distribution of macroinvertebrates in general.

The only large gastropod observed below 3 m by Schiel et al. (1986) was the trochid *T. royanus*, which occurred in very low numbers. Similar findings are reported by Cole et al. (1992) who observed *T. royanus* at all depths to 18 m, but noted that it was not abundant. Our data for this endemic top shell are in agreement with these previous findings, the maximum density we observed was 0.75 individuals m^{-2} (at Meyer, 6–9 m), and there was no evidence of depth-stratification for this species. The most abundant mollusc we observed was the predatory whelk *M. smittii* which we observed at all depths, and which showed some evidence at both sites of a negative relationship between abundance and increasing depth. Schiel et al. (1986) made note of a few individuals of *M. smittii* at Boat Cove, whereas Cole et al. (1992) did not, apparently, encounter this species. Of the other subtidal molluscs that we observed, the endemic spiny oyster *S. raoulensis* was rare (we only observed one in our survey of both sites, but did see several more beyond the surveyed areas), as was the endemic chiton *L. mestayerae*, and an unidentified nudibranch (we only saw one of each in total), whereas the cone shells were much more abundant generally (Brook (1998) reports 28 species), although rare in our surveyed areas.

This, and earlier studies, have noted that small colonies of hard and soft corals are relatively abundant in shallow water (<30 m) around the Kermadec Islands. Schiel et al. (1986) and Brook (1999) observed hard corals (maximum of 20% cover) at all depths down to 20 m, but the patterns of depth-related distribution were quite different. Our surveys revealed values of percentage cover for hard coral species comparable with these two previous studies, but at both our sites we observed a reasonably pronounced inverse relationship between percentage cover and increasing depth. Such a relationship was also observed by Brook (1999) with the exception of an increase in percentage cover from 15 to 20 m, whereas Schiel et al. (1986) observed a peak of percentage cover at 3 m depth, followed by a drop at 5 m depth, and then a pronounced increase from 12 to 18 m depth. The pattern of percentage cover estimates of soft corals as a function of depth were very similar between the studies of Schiel et al. (1986) and Brook (1999), even if the actual values were not. Both studies observed very low values at shallow depths (<5 m depth), which increased rapidly with increasing depth (to a maximum value of 15% and 3%, respectively), held reasonably constant until 13–15 m, and then decreased to 0% by 18–20 m depth. Our estimates of soft coral percentage cover at Meyer Island were comparable to the values reported by Schiel et al. (1986), whereas our estimates at West Chanter Island were comparable to those reported by Brook (1999). In neither instance however, did we observe the same pattern of depth-related abundance as reported by these two studies. At Meyer Island the soft coral percentage cover values were relatively constant for depth, whereas at West Chanter Island there was evidence of a positive relationship between soft coral abundance and depth (values increased in a linear manner from 0% to 5.3% with increasing depth; Table 4). Other subtidal faunal groups observed by us included barnacles (*Tesseropora* sp.), hermit crabs (*Calcinus* spp.), sponges, ascidians, bryozoans, anemones, a tube-dwelling polychaete, and an unidentified shrimp. These all occurred at low abundance, often at only one of the two sites, making it difficult to determine ecological patterns of distribution.

Our two study sites were only 2 km apart, and superficially were very similar in substrate type, depth, and exposure. However, our analyses identified pronounced differences in benthic community composition between the two sites during our snapshot survey. Significant differences existed in depth-related mean number of groups between the sites, and also in the mean number of groups regardless of depth, indicating that diversity was significantly higher at Meyer than

at West Chanter. Although the difference in the number of groups was significant between the sites, this difference was relatively small compared to the variance. There is therefore evidence of large within-site variability in community structure which is attributable to small-scale patchiness, and in an ecological sense, may well be as important as between-site differences in community structure. Multivariate analyses of abundance and percentage cover data also indicated that significant differences existed in benthic community structure between the sites. Cluster analysis revealed that the four Meyer depth strata formed a subgroup, and that the West Chanter 9–12 m and 12–15 m depth strata exhibited greater similarity to the Meyer subgroup than to the subgroup formed by the West Chanter shallow depth strata (i.e., 3–6 m and 6–9 m). MDS analysis indicated that the four Meyer depth strata were reasonably close together (i.e., similar) and separate from the West Chanter depth strata, whereas these latter depth strata were somewhat spread out (i.e., dissimilar) across the ordination, with the West Chanter depth strata 9–12 m and 12–15 m being closer to the Meyer depth strata than to the West Chanter depth strata 3–6 m and 6–9 m. Finally, ANOSIM indicated that all 16 comparisons between depth-strata at Meyer and West Chanter were significantly different, whereas 5 of 12 within-site comparisons were not significantly different. Overall, these analyses clearly indicate a significant difference in benthic community structure between the two sites despite their proximity and apparently very similar physical characteristics.

Because of logistical limitations we had only 5 working days at KIMR and were able to survey only two sites using a depth-stratified approach. This limitation is a common problem faced by researchers at this location (e.g., Schiel et al. 1986; Cole et al. 1992) and others like it, and may confound our interpretation of the results. We surveyed 16 quadrats (50×50 cm) in each of four depth strata at the two sites. Two-way ANOVA revealed that site ($P < 0.001$) explained far more variation in the data set than depth ($P = 0.045$), and that the site x depth interaction term was significant ($P = 0.019$) (Table 2). Inspection of the data in Table 4 reveals the existence of a number of rare species at either site and in all four depth-strata which may have contributed disproportionately to the statistical differences observed between sites. Such a contribution may have arisen as a consequence of under-sampling. However, ANOSIM results (Table 5) and the cluster analysis (Fig. 3) both suggest that there is more structure to the data than one would expect by chance alone. For the ANOSIM, all between-site comparisons were statistically significant, whereas non-significant results were only observed between depth-strata within a site (Table 5). Consistent with this, the dendrogram (Fig. 3) identified the four Meyer Island depth-strata as being most similar, with the West Chanter 9–12 and 12–15 m groupings showing next greatest similarity, and with the West Chanter 3–6 and 6–9 m groupings being greatest distance from (i.e., most dissimilar to) all other groupings. This kind of structure in the data set is unlikely to exist if rare species contribute disproportionately to the outcomes as a consequence of under-sampling at all depth-strata at both sites. Our interpretation is that the ecological differences that we have seen between sites are real and are not generated by under-sampling, but we acknowledge that under-sampling is a problem in this type of study. We suggest that greater sampling effort is required both within-sites and at a greater number of sites at KIMR to better understand the natural variability of biological communities that exists within this group of islands and to further our understanding of the biological context of the Kermadec Islands in the South Pacific.

Meaningful comparison of benthic community structure at the Kermadec Islands (29–31°S) is limited to a handful of Pacific island sites such as the Pitcairn Islands (24–25°S), Easter Island (27°09′S), Lord Howe Island (31°33′S), and the Galapagos archipelago (01°40′N–01°25′S). Paulay (1989) noted the significant extent of inter-island variation in benthic community structure within the Pitcairn group (Pitcairn, Henderson, Ducie, and Oeno islands) and attributed this to the group's peripheral location within the subtropics, its diverse geological history and physiography, and the attendant instability of its fauna. This faunal instability was reflected in the large short-term changes in coral cover at Ducie, the large temporal changes in species composition at Henderson, and the considerable differences between the faunas of neighbouring Ducie and Henderson which are 360 km apart (Paulay 1980). Similar faunal differences have been reported between Easter Island and Sala-y-Gómez (Rehder 1980; DiSalvo et al. 1988) which are 415 km apart, and are the most isolated landmasses in the Pacific Ocean. Rates of faunal turnover at Easter Island were high and resulted in profound ecological and habitat change over time scales of only a few years (DiSalvo et al. 1988). However, no great differences

among sites in the distributions of intertidal molluscs based on Sorensen's index of similarity were reported at Easter Island for the period January to September 1986 (Osorio & Cantuarias 1989). Coral communities at Lord Howe Island (which is surrounded by the southern-most coral reefs in the Pacific Ocean) clustered according to habitat type (e.g., seaward versus reef flat versus lagoonal hole and slope sites; Harriott et al. 1995) and generally did not exhibit between-site variation in structure comparable to that observed at KIMR. Although the abundances and distributions of dominant coral species at Lord Howe Island were relatively stable over time, the rarer species were appearing and then disappearing over time, indicating some degree of faunal instability (Harriott et al. 1995) which would contribute to both small and large spatial scale differences in benthic community structure. Regional biogeographic analyses of the shallow water reef fauna of the Galapagos archipelago revealed five major marine bioregions among the islands (Edgar et al. 2004). Four of these zones result from local environmental conditions and connectivity of larval propagules with external source regions, but one probably results from high levels of phytoplankton primary productivity which appear to give the ecosystem its distinctive biological character (Edgar et al. 2004). Brook (1998) pointed out that the species composition of the Kermadec Islands reflects their biogeographic isolation, their subtropical location, the small range of habitats present, and also their geological history which has given rise to high rates of faunal turnover and allopatric speciation. Analyses of small, isolated and often peripheral islands in the Pacific Ocean indicate that high faunal turnover rates (= faunal instability) are a major factor contributing to differences in community structure in time and space at these locations. We cannot at present quantify the contribution of faunal instability as an explanation for benthic community differences that we observed, but we suggest that it may be significant. An analysis of species-specific settlement patterns at KIMR sites would help address this point. Another possible explanation for differences in macrocommunity structure between sites only 2 km apart is differences in localised oceanographic conditions (in particular, the supply of particulate food material) which have been demonstrated to profoundly influence intertidal and shallow subtidal community structure in other regions (e.g., Dahlhoff & Menge 1996; Menge et al. 1999; Gardner 2000; Edgar et al. 2004; Helson et al. unpubl. data; Helson & Gardner unpubl. data). This physical interpretation

is consistent with the somewhat "patchy" nature of the macrobenthic community reported here, and also by earlier studies (Schiel et al. 1986; Cole et al. 1992; Brook 1999). Both sets of processes (the biological phenomenon of faunal instability and physical phenomenon of site-specific hydrographic processes) are likely to be operating at KIMR and both may contribute to the observed small spatial scale differences in benthic community structure that we observed.

The water column data presented here are the first of their type for the KIMR. The scarcity of such data from KIMR sites and also from other oceanic, subtropical islands makes establishing the context of these data difficult, and emphasises the need for a comprehensive survey of the water column of the KIMR. Although statistically significant differences were observed for all four water column variables (conductivity, temperature, turbidity, and chlorophyll) among the four locations (Meyer 3 m and 8 m; West Chanter 3 m and 8 m), in an ecological sense most of the differences were often small. The apparent coupling of variation between chlorophyll concentration and turbidity at 3 m depth at both sites, and their uncoupling at 8 m depth at both sites, suggests that the surface water (0–5 m) is well mixed and that the extent of mixing is much less at 8 m depth. The generally higher levels of turbidity and lower levels of chlorophyll at West Chanter compared to Meyer may be attributable to the greater current strength at the former site (as judged by our divers, but not quantified in any way). We suggest that further analyses of water column properties may prove to be useful in explaining biotic differences between sites (e.g., differences in the abundance of suspension feeding species).

SUMMARY

Comparison of our data with those of three other surveys of the Kermadec Islands reveals a high degree of similarity among the species observed, but often a low degree of similarity in species abundance or percentage cover as a function of depth. Whether these dissimilarities are real and reflect ecological change over time or perhaps the patchy distributions of uncommon species, or are simply the product of infrequent sampling at small scales and over short time periods remains open to question. Future research should focus on: (1) surveying benthic community structure at a greater number of sites within each island group to establish the extent

of small spatial scale differences in community structure; (2) surveying sites within the northern, middle and southern island groups to establish the extent of large spatial scale differences in community structure; and (3) determining water column characteristics at these locations with the intention of testing for a relationship between water column productivity and benthic community structure. Finally, we strongly recommend the establishment of a long-term monitoring programme at KIMR to permit quantification of temporal changes in community structure of what is likely to be an inherently unstable biota given the remote location of the islands, their relative geological youth, and the peripheral location of the islands within marine Polynesia.

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