Spatial patterns and regional affinities of coral communities at the Kermadec Islands Marine Reserve, New Zealand — a marginal high-latitude site

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ABSTRACT: The Kermadec Islands Marine Reserve (29 to 31° S), New Zealand, harbours one of the world's highest latitude scleractinian coral communities, situated close to the lower thermal limits for coral survival. An understanding of how and why similarities and differences exist between so-called 'marginal' coral communities can provide insight into the physical and biological factors that influence coral distributions. In this study, a depth-stratified survey of benthic community structure and coral species assemblages was conducted at 9 sites around the Kermadec Islands. All coral species identified were subtropical non-reef building species, or species with a wide geographic range. Scleractinian coral cover (16 species) was low and variable between sites and depths (5.3 ± 13.9 %, mean ± SD) with macroalgae contributing between 36 to 95 % of the benthic cover. Multivariate analyses revealed small-scale spatial variability between closely located sites. Resulting data on coral species diversity were compared to published data from coral communities at other 'marginal' locations, as well as those from a range of Australian locations. On a global scale, the Kermadec Islands coral community exhibits greatest affinity with southeastern Australian sites. In comparison, there was a lack of affinity for Australian tropical sites and other high latitude sites, both in Australia and globally. Our analyses suggest that the low diversity, highly variable coral communities of the Kermadec Islands are likely shaped by their isolation and high wave energy, in addition to the low annual temperatures experienced.

KEY WORDS: High latitude · Coral community · Kermadec Islands · Regional affinities · Subtropical · New Zealand

INTRODUCTION

Marginal coral reefs and communities exist near or beyond the normal limits of reef distribution, close to the environmental thresholds for coral survival (Kleypas et al. 1999). Marginal reefs are defined as those where 3-dimensional, biologically influenced build-ups of coral framework and carbonate sediments have occurred. Marginal communities, however, are assemblages of organisms growing on substrates other than their own and which do not produce framework. The lack of framework in these communities is attributable to a lack of significant accretion of calcium carbonate (Buddemeier & Smith 1999), with corals in these communities attaching to hard substrata, appearing as isolated colonies growing on exposed bedrock (e.g. Macintyre 2003). Coral communities can have similar species diversities to true coral reefs (>140 spp; Sheppard & Sheppard 1991, Perry 2003), though in most cases species diversities are much lower (< 90 spp; Harriott & Banks 2002, Moyer et al. 2003, Nozawa et al. 2008).

Marginal reefs and communities frequently occur at high latitudes (subtropics) i.e. above 25°S and 25°N, with well known examples being those of the Persian Gulf, Bermuda, Japan and Lord Howe Island, Australia. Development and coral species diversity of these high-latitude assemblages, at both biogeographic and local scales, are largely regulated by low mean annual and seasonally variable temperatures and irradiances, and the low aragonite saturation state (Buddemeier 1997, Kleypas et al. 1999). Other parameters with local importance include wave exposure (Harriott et al. 1994, Benzoni et al. 2003, Nozawa et al. 2008), low and variable salinity and high turbidity (Harriott & Smith 2002, Manzello & Lirman 2003). Macroalgae play a dominant role in many of these high latitude coral assemblages, their rapid growth out-competing corals for space (Johannes et al. 1983). Further, many high latitude coral assemblages are small and isolated (e.g. Babcock et al. 1986, Brook 1999, Hughes et al. 2002), meaning that they are likely to be largely self-seeding in terms of larval supply (Ayre et al. 1997).

Patterns of diversity and distribution in high latitude coral communities, which exist close to the environmental limits of survival, are poorly documented. Given that these communities occupy a transitional tropical–temperate ecological niche, studies of such sites, and their relatedness to coral communities and reefs elsewhere can provide important information about the processes underlying the distributional limits of coral species and coral reefs (Harriott & Banks 2002). Further, they can provide essential information for conservation and management strategies, which need to take into account physical and biological factors that are important in high-latitude systems (Harriott & Banks 2002).

To address the patterns of coral diversity and distribution at high latitudes, we focused on one of the South Pacific's high-latitude coral community sites, the Kermadec Islands Marine Reserve, 750 km off the northeast coast of New Zealand's North Island (Fig. 1) and 3000 km from the Great Barrier Reef (GBR). The isolation of the Kermadec Islands, coupled with the lack of terrestrial inputs or a resident human population, means that they are relatively free from anthropogenic stressors to which other reefs are exposed, such as concentrated over-fishing or terrestrial runoff. However, little is known of the biodiversity variability within the marine reserve (among islands, or among sites within islands), which spans a range of latitudes (29 to 31°S) and sea surface temperatures (14 to 18°C annual minima, 23 to 26°C annual
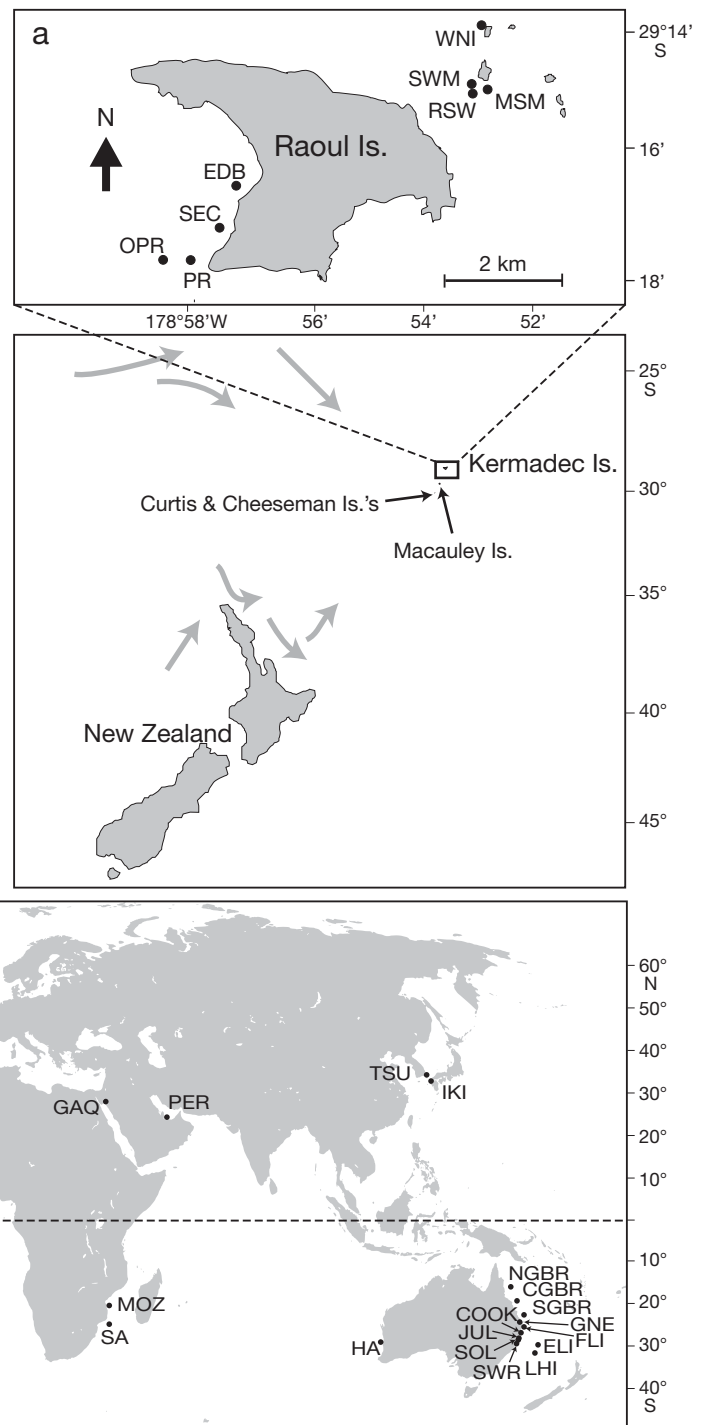

Fig. 1. (a) Kermadec Islands, northeastern New Zealand. Inset: 8 sites within the Kermadec Islands Marine Reserve; for site abbreviations see Table 1. Arrows: major oceanic currents (Schiel et al. 1986); (b) location for which data from published records were used to analyse regional affinities of Kermadec Island coral community. Global site abbreviations: GBR, Great Barrier Reef (N, North; C, Central; S, South); GNE, Gneering Shoals; JUL, Julian Rocks; COOK, Cook Island; SOL, Solitary Islands; SWR, Southwest Rocks; LHI, Lord Howe Island; ELI, Elizabeth Reef; HA, Houtman Abrolhos; MOZ, Mozambique; SA, South Africa; PER, Persian Gulf; GAQ, Gulf of Aqaba; IKI, Iki Island, Japan; TSU, Tsushima Island, Japan

maxima; Francis et al. 1987). The lack of a comprehensive study of temporal and spatial variation in community structure of the benthic (coral and noncoral assemblages) at the Kermadec Islands is due to their inaccessibility; their isolation, and intense wave exposure (Gardner et al. 2006). We aimed to (1) assess the spatial patterns of coral distribution in terms of cover and species diversity and richness at this high latitude location; (2) determine if different assemblages exist between neighbouring sites at the Kermadec Islands and how these communities vary with latitude; and (3) identify similarities between coral diversity at the Kermadec Islands and other coral communities and reefs to quantify the contribution of latitude in governing coral species distributions. The latter point is developed in analyses of published data of coral biodiversity at a latitudinal range of Australian sites, and marginal sites on a global scale, including high latitudes.

MATERIALS AND METHODS

Study area. The study was conducted at 2 locations at the Kermadec Islands, 120 km apart and situated between 29° and 30° S, in November 2004. The 11 islands form 3 discrete groups (Fig. 1), the northern group around Raoul Island (29° 12′ S, 177° 55′ W), the middle group around Macauley Island (30° 14′ S, 178° 25′ W), and the southern group of Curtis and Cheeseman Islands (31° 21′ S, 178° 41′ W). Although corals are present at the southern group, the area was not surveyed, because it was inaccessible at the time of study. As the islands are volcanic in origin, sites were characterised by steeply sloping rock substrata dominant in the shallow sub-tidal zone down to 10 m. The Kermadec Islands also feature gently sloping reef areas of smooth rock and large boulders common to depths of 20 to 30 m. Eight of the 9 sites surveyed are situated in the northern group, which includes Raoul, Meyer, North Chanter, South Chanter, West Chanter, Napier and Nugent Islands. One site was located close to Macauley Island in the middle group. Sites were chosen on the basis of accessibility and repeatability.

Equidistant between temperate New Zealand and tropical Tonga, the Kermadec Islands are one of the few subtropical island groups in the western South Pacific Ocean, and form New Zealand's largest marine reserve (748 000 ha). The main oceanographic influence on the Kermadec Islands is poorly known (Gardner et al. 2006), but is suggested to be either from the East Australian Current, flowing from New South Wales (eastern Australia) to Norfolk Island and on to the Kermadec Islands (Marshall 1979, Schiel et

al. 1986), or from the northwest route of New Caledonia, Fiji and Tonga (Fig. 1; Gardner et al. 2006). Little is known of localised oceanographic patterns. Previous surveys of benthic species diversity at the Kermadec Islands have reported a mix of tropical, subtropical and temperate species of Southwest Pacific origin (Schiel et al. 1986, Brook 1999, Gardner et al. 2006), with corals generally restricted to depths of <30 m (Brook 1999).

Sampling. At each of the Kermadec sites, quantitative benthic surveys were carried out at 4 depth strata, 3–6, 6–9, 9–12 and 12–15 m, consistent with previous surveys (Schiel et al. 1986, Gardner et al. 2006). Sampling was conducted by photographing 16 haphazardly located quadrats of 50×50 cm (total area sampled = 4 m^2 per stratum) using a Canon S60 camera. From the digital images, percent cover (±SD) was determined using the 100 random dot method for 9 benthic groups: sand/rubble, filamentous/fleshy algae, encrusting red algae, hard coral, soft coral, bryozoans, sponges, ascidians and anemones. Corals present were identified to family and, where possible, to species, and their percent cover was recorded.

Regional affinities. For multivariate analysis of coral community structure in relation to other geographic locations, data on scleractinian coral species richness in the form of number of species per family was collated from 18 additional locations. These were 12 Australian regions or sites from the tropics to subtropics (Fig. 1; 10 published by Veron 1993a,b cited in Harriott & Banks 2002, the other 2 in Veron & Marsh 1988, Oxley et al. 2004), and 6 marginal/isolated sites from around the world: Tsushima Island and Iki Island Japan (34° and 33° N respectively; Sugihara & Yamano 2004, Yamano et al. 2004 respectively), the Persian Gulf (26° N; DeVantier & Pilcher 2000), the Gulf of Aqaba (28° N; Sheppard & Sheppard 1991), South Africa (east coast, 26° S) and southern Mozambique (27° S; both Riegl 1996). Coral species counts from the present study for the Kermadec Islands were supplemented with records from Brook (1999), who identified 8 additional species. Where possible, percent coral cover, survey depth, and average minimum and maximum annual temperatures for the sites were noted. Most temperature data were collated from ReefBase GIS information (http://reefgis.reefbase.org), with data for Japan from Yamano et al. (2001).

Data analysis. *Kermadec Islands:* Mean (±1 SD) of percent cover for each benthic category was estimated for the 16 replicate quadrats at each site. Percent cover of each coral species identified was estimated for each quadrat, and means calculated for each site/depth stratum. Total number of species per site was recorded.

Significance of differences in coral cover (hard and soft corals separately) between sites and depths was determined using a 2-way ANOVA test, following normality (Kolmogorov-Smirnov test) and equal variance testing (Levene's test).

Multivariate analyses of similarities and differences among sites and depths were performed on percent cover of (1) all benthic categories and (2) scleractinian coral species only. Data analysis was performed using the PRIMER package v6.0 with permutational multivariate analysis of variance (PERMANOVA) add-on (Plymouth Marine Laboratory). All benthic group and scleractinian coral species percent cover values were pre-treated with a dispersion weighting transformation in which the abundances of the different species were differentially weighted on the basis of their observed variability in replicate samples. This method compensates for the spatial clustering common in coral community studies (Clarke et al. 2006a). Similarities were calculated using the zero-adjusted Bray-Curtis similarity measure (Bray & Curtis 1957) to account for samples with depauperate assemblages (see Clarke et al. 2006b). PERMANOVA, with 9999 permutations, was used to determine differences in coral assemblages between sites and depths within sites, and separately between sites at each depth strata. This analysis is unconstrained by the assumptions of normality and homogeneity of variance that limit the use of traditional MANOVA, and relies on comparing the observed value of a test statistic (pseudo *F*-ratio) against a recalculated test statistic generated from random re-ordering (permutation) of the data (Anderson 2001). Patterns in the data were visualised using a canonical analysis of principal coordinates (CAP), and similarity percentage analysis (SIMPER) established the species causing the dissimilarities between the majority of sites and any outlying sites and depth combinations.

Regional affinities: To gain insight into the regional affinities of the coral families and diversity patterns seen at the Kermadec Islands, multivariate analyses of similarities and differences were conducted on the total number of species in each family present at each of the aforementioned Australian and marginal locations, using the PRIMER software package. Analysis was conducted on untransformed and 4th root-transformed data, to identify the role of dominant and rare families, respectively. Following calculation of similarities using the Bray-Curtis similarity measure, significant groupings in the multivariate space at the 95% level were identified using the similarity profile permutation test SIMPROF, with SIMPER analyses used to assess the contribution of each family to the similarities within clusters.

RESULTS

Kermadec Islands

We identified 17 coral species in this survey (Table 1): 16 hard (scleractinian) corals and 1 soft coral (*Sinularia* sp.). The most common species observed were *Montastraea curta*, *Hydnophora pilosa* and an encrusting *Montipora* sp. Small spatial scale geographical divisions were observed for some coral species, with 1 species only found at the southern sites (*Rhizopsammia* sp), and 3 limited to the northeast region (*H. pilosa*, *Tubastrea* sp. and *Dendrophyllia* sp). Coral colonies were generally small, their diameters ranging from 20 (e.g. *Cyphastrea serailia*) to 1000 mm for soft corals. Total number of scleractinian species was greatest at the northernmost site of West Napier Island (9), and lowest at the southernmost site of Macauley Island (3). The soft coral *Sinularia* sp. was present at all sites excluding Macauley Island.

Soft corals were less abundant than hard corals, with an average (± SD) of 2.9 ± 11.9 versus 5.2 ± 13.9% cover respectively, averaged over all depths at all sites. Both hard and soft coral cover were significantly different between sites (Fig. 2; hard: F = 9.7, p < 0.01; soft: F = 13.9, p < 0.01). Southeast Denham Bay had the greatest mean cover of hard corals (18%), with only 0.2 ± 0.9% hard coral cover recorded at Macauley Island. Rocks Southwest Meyer had the greatest mean soft coral cover (13 ± 26.5%; Table 1), with less than 1% recorded at East Denham Bay and the northernmost site of West Napier Island.

Coral cover was less than macroalgal cover in all sites surveyed. Macroalgae accounted for 57 to 94% of the benthic cover (Southwest Meyer and Macauley Island, respectively; Table 1). Filamentous/fleshy macroalgae observed included genera such as *Caulerpa*, *Enteromorpha*, *Codium* and *Corallina*, with encrusting species such as *Lithothamnion* sp. and *Apophloea* sp. also being common. Filamentous/fleshy macroalgal cover declined with decreasing latitude, accounting for only 36% of the benthic cover at West Napier Island (29° S), compared to 94% at Macauley Island (30° S) though it was highly variable between neighbouring sites. For example, the 3 sites south of Meyer Island ranged from 37 to 57% filamentous/fleshy macroalgal cover, even though all were within a 20 km radius.

Both hard and soft coral cover were significantly different between depths within sites (Fig. 2; hard: F = 4.1, p < 0.01; soft F = 9.6, p < 0.01). Overall, mean hard coral cover (±SD) was lowest in the 12 to 15 m zone (2 ± 2% of cover averaged over all sites), although the 2 sites around Parsons Rock had their highest recorded coral covers in this depth zone (Parsons Rock = 8.2 ±

Table 1. Mean percent cover ± SD of the benthic categories and coral species at 9 sites at the Kermadec Islands. Means averaged over all depths at each site (n = 64 per site, excluding SEC where n = 48 as no data for 3 to 6 m). Site codes are in brackets. Blank cells represent an absence of the benthic category/species. ENC-RED-ALG, encrusting red algae. FIL/FLE-ALG, filamentous/fleshy algae

|	W. Napier Is. (WNI) 29° 14′ S	Mid S. Meyer (MSM) 29° 14′ S	Rocks SW Meyer (RSW) 29° 15′ S	SW Meyer (SWM) 29° 15′ S	SE Denham Bay (SEC) 29° 17′ S	East Denham (EDB) 29° 18′ S	Outer Parsons Rock (OPR) 29° 18′ S	Parsons Rock (PR) 29° 18′ S	Raoul Is. (mean ± SD for 8 sites)	McCauley Is. (MCI) 30° 17′ S
RUBBLE/SAND	3.4 ± 4.0	4.8 ± 8.1	14.1 ± 22.6	13.3 ± 17.0	10.4 ± 13.8	23.0 ± 25.6	5.2 ± 3.9	7.2 ± 8.2	10.2 ± 6.5	2.7 ± 5.6
FIL/FLE-ALG	35.6 ± 31.7	57.9 ± 21.9	36.0 ± 30.4	48.1 ± 22.5	51.6 ± 28.6	66.1 ± 25	61.9 ± 26.6	75.6 ± 26	54.1 ± 14.1	78.4 ± 20.9
ENC-RED-ALG	49.7 ± 34.6	16.0 ± 16.8	20.8 ± 22.5	19.7 ± 25.6	18.1 ± 24.9	6.7 ± 14.9	17.8 ± 21.7	5.5 ± 13.1	19.3 ± 13.6	15.8 ± 17.8
HARD CORAL	3.2 ± 11	4.8 ± 11.2	10.2 ± 17	5.8 ± 14.7	18.0 ± 26.0	2.6 ± 8.1	1.2 ± 6.9	3.5 ± 11	6.2 ± 5.5	0.2 ± 0.9
SOFT CORAL	0.1 ± 0.6	10.5 ± 18	13.1 ± 26.5	0.4 ± 2.1	0.3 ± 1.6	0.1 ± 0.3	0.2 ± 0.9	0.6 ± 2.3	3.2 ± 5.4	–
BRYOZOAN	–	0.4 ± 2.3	<0.1 ± 0.1	–	–	–	0.1 ± 0.9	–	0.1 ± 0.1	0.1 ± 0.5
SPONGE	3.6 ± 5.5	3.0 ± 3.7	3.0 ± 3.6	6.6 ± 11.2	0.6 ± 1.2	0.3 ± 0.8	8.3 ± 15.8	3.6 ± 7.4	3.6 ± 2.7	0.7 ± 1.0
ASCIDIAN	0.4 ± 1.2	<0.1 ± 0.2	<0.1 ± 0.2	0.1 ± 0.4	–	–	0.5 ± 1.5	0.4 ± 1.6	0.2 ± 0.2	0.1 ± 0.5
ANEMONES	–	–	–	–	–	–	0.8 ± 3.1	–	0.1 ± 0.3	–
TOTAL ALGAE	85.4 ± 14.9	74.0 ± 22.2	56.8 ± 30.3	67.8 ± 19.3	69.7 ± 23.9	72.8 ± 29.1	79.7 ± 20.1	81.2 ± 19.0	73.4 ± 9.0	94.2 ± 14.4
Acroporidae										
Montipora spp.	0.2 ± 0.0	0.4 ± 2.9	0.1 ± 0.9	0.2 ± 1.2	10.1 ± 24.0	–	–	0.4 ± 3.0	1.4 ± 3.5	<0.1 ± 0.1
Caryophyllidae										
Coenocyathus brooki	–	–	–	–	–	–	–	<0.1 ± 0.1	<0.1 ± 0.1	–
Pocilloporidae										
Pocillopora damicornis	0.1 ± 0.5	–	0.9 ± 3.3	0.2 ± 1.4	–	0.1 ± 0.8	–	–	0.1 ± 0.3	–
Dendrophylliidae										
Dendrophyllia sp.	<0.1 ± 0.1	–	–	–	–	–	–	–	<0.1 ± 0.1	–
Tubastrea sp.	0.2 ± 0.8	–	–	<0.1 ± 0.1	–	–	–	–	<0.1 ± 0.1	–
Turbinaria sp.	0.9 ± 6.2	0.9 ± 6.7	–	–	–	–	0.2 ± 1.5	–	0.2 ± 0.4	–
Rhizopsammia sp.	–	–	–	–	–	–	–	–	–	<0.1 ± 0.1
Faviidae										
Cyphastrea sp.	–	<0.1 ± 0.1	–	<0.1 ± 0.1	–	–	<0.1 ± 0.3	<0.1 ± 0.1	<0.1 ± 0.1	–
Goniastrea sp.	–	–	<0.1 ± 0.2	0.1 ± 0.3	3.2 ± 7.8	2.1 ± 7.8	0.8 ± 6.4	0.1 ± 0.4	0.7 ± 1.3	–
Leptastrea sp.	–	–	–	–	–	–	–	–	0.1 ± 0.3	–
Montastraea curta	1.7 ± 8.0	0.1 ± 0.3	3.1 ± 9.3	2.0 ± 9.2	3.4 ± 6.7	0.2 ± 1.6	–	3.0 ± 10.8	1.7 ± 1.4	<0.1 ± 0.4
Merulinidae										
Hydnophora pilosa	–	3.1 ± 8.9	6.1 ± 14.3	3.2 ± 10.9	1.2 ± 5.6	0.1 ± 0.8	–	–	1.7 ± 2.2	–
Poritidae										
Alveopora spongiosa	–	–	–	–	0.1 ± 0.5	<0.1 ± 0.1	–	–	<0.1 ± 0.1	–
Agariciidae										
Leptoseris sp.	–	–	<0.1 ± 0.1	–	<0.1 ± 0.1	–	–	–	<0.1 ± 0.1	–
Pavona explanulata	–	<0.1 ± 0.0	–	–	–	–	–	–	<0.1 ± 0.1	–
Alcyoniidae										
Sinularia sp.	0.1 ± 0.6	10.8 ± 18.4	13.1 ± 26.5	0.4 ± 2.1	0.3 ± 1.6	0.1 ± 0.4	0.2 ± 0.9	0.6 ± 2.3	3.2 ± 5.4	–
Unidentified	<0.1 ± 0.1	<0.1 ± 0.1	<0.1 ± 0.2	0.1 ± 0.4	0.1 ± 0.4	0.1 ± 0.4	0.2 ± 0.8	0.1 ± 0.3	<0.1 ± 0.1	0.2 ± 0.8
Total no. hard coral spp.	**9**	**7**	**7**	**8**	**8**	**6**	**4**	**6**	**15**	**4**
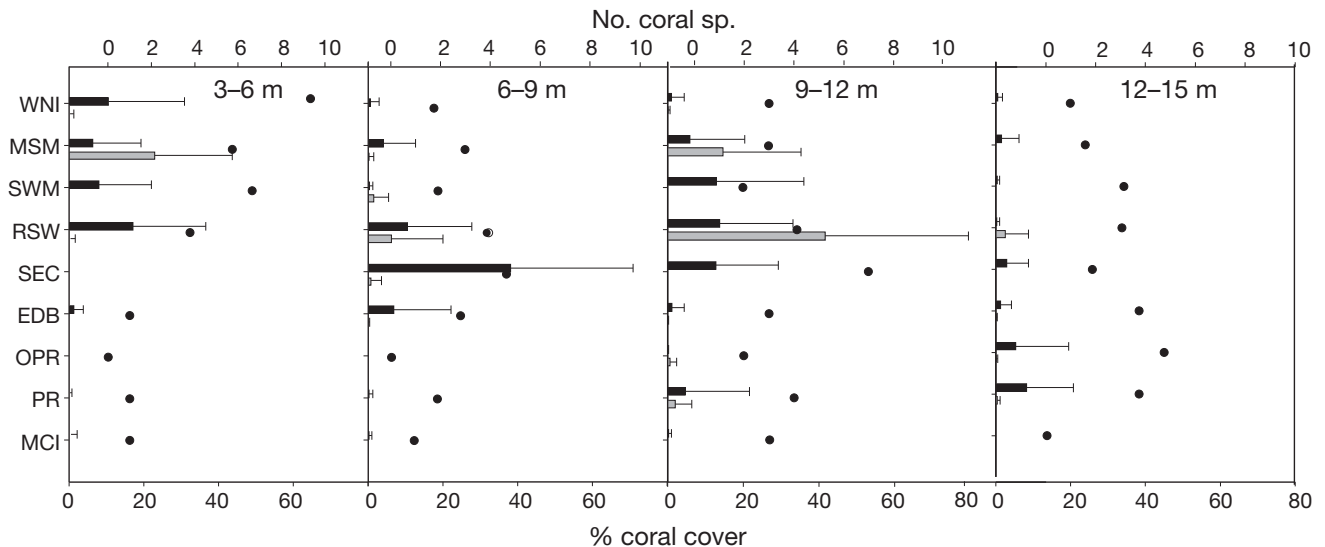
Fig. 2. Mean percent coral cover ± SD of scleractinian (dark bars) and soft corals (light bars – bottom axis), and number of species (dots – top axis) present at each of the 9 sites (left axis) in the 4 depth strata surveyed at the Kermadec Islands (for site abbreviations see Table 1). Sites ordered from north to south (top to bottom)

12.5%, Outer Parsons Rock = 5.3 ± 14.1%). These deeper assemblages around Parsons Rock were dominated by *Leptastrea* sp. and *Montastraea curta*. *M. curta, Goniastrea favulus,* and *Hydnophora pilosa* were present at all depths surveyed, varying in cover and presence by site. *Pocillopora damicornis* was only present in the 3 to 9 m zone, at 0.2 to 3.4% of benthic cover. Mean soft coral cover was greatest in the 9 to 12 m zone, averaging 7 ± 14% over all sites, with the highest cover of 42 ± 38% being recorded at Rocks Southwest Meyer. Lowest mean soft coral cover was recorded in the 12 to 15 m zone (0.45 ± 0.8%), averaged over all sites. Mean cover of filamentous algae decreased with depth from 63.6 ± 18.9% in the 3 to 6 m zone to 52.9 ± 17.3% in the 12 to 15 m zone.

Multivariate analysis of both benthic composition and scleractinian coral species assemblages for the 9 sites (in 4 depth strata) around the Kermadec Islands revealed significant differences among sites and depths within sites (Table 2; PERMANOVA, p < 0.01 for all tests). However, only 13 of 36 and 8 of 36 possible site comparisons had significantly different benthic compositions and coral community structures, respectively. Analysis of significant differences in coral assemblages between sites at each depth revealed the greatest variability between assemblages at the 3 to 6 m strata, with all sites significantly different from each other (Table 2). Least variability was observed in the 6 to 9 m strata, with only

26 of the 36 site combinations showing significant differences (Table 2). Canonical ordination shows a lack of groupings of sites and depths according to their coral assemblage similarities, with a clear overlap of most sites due to their dominance by macroalgae and coral species scarcity. The few outliers identified by CAP analysis were sites with high abundances of hard or soft corals (e.g. Rocks Southwest Meyer 9 to 12 m had 41% soft coral cover, data not shown).

The taxa that contributed most to the dissimilarity between the main grouping and the outliers for benthic and scleractinian coral assemblages were defined by SIMPER analysis. The site of Mid South Meyer was significantly different to most other sites, due to its abundance of soft corals (19% mean cover) in addition to the hard coral *Hydnophora pilosa* (3% mean cover). The other outliers were characterised by their abun-

Table 2. Results of PERMANOVA of similarities in coral community assemblages for 2-way nested site and depth among sites, and separate analysis for each depth stratification at 9 sites at the Kermadec Islands, New Zealand. Pairwise difference for sites in each depth stratification significant at p < 0.05

Factor	DF	SS	MS	Pseudo-F	p	Significant pairwise differences
Site	8	44323	5540	2.21	<0.01	
Depth	3	8814	2938	5.28	<0.01	
Depth (Site)	26	65549	2521	6.61	<0.01	
3–6 m Site	7	37313	5330	8.3	<0.01	All sites
6–9 m Site	8	71441	8930	12.5	<0.01	26 of 36 combinations
9–12 m Site	8	73728	9216	11.5	<0.01	35 of 36 combinations
12–15 m Site	8	55498	6937	8.6	<0.01	30 of 36 combinations

dance of rare species (e.g. Outer Parsons Rock 12 to 15 m had 4% *Leptastrea* sp.), or the relatively high abundance of one species (e.g. Rocks Southwest Mayer 3 to 6 m had 14% *Montastraea curta*). Two site/depth combinations were significantly different to other site/depth strata in both benthic (including coral) and coral species community structure: Rocks Southwest Meyer 9 to 12 m, which was dominated by soft coral (42% cover), *H. pilosa* (13% cover) and filamentous/fleshy macroalgae (23% cover); and Southeast Denham Bay 6 to 9 m with 38% hard coral cover (including 28% *Montipora* sp.). The southern site of Macauley Island was not significantly different in community structure to 5 of the other 8 sites, despite its geographical isolation. Overall, the coral assemblage at Macauley Island exhibited the lowest coral cover, lowest coral species diversity and an absence of soft corals. However, the lack of clear groupings in all 9 sites suggests a variable benthic community among sites and depths, rather than a clear latitudinal delineation.

Regional affinities

Cluster analysis (Fig. 3) of the regional affinities of the coral species and diversity patterns seen at the Kermadec Islands revealed the existence of pronounced divisions between the tropical Australian sites and the high latitude sites. Analyses of coral assemblages using both untransformed and transformed data gave the same clusters, at comparable similarity levels. SIMPROF grouped sites based on the abundance of each coral family into 5 clusters at p < 0.01, loosely defined as: A – Northern and Central GBR, B – Gulf of Aqaba/Houtman Abrolhos, C – Australasian high latitude (incl. the Kermadec Islands), D – Japan, E – high latitude, plus the 2 outliers of Southwest Rocks (Australia) and the Southern GBR.

The Kermadec Islands showed closest affinity in terms of coral family composition with the high latitude sites of Cook Island (28° 12′ S, 153° 34′ E) and Julian Rocks (28° 38′ S, 153° 36′ E), both in New South Wales (NSW), Australia. The coral assemblages of the Kermadec Islands and the 2 Australian high latitude sites were significantly different to all other tropical, subtropical and high latitude clusters (p < 0.05). These 2 Australian high latitude sites have similar coral cover to the Kermadec Islands (8%) with 8 and 5%, respectively, though their species counts are higher than at the Kermadec Islands (24 species) with 33 and 30 spe-
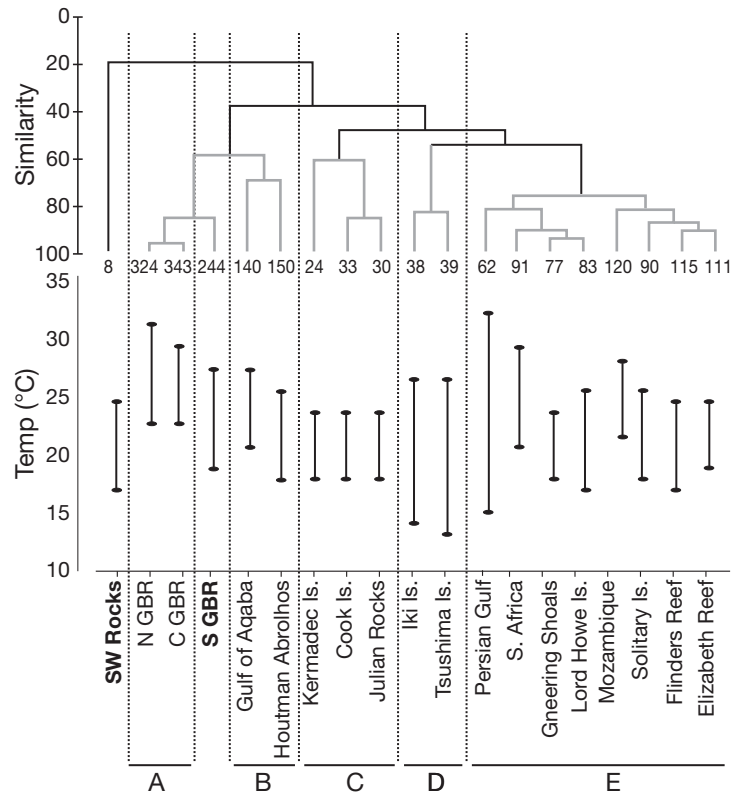

Fig. 3. Cluster analysis of similarities in coral family assemblages of the Kermadec Islands (present study and Brook 1999), and from documented locations in Australia and other high latitude sites, with annual minimum and maximum temperatures sourced from Reefbase.org and Yamano et al. (2001). Temperatures of each specific Great Barrier Reef (GBR) region are maximum and minimum over the whole latitudinal range. Number of species present at each site/region are noted under branch of cluster. Bold text indicates outlying sites/regions

cies, respectively. The closest affinity of coral assemblages in this cluster was with the cluster of high latitude sites of Japan (Iki Island 33° 47′ N, 129° 43′ E and Tsushima Island 34° 25′ N, 129° 20′ E), Australia, South Africa, Mozambique and the Persian Gulf. Notably, the western high latitude Australian site, Houtman Abrolhos, showed closest affinity with the Gulf of Aqaba, in terms of coral family composition. This latter cluster showed closer affinity with all GBR regions than with other high latitude sites, despite the Persian Gulf being closely located to the Gulf of Aqaba, and the African sites in the same ocean as Houtman Abrolhos (though admittedly many thousands of km apart). Additionally, the southernmost mainland site of Australia, Southwest Rocks (30.56° S, 152.0° E), was separate in coral assemblage similarity to all other groups (similarity of ~20%) due to the species-depauperate nature of the site (only 8 species).

SIMPER analysis revealed that the Faviidae (25%), Dendrophylliidae (25%) and Acroporidae (18%) con-

tributed most to the similarity of the coral assemblages at the Kermadec Islands and the 2 southern Australian sites (Table 3). The dissimilarity of the high latitude Australasian cluster to the Japanese sites was attributed to the abundance of species from the Faviidae at the latter (mean of 19 species compared to 7 species) and the high counts of species from the Dendrophylliidae at the former (mean of 6 species compared to 1 species at the Japanese sites). The abundance of acroporids on the GBR, and their absence at the Kermadec Islands, explained the different coral assemblage of the Kermadec Islands versus the GBR clusters. Furthermore, the abundance of species in general, and specifically of acroporid and faviid species at the remaining high latitude sites (cluster E) explained the separation of this group from the 2 Australian high latitude sites and the Kermadec Islands.

After assessing survey depth at each location (where possible), no distinct patterns were found between depth and affinities of coral assemblages. Despite the surveys of all coastal eastern Australian sites being conducted at 8 to 12 m (Harriott & Banks 2002), as opposed to the 0 to 40 m at the Kermadec Islands (Brook 1999), 2 of these Australian sites still showed closer affinity with the Kermadec Islands than with other Australian sites. Survey depths at other high latitude sites range from 0 to 20 m (Elizabeth Reef) to 0 to 50 m (Gulf of Aqaba).

A clear pattern exists between the clustering of tropical sites versus high latitude sites, and their annual temperature ranges (Fig. 3), with the coral assemblages of the warmer GBR sites clustering together. However, similarities also exist in temperature ranges between distinct high latitude clusters. Five of the 8 sites in the high latitude cluster (E) have a similar annual temperature range to the Kermadec Island cluster (C; 18 to 24°C), yet exhibit a lack of affinity with respect to their coral assemblage. However, sites in the Kermadec Islands cluster have the lowest annual maximum of 24°C, whereas the annual maxima at the other high latitude sites range from 25 to 30°C. Further, the Kermadec Islands and southern Australian sites all host coral communities as opposed to reefs. The Japanese sites, loosely clustering with the Kermadec Islands, are located at a higher latitude (34°N) than the Kermadec Islands and are subject to average annual temperatures of 13 to 27°C. The other 3 sites in the high latitude cluster (E) are all subject to either higher or wider ranging annual temperature ranges than the Kermadec Islands (Persian Gulf 15 to 33°C, S. Africa 21 to 30°C, Mozambique 22 to 28°C).

DISCUSSION

The coral assemblages of the Kermadec Islands are dominated by subtropical species and feature low coral species diversity and overall low cover, as might be expected at such a high latitude location (Harriott & Banks 2002). We identified 16 scleractinian and 1 soft coral species, with considerable differences in assemblages between closely located sites (<1 to 4 km). Although located at a high latitude (29 to 31°S), and subject to low annual sea surface temperatures (SST; 18 to 24°C annual range), the variability in coral diversity and cover at the Kermadec Islands suggests that local-scale variations in the environmental and biological regime are important for controlling the structure of this marginal community. On a regional scale, the Kermadec Islands coral assemblage was most similar to 2 rocky subtropical sites of southeastern Australia (NSW); there was a lack of affinity with tropical sites, and a lesser affinity for other high latitude sites. These different affinities are likely explained by local environmental factors such as wave energy (and associated algal whiplash) and water quality, rather than latitude and its associated influence on temperature (Wells 1957). Additionally, larval supply, and historical and evolutionary factors

Table 3. Coral families contributing to SIMPROF groupings (Fig. 3) of similarities in coral assemblages at Australasian and marginal sites, calculated with Bray-Curtis Similarity. Families are listed in order of % contribution to within-site similarity. Letters in brackets under site refer to groupings in text. Numbers in brackets beside families indicate average number of species per group in site assemblage. N and C GBR: Northern and Central Great Barrier Reef. KI: Kermadec Islands

Group	N GBR/C GBR (A)	Gulf of Aqaba/ Houtman Abrolhos (B)	Australasian high latitude (inc. KI) (C)	Japan (D)	Australian and African high latitude (E)
Within group similarity	97%	69%	69%	83%	79%
Family contributing (mean number spp.)	Acroporidae (108) Faviidae (63) Poritidae (37) Fungiidae (31)	Acroporidae (58) Poritidae (16) Merulinidae (11) Siderasteidae (7)	Faviidae (7) Dendrophylliidae (6) Acroporidae (6) Siderasteidae (3)	Faviidae (19) Poritidae (6) Pectiniidae (4) Acroporidae (2)	Acroporidae (32) Faviidae (22) Poritidae (9) Dendrophylliidae (6)

(Harriott & Banks 2002) will have influenced the formation of the modern-day coral assemblages at the Kermadec Islands.

The low coral diversity at the Kermadec Islands (24 species, Brook 1999) is seemingly linked to the physiological tolerances of coral species to low temperatures. Many reef-building species cannot grow and survive outside the tropics (Harriott et al. 1994, 1995), as exemplified by the absence of some major reef-building taxa (e.g. staghorn *Acropora* and massive *Porites*) at the Kermadec Islands and at most subtropical Australian sites. However, coral communities with higher species diversity and cover have been observed in regions subject to lower annual SST minima than those seen at the Kermadec Islands. For example, along the coast of Japan, coral communities with up to 40 species and 20 to 30% cover have been recorded (Yamano et al. 2004). These are usually subject to an annual average SST minimum of 17°C (compared with 18°C at the Kermadec Islands), and the most northerly of them are subject to a lowest annual SST of 13.3°C (Yamano et al. 2001). Additionally, coral communities on the east coast of Australia separated by <50 km, but with similar annual temperature regimes, have highly variable species diversity and cover (Harriott & Banks 2002). The low temperatures experienced at the Kermadec Islands will also limit coral reef formation and cover by causing coral mortality (Veron & Done 1979, Burns 1985), and reducing the rates of growth (Grigg 1982, Harriott 1999), fecundity (Wells 1957, Hughes et al. 1999) and recruitment (Veron & Done 1979, Grigg 1983). However, while low temperature goes some way towards explaining the low diversity and cover of corals at the Kermadec Islands, alone it cannot explain the lack of similarity between coral assemblages at sites from similarly high latitudes. Other, more local factors must play a role.

The hydrodynamic conditions, in terms of exposure to high wave energy, at the Kermadec Islands create a challenging environment for habitation, with the absence of shallow, sheltered rocky reefs and lagoons limiting the substrate available for coral settlement. Locally, the southern site of Macauley Island is exposed to unrefracted ocean swell and storm surges (Brook 1999), and the species assemblage present reflects this challenging environment: macroalgae dominate with no soft corals present and <1% hard coral cover. The high wave energy experienced at the Kermadec Islands is also experienced at the rocky benthic communities of Julian Rocks and Cook Island (NSW, Australia; Harriott et al. 1999), with which the Kermadec Islands showed the closest affinity in the present study. These sites are located 2 km and 600 m offshore, respectively. Reef accretion at these sites is also likely to be inhibited by the removal of living and dead coral skeletal material by episodes of severe waves (Harriott & Smith 2002). Further, the dislodgement of colonies from the substrate by storm surge will be facilitated by the relatively smooth surfaces of rocks at high latitudes (Banks & Harriott 1995, Nozawa et al. 2008).

Environments with high wave energy favour compact growth forms of corals (Veron 1993b), with only those coral species that can withstand exposure to swell and storm surge able to establish there. Thus, the low abundance of branching species at the Kermadec Islands, Julian Rocks and Cook Island (e.g. acroporids, pocilloporids) may be due to the high degree of wave exposure. Comparatively, at Lord Howe Island, Australia, reef-building species are able to establish, but only in the lagoonal areas; they are uncommon on the seaward slopes where reef accretion capacity is very limited (Harriott et al. 1995). In addition to Lord Howe Island, the other high latitude sites considered here, all of which show greater species diversity than the Kermadec Islands, all feature sheltered areas, which potentially allow more fragile species to establish. The lack of sheltered areas at the Kermadec Islands means that even if temperatures are sufficient to allow colonization by reef-building species, hydrodynamic conditions may prevent their long-term establishment.

The high wave energy at the Kermadec Islands also favours dominance by calcareous algae, which can establish in wave-exposed areas, and out-compete corals for space and light (Hustan 1985). At high latitudes, competition between corals and algae plays a significant role in regulating coral assemblages (Birkeland 1977, Birkeland & Randall 1981) because subtropical conditions (i.e. relatively low SST) favour algae over corals. The dominance by macroalgae, at the Kermadec Islands, Julian Rocks and Cook Island (76, 45 and 67%, respectively, compared to 25% on the GBR) suggests that algae are successfully out-competing corals for space at these sites, perhaps by overgrowth of the live coral tissue (McCook et al. 2001). Chemical degradation and physical damage by abrasion have also been shown to be involved in a number of direct competitive interactions between corals and algae, the mechanism dependent on the coral and algal species concerned (de Nys et al. 1991, McCook et al. 2001, Jompa & McCook 2003, Nugues & Bak 2006). In areas of high flow, such as many of the shallow exposed sites at the Kermadec Islands, macroalgae can have a whiplash effect on the corals, causing physical damage by abrasion (Coyer et al. 1993) and reduced coral growth (River & Edmunds 2001). On the other hand, corals have also been shown to inhibit algal growth and overgrow algae (Meesters & Bak 1993, McCook et al. 2001). For example, Jompa & McCook (2002) reported a mutual competitive interaction between the

coral *Porites cylindrica* and the creeping form of the brown alga *Lobophora variegata;* the alga induced tissue mortality of the coral, which was also able to inhibit the growth of this alga, though to a lesser degree.

The impact of wave surge and algal competition on coral cover will also be depth dependent (McCook et al. 2001). As wave surge decreases with depth, the reduced algal whiplash at these depths may create a more habitable environment for corals (cf. McCook et al. 2001). Additionally, algal growth rates decline with depth and illumination (cf. Markager & Sand-Jensen 1992). As a result, the alga has a reduced competitive advantage, and thus coral cover increases with depth until light becomes limiting (Burns 1985, Riegl et al. 1995). This pattern was observed at some of the sites at the Kermadec Islands, but was not consistent across all sites.

The competition between algae and corals at high latitudes, and indeed any location, is linked to nutrient concentrations as, in general, inshore and higher latitude waters have greater nutrient concentrations than do offshore and lower latitude waters, which allows for enhanced growth rates of macroalgae (Crossland 1983). Additionally, any variation in nutrient availability between sites will affect community structure, as nutrients enhance growth and hence the competitive ability of macroalgae (Kojis & Quinn 1984, Hughes 1989, Nugues & Roberts 2003). Turbidity, a reflection of nutrient levels (Koenings & Edmundson 1991), is indeed known to be variable between sites at the Kermadec Islands (0 to 3 Formazin Turbidity Units, FTU, J. Gardner unpubl. data); however, long-term measurements of turbidity and/or nutrients are not available and so further study is needed to assess the role that nutrient levels play in shaping the coral assemblages at this location.

The geological history of the Kermadec Islands and the rate of dispersal of larvae to this isolated site are additional, intertwined factors that limit the species present. In a study of genetic connectivity between Lord Howe Island and the GBR (700 km apart), Ayre & Hughes (2004) showed that expanses of open ocean between isolated reefs are far more effective barriers to dispersal than are similar distances within continuous reef systems. This highlights the potential for limited recruitment of coral larvae at the Kermadec Islands, given that they lie at a minimum distance of 750 km from any landmass, and are approximately 3000 km from the GBR. Indeed, at the Kermadec Islands, there is evidence of limited connectivity between even closely located sites (<1 km), most likely associated with the hydrographic regime (Wood & Gardner 2007). The low diversity of the Kermadec Islands may also reflect their geological history, with

no evidence of a land bridge at any time (Brothers & Searle 1970). Additionally, there appears to be a decline in coral recruitment with increasing latitude, linked to low water temperatures (Hughes et al. 2002, Nozawa et al. 2006), which at the Kermadec Islands likely compounds the problems associated with their remoteness. Finally, although a heavily debated issue, the mode of transmission of coral species is likely to affect their likelihood of recruitment to and within the Kermadec Islands. Most brooding corals have larvae that are competent to settle within a few hours or a few days after release (Richmond 1987, Harrison 2006, Gilmour et al. 2009), which promotes settlement on, or close to, the natal reef (e.g. Tioho et al. 2001). However, spawning corals and some brooding corals produce a small proportion of larvae that have extended competency periods of over 100 d in the water column (e.g. Nozawa & Harrison 2002), with an associated dispersal potential of hundreds of km (Harrison & Wallace 1990, Harrison & Booth 2007). Whilst over 85% of coral species on the GBR are spawners (reviewed by Hughes et al. 2002), approximately half of the species present at the Kermadec Islands are brooders. Many high latitude locations are dominated by brooding species, including the Solitary Islands (Harriott & Banks 1995), Lord Howe Island (Harriott 1992) and Gneering Shoals (Banks & Harriott 1996); locations which show a lack of affinity, in terms of their species assemblages, with the Kermadec Islands.

It is important to note that small, isolated, and often peripheral islands in the Pacific Ocean are usually subject to high faunal turnover rates, which are a major factor contributing to differences in community structure in time and space at these locations (Pauley 1989, Harriott et al. 1994, 1995). Temporally, little is known of the variability in community structure at the Kermadec Islands, as due to their isolation and inaccessibility, longer-term monitoring has not been possible. Two previous short-term studies have found large within-site variability (surveys 1991 to 1992, Brook 1999; survey 2002, Gardner et al. 2006), while variability with depth is apparent when these 2 studies are compared; however, repeat sampling of the same sites has not been undertaken. Crucially, though, the present study identified the same coral species present at the Kermadec Islands as were reported by Brook (1999), which suggests that, although coral cover may be temporally variable, species presence is not (at least in the short to mid term). Hence, our analysis of regional species affinities remains valid, even if the extent of coral cover may vary over time and the associated comparisons should be treated with caution.

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 (cf. Sandin et al. 2008). Thus, our study provides valuable data on a marginal coral community that is relatively free from anthropogenic impact. Ongoing monitoring at this site will not only improve our understanding of the ecology of high latitude coral communities, but provide a pristine comparison for assessing the impacts of environmental degradation on other high latitude coral systems.

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