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# The coastal scleractinian coral fauna of the Kermadec Islands, southwestern Pacific Ocean

F. J. Brook\*

The species diversity of the coastal scleractinian coral fauna at the subtropical Kermadec Islands attenuates southwest along the island chain from 17 hermatypic (zooxanthellate) species and 7 ahermatypic (azooxanthellate) species at the northern end (Raoul Island 29°2'S), to 2 hermatypes and 2 ahermatypes in the south (L'Esperance Rock 31°1'S). Biogeographic affinities are with other subtropical southwestern Pacific islands rather than with New Zealand.

The majority of the Kermadec hermatypic species are restricted to depths shallower than 20–30 m, and encrusting growth forms predominate. Hermatypic corals form scattered colonies on volcanic substrata, and there is no contemporary reef formation. Coral cover is highest around Raoul Island, peaking at 20–40% of benthic cover at 1–6 m depth, with a subsidiary peak at about 15–25% of benthic cover between 18 m and 25 m depth at some sites. Hermatypic corals form less than 1% of benthic cover around islands further south in the group. Kermadec coastal ahermatypic species are largely restricted to caves and overhangs.

The asteroid *Acanthaster planci* is recorded from Raoul and Macauley Is. It is common at Raoul, and is evidently an important modifier of hermatypic coral communities there.

**Keywords** Kermadec Islands, subtropical, scleractinian corals, hermatypes, ahermatypes, biogeography

## INTRODUCTION

The Kermadec Islands are a NNE-trending chain of volcanic islands in the southwestern Pacific Ocean, located northeast of the New Zealand mainland between 31°3'S 178°8'W and 29°2'S 177°8'W (Fig. 1). The largest of the Kermadec Islands, Raoul I., is located at the northern end of the chain. It is fringed on its northeastern side by a series of small islands and rocks, including Meyer, Napier, Nugent, Dayrell and Chanter Is. (Fig. 2). Raoul and nearby islands (2938 ha total area) are 100 km NNE of Macauley I. and adjacent Hazard Islet (306 ha total area), which in turn are 35 km NNE of Curtis and Cheeseman Is. (59 ha total area). L'Esperance Rock (5 ha) and submerged Havre Rock at the SSW end of the Kermadec chain are 80 km distant from Curtis and Cheeseman Is.

The shallow water (<50 m depth) marine biota at the Kermadecs is of considerable biogeographic and ecological interest on account of the islands' physical isolation and geological setting, the range of latitude over which they extend and their location midway between temperate New Zealand coasts and the tropical Tonga Islands (Oliver 1915, Nelson & Adams 1984, Schiel et al. 1986, Francis et al. 1987, Cole et al. 1992, Francis 1993, Brook

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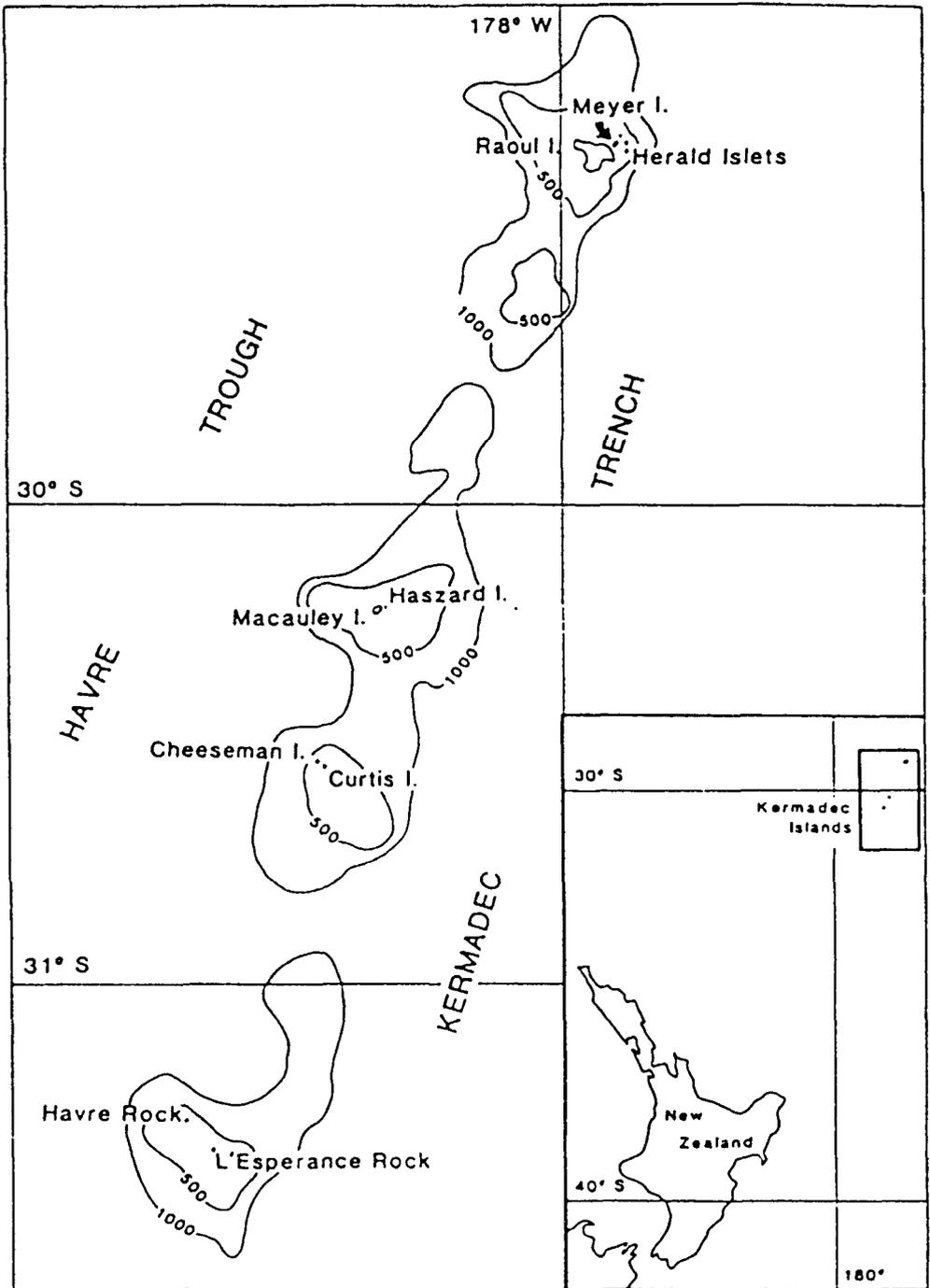


Fig. 1 Kermadec Islands. Bathymetry in metres.

1998a) The biota comprises a mix of tropical, subtropical, temperate and endemic species. Hermatypic corals are present, but there are no coral reefs such as are common at tropical latitudes in the western and central Pacific Ocean.

The first account of the Kermadec Islands coral fauna recorded six hermatypic species from shore and dredge collections made at Raoul and Meyer Is in 1908 by W. R. B. Oliver and R. Bell, and a further four hermatypic species from fossil material collected by Oliver on Raoul, Napier and Dayrell Is (Vaughan 1917). Those species records have subsequently been quoted in a number of studies concerned with the present-day distribution of hermatypic genera and regional variation in generic diversity (Wells 1954, Stehli & Wells 1971, Rosen 1984, Veron 1985a, 1993). Morton & Miller (1973) briefly mentioned hermatypic corals seen in rock pools and subtidally at Meyer I. Schiel et al. (1986) surveyed the depth distribution, colony size and percent cover of scleractinian corals at 0–20 m depth along a single transect on the southeastern coast of Raoul I, but their data set did not differentiate coral species. Kosmynin (1994) recorded 13 species of hermatypic and one ahermatypic scleractinian species from Raoul and adjacent islands, and Cairns (1995) recorded two coastal ahermatypic species from the Kermadec group.

The present study concerns the taxonomic composition, ecological setting, zonation and biogeographic relationships of the present-day scleractinian fauna at the Kermadec Islands. A geological and paleoenvironmental study of Early Pleistocene coral-bearing volcanic-sedimentary rock units at the northern Kermadec Islands was carried out concurrently (Brook 1998b).

## PHYSICAL SETTING

The Kermadec Islands are the emergent crowns of large volcanic mountains that rise more than 1 km above the crest of the NNE-trending submarine Kermadec Ridge. That ridge extends between northeastern New Zealand and the Tonga Islands, and is situated above an active WNW-dipping subduction zone at the boundary between the Indian and Pacific crustal plates (Karig 1970, Ewart et al. 1977). It is flanked to the east by the 8000–10 000 m-deep Kermadec Trench, and to the west by the 2500–3000 m-deep Havre Trough, which separates the Kermadec Ridge from the parallel submarine volcanic Colville Ridge 175–200 km to the west-northwest. The Kermadec Islands themselves are of Pleistocene and Holocene age (Brothers & Martin 1970, Brothers & Searle 1970, Doyle et al. 1979, Lloyd & Nathan 1981), but sedimentary rocks containing reworked microfossils as old as earliest Miocene have been dredged from the top and flanks of the Kermadec Ridge (P. F. Ballance pers. comm. 1997). The Havre Trough is a back-arc basin that is thought to have begun opening in the Pliocene (Caress 1991, Wright 1993).

There is a limited range of physical habitat types at shallow subtidal depths at the Kermadec Islands, and no shelter from oceanic swell and storm waves. Smaller islands within the group are encircled by rocky coasts, but boulder and gravelly sand beaches are present around parts of Raoul and Macauley Is. Steeply sloping rock substrata, commonly with crevices, caves and overhangs, dominate in the shallow subtidal zone (down to 10 m depth or more) at L'Esperance Rock, and Curtis, Cheeseman, Meyer, Napier, Nugent, Dayrell and Chanter Is, and in places around Macauley and Raoul Is. Gently sloping reef areas of *in situ* rock and/or large boulders are present locally around Raoul, Meyer, Chanter, Macauley and Curtis Is to depths of approximately 20–30 m. Gravelly and sandy sediments offshore from beaches and reefs at the Kermadec Islands are predominantly volcanoclastic, but mixed volcanoclastic-bioclastic sediments are present below approximately 10–20 m depth adjacent to reefs and in erosional gutters and channels between reefs. Bioclastic-dominated sediments are present locally below 15 m depth around Raoul and adjacent

islands. They include aprons of coral rubble to seaward of reefs, and lenses of detrital gravelly sand ponded on reefs and at the base of steeply sloping to overhanging submarine rock faces. No muddy sediments are known from intertidal or shallow subtidal depths around the Kermadec Islands.

Water clarity around the Kermadecs is generally high except on gently shelving coasts around Raoul and Macauley Is., where wave action and/or terrestrial runoff can at times increase turbidity levels. Sea surface salinity around the islands is typically high (Ridgway & Heath 1975).

Satellite-derived sea surface temperature data for the Kermadec region summarised in Francis et al. (1987) indicate that surface waters have an annual temperature range of approximately 16–26°C at the northern end of the island chain, and a range of approximately 14–26°C at L'Esperance Rock in the south. Monthly means range from minima of 18°C and 17°C in August–September to maxima of 24°C and 23°C in February–March, at the northern and southern ends of their chain respectively.

Circulation of surface and near-surface waters in the Kermadec region is complex and poorly known. The overall pattern of oceanic circulation in the southwestern Pacific is dominated by a large subtropical anticyclonic gyre. At low latitudes, the Trade Wind Drift field generates an overall westward flow towards the Coral Sea and northwestern Australia, whereas at higher latitudes the return flow is predominantly to the east and northeast (Wyrski 1960). In summer months, the Trade Wind Drift field is pushed south by the northerly monsoon, and at times the northern part of the Kermadec chain is warmed by south to southwest-flowing tropical water (Wyrski 1960; Stanton 1969; Ridgway & Heath 1975). However, for most of the year the islands are in the path of the return flow of the subtropical gyre, and are influenced by eastward-flowing subtropical watermasses or by cooler subtropical watermasses flowing north to NNE from northeastern New Zealand (Heath 1975, 1980, 1985; Ridgway & Heath 1975; Reid 1986; Roemmich & Cornuelle 1990). Additional evidence for the existence of surface currents flowing from New Zealand to the Kermadec Islands is given by the periodic washup on beaches at Raoul and Macauley Is. of drift algae, seeds, logs and flotsam derived from New Zealand (Oliver 1910; Sykes & Godley 1968; Nelson & Adams 1984).

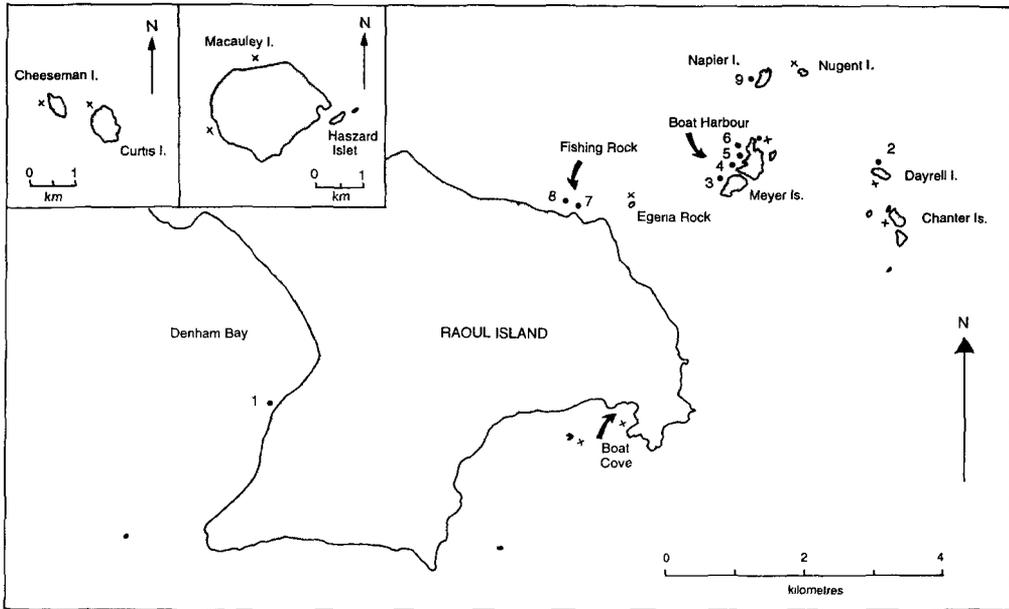
## METHODS

### Coral surveys

This study describes scleractinian coral faunas between the intertidal and 45 m depth at the Kermadec Islands. It is based on coral specimens collected by M. P. Francis in October 1985 and my own field surveys using SCUBA carried out in September 1988, May–June 1991, June 1992 and May 1995, involving qualitative observations of species distribution and ecology and depth-stratified quantitative surveys of coral abundance. During the course of the field surveys, a representative collection was made of species seen, and that material has been deposited at the Auckland War Memorial Museum.

Identification of hermatypic species follows the taxonomy of 'Scleractinia of Eastern Australia' parts 1–5 (Veron & Pichon 1976, 1980, 1982; Veron et al. 1977; Veron & Wallace 1984) and also Veron (1985b, 1986). Some of the ahermatypes and hermatypes collected were identified by S. D. Cairns, and J. E. N. Veron respectively.

Qualitative surveys of coral faunas were undertaken at locations shown in Fig. 2. A range of physical habitat types and exposure settings were surveyed around eastern Raoul and adjacent islets, but information on L'Esperance Rock, Curtis and Cheeseman Is. is based on single locations at each, and that for Macauley I. is based on two locations. At each location, an attempt was made to search all microhabitats present over as great a depth range as



**Fig. 2** Cheeseman, Curtis, Macauley and Raoul Is. showing locations of dive sites. Numbered dots and crosses denote sites of quantitative and qualitative surveys respectively.

practicable. In most cases dives were limited to depths shallower than 20–30 m, but deeper reefs were surveyed at Macauley, Napier and Dayrell Is. During each dive a list of coral species seen was compiled and notes were made on depth range and habitat of each species, their estimated relative abundance, corallum size and growth form (Appendix 1). The distribution of the corallivorous asteroid *Acanthaster planci* (Linnaeus) and its feeding traces on hermatype colonies were also recorded at each location. Quantitative abundance data for *A. planci* were obtained at a few locations around Raoul in May 1995 and will be reported elsewhere (R. Babcock & F. Brook unpub. data).

Quantitative surveys of sessile benthic cover were made at nine locations and 23 sites at depths of 1–3 m, 5 m, 15 m and 20 m around Raoul and adjacent islets in 1991 and 1992 (Fig. 2). Surveys were carried out on gently sloping substrata at set depths for comparison of depth-related trends in coral cover and community composition between locations. All sites were on bedrock reefs except for the shallowest site at location 8, which was on large boulders and lacked corals. Location of surveyed areas was chosen with the aim of sampling as wide a range of exposure settings as possible (re aspect and overall reef slope) and given the constraints of time and sea conditions. At most locations two or more sites were sampled at different depths along profiles, but sea conditions limited the survey of Napier I. to a single depth stratum. At each site the cover of scleractinian coral species, crustose red algae, filamentous and frondose algae, the fleshy red alga *Galaxaura filamentosa*, soft corals and zoanthids was estimated in twenty haphazardly placed 0.25 m<sup>2</sup> quadrats (total area of 5 m<sup>2</sup> per site).

### Statistical analysis

To facilitate comparison of coral associations among sites, the species percent cover data for sites at Raoul were transformed to percent relative cover. The actual cover of each species

was divided by the total hermatype cover for the site and the resultant figure was multiplied by 100. I then carried out an unweighted pair group cluster analysis using arithmetic averages of a Bray-Curtis distance matrix of this transformed data to produce a dendrogram classification of sites based on similarity of faunal composition. A mathematical definition of the Bray-Curtis coefficient is given in Rohlf (1989) and the cluster analysis was computed using the NTSYS statistical package (Rohlf 1989).

### Biogeography

I assessed the biogeographic relationships of the coastal coral fauna in terms of the wider distribution of species present at the Kermadecs, and by comparison with subtropical faunas of eastern Australia and other South Pacific islands. Information on regional species distribution and faunal diversity was obtained from published records (all listed in the References), and for Norfolk Island from my own unpublished data. A comparison was also made between the coastal ahermatype and deep water Kermadec coral faunas based on distribution information in Cairns (1995).

## RESULTS

### Coral distribution

Seventeen hermatypic species (in 15 genera) and 7 coastal ahermatypic species (in 6 genera) are recorded here from the Kermadec Islands (Appendix 1). The geographic distribution of species is summarised in Table 1. Total species diversities were highest at Raoul and adjacent islands (17 hermatypes, 7 ahermatypes), and lowest at L'Esperance Rock (2 hermatypes, 2 ahermatypes) and Curtis and Cheeseman Is. (2 hermatypes, 3 ahermatypes). The most abrupt latitudinal change in hermatype diversity was between Macauley I. (10 species) and Curtis and Cheeseman Is. (2 species), whereas the greatest change in ahermatype diversity was

**Table 1** Geographic distribution of coastal scleractinian coral species at the Kermadec Islands. 1 Raoul and adjacent islets, 2 Macauley Island, 3 Curtis and Cheeseman Islands, 4 L'Esperance Rock

	1	2	3	4		1	2	3	4
<b>Hermatypes</b>					<b>Ahermatypes</b>				
<i>Pocillopora damicornis</i>	x	x			<i>Culicia rubeola</i>	x	x	x	x
<i>Montipora capricornis</i>	x	x	x		<i>Coenoclyathus brooki</i>	x	x	x	x
<i>Montipora spongodes</i>	x	x	x	x	<i>Cladopsammia eguchi</i>	x			
<i>Alveopora ?spongiosa</i>	x	x		x	<i>Dendrophyllia yamai</i>	x			
<i>Coscinaria columnna</i>	x				<i>Rhizopsammia</i> sp. cf. <i>R. verrilli</i>	x			
<i>Psammocora haimeana</i>	x				<i>Tubastrea coccinea</i>	x			
<i>Leptoseris scabra</i>	x				<i>Tubastrea diaphana</i>	x	x	x	
<i>Pavona explanulata</i>	x	x							
<i>Cycloseris vaughani</i>	x								
<i>Hydnophora pilosa</i>	x	x							
<i>Cyphastrea serailia</i>	x								
<i>Goniastrea australensis</i>	x	x							
<i>Leptastrea bewickensis</i>	x								
<i>Montastrea curta</i>	x	x							
<i>Plesiastrea versipora</i>	x	x							
<i>Tubinaria frondens</i>	x								
<i>Tubinaria radicalis</i>	x	x							

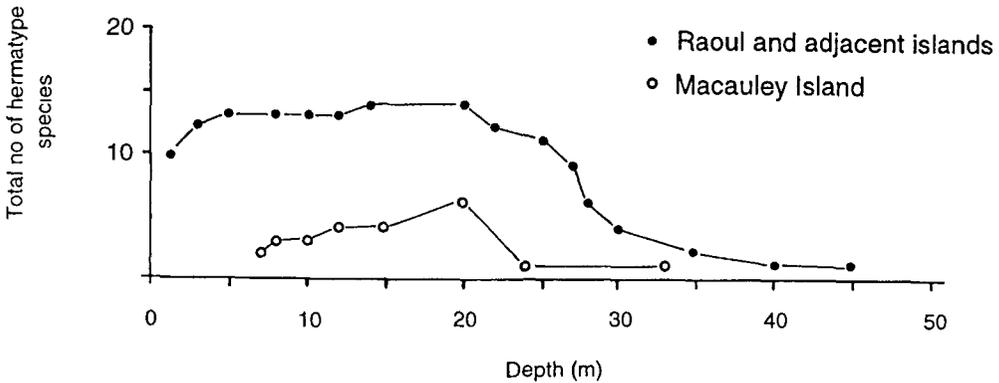


Fig. 3 Total hermatype species number plotted against depth for Raoul and Macauley Is

between Macauley I (3 species) and Raoul and adjacent islands (7 species). The latitudinal species diversity gradient among Kermadec coastal coral faunas represents a simple addition rather than replacement of species from southwest to northeast along the chain, all of the shallow water coral species present at L'Esperance Rock, Curtis, Cheeseman and Macauley Is also live off Raoul and adjacent islands. The hermatypes *Alveopora* ?*spongiosa*, *Montipora spongodes* and ahermatypes *Culicea* ?*rubeola* and *Coenocyathus brooki* are the only species known to have a distribution extending throughout the Kermadec chain.

The depth distribution of coral species is listed in Appendix 1, and the variation in hermatype species diversity with depth at Macauley I, Raoul and adjacent islets is summarised in Fig. 3. At Raoul most hermatype species were restricted to depths shallower than 25–30 m, and adults of two species (*Pocillopora damicornis*, *Montastrea curta*) were not seen below 10 m. *Plesiastrea versipora* was the only Kermadec hermatype found deeper than 40 m, its lower depth limit was not determined, but was beyond 45 m. Overall hermatype species diversity at Raoul was highest at 5–20 m, and decreased abruptly shallower than 5 m, and from 20 m to 35 m. The situation at Macauley I was rather different. There, no hermatypes were seen shallower than 7 m, two species (*Pocillopora damicornis*, *Montastrea curta*) were restricted to approximately 7–8 m depth, and only one species (*Alveopora* ?*spongiosa*) extended deeper than 20 m, down to at least 33 m. Three species (*Pavona explanulata*, *Plesiastrea versipora*, *Turbinaria radicalis*) were found only at around 20 m, and overall species diversity was also highest at that depth. The upper depth limit of hermatypes further south in the Kermadec chain was deeper still, with corals living at 15–30 m depth at Curtis and Cheeseman Is and at approximately 18–21 m at L'Esperance Rock.

No ahermatypic corals were found shallower than 6 m depth at the Kermadecs. Three of the seven coastal species (*Culicea* ?*rubeola*, *Coenocyathus brooki*, *Rhizopsammia* sp. cf. *R. verrilli*) extended below 45 m (Appendix 1), but the other four were not found deeper than 25–30 m and one (*Cladopsammia eguchii*) was seen only at 6–8 m.

### Hermatypic growth form and size

#### *Raoul and adjacent islets*

Encrusting growth forms predominated subtidally around Raoul and adjacent islets (Appendix 1). A few species were exclusively encrusting (*Psammocora haimeana*, *Leptastrea bewickensis*, *Montipora capricornis*, *Turbinaria radicalis*), whereas some others formed encrusting colonies that commonly had stout columns projecting from the upper surface (*Montipora spongodes*, *Pavona explanulata*, *Hydnophora pilosa*). The two last-named species, and also *Coscinaraea*

*columna*, *Cyphastrea serailia* and *Goniastrea australensis*, were mostly encrusting on gently sloping rock surfaces, but were commonly explanate on steep rock faces. Rare submassive colonies of *Cyphastrea serailia* and *Goniastrea australensis* were present locally at shallow depths, and similarly *Monastrea curta*, which was predominantly encrusting, also formed submassive colonies in shallow water.

The only branched species in the fauna, *Pocillopora damicornis*, formed low, compact colonies. *Turbinaria frondens* was encrusting to vasiform at shallow depths, formed foliaceous colonies with nested whorls between about 8 m and 25 m depth, and was crateriform between about 25 m and 30 m depth. *Plesiastrea versipora* was mostly encrusting above 10 m depth, formed tall, massive colonies between about 10 m and 25 m, and was submassive to encrusting in deeper water. *Alveopora ?spongiosa* formed minute hemispherical colonies.

The majority of hermatype species had a maximum colony size of between 30 cm and 60 cm, but *Plesiastrea versipora* and *Turbinaria frondens* formed colonies more than 100 cm in diameter, *Alveopora ?spongiosa* and *Psammocora haimeana* were consistently less than 10 cm in diameter, and *Leptoseris scabra* is known only from a single dead juvenile corallum 40 mm in diameter.

#### *Southern islands*

Species growth forms were closely comparable with those at Raoul. *Montipora capricornis* and *Montipora spongodes* formed encrusting colonies with or without short projecting columns, *Alveopora ?spongiosa* formed minute hemispherical colonies, *Pocillopora damicornis* formed low, compactly branched colonies, *Turbinaria radicalis* and *Montastrea curta* were encrusting, and *Pavona explanulata*, *Hvdnophora pilosa* and *Goniastrea australensis* were encrusting to explanate. The first five of those species formed colonies of comparable size to those at Raoul, but the four last-named were consistently smaller at Macauley with none larger than 15 cm diameter being seen. Similarly, the Macauley record of *Plesiastrea versipora* is based on hemispherical coralla only a few centimetres in diameter.

#### **Benthic cover off Raoul and adjacent islets**

Hermatypic coral cover was less than algal cover at all of the reef sites surveyed around Raoul and adjacent islets (Fig. 4). No fucalean or laminarian kelps were seen subtidally but several species of frondose algae were common. Filamentous and frondose algae dominated the benthic cover at most sites and crustose red algae were also common, albeit with high variance in percent cover among sites of equal depth. The tufted red alga *Galaxaura filamentosa* was locally abundant, forming 17–30% cover at 5 m depth at locations 1 and 4, and 11–69% cover at 15 m depth at locations 3–6 off the west side of Meyer I. At other sites, that species was absent or accounted for less than 1% cover. The soft coral *Efflatounaria* sp. had highest cover at 5–15 m depth but was nowhere common.

The percent cover of hermatypic corals recorded at locations around Raoul and adjacent islets is shown in Fig. 5. At locations 2–5, coral cover peaked at 22–40% between 1 m and 3 m depth, and decreased abruptly to 10% or less below that, whereas at location 7 coral cover increased from 18% at 1–5 m depth to 40% at 6 m. All of the sites with relatively high coral cover at immediate subtidal depth were on bedrock substrata. In contrast, corals were rare above 3 m depth on boulder coasts such as at locations 1 and 8. Data from location 6 and qualitative observations made elsewhere indicate that there was another peak in coral cover at approximately 18–25 m depth on some rocky reefs around Raoul and adjacent islets.

The percent cover of individual hermatype species on reefs around Raoul and adjacent islets is shown in Fig. 6. Two species (*Montastrea curta*, *Pocillopora damicornis*) reached their peak mean cover at immediate subtidal depths (<3 m) and were rare below that at most

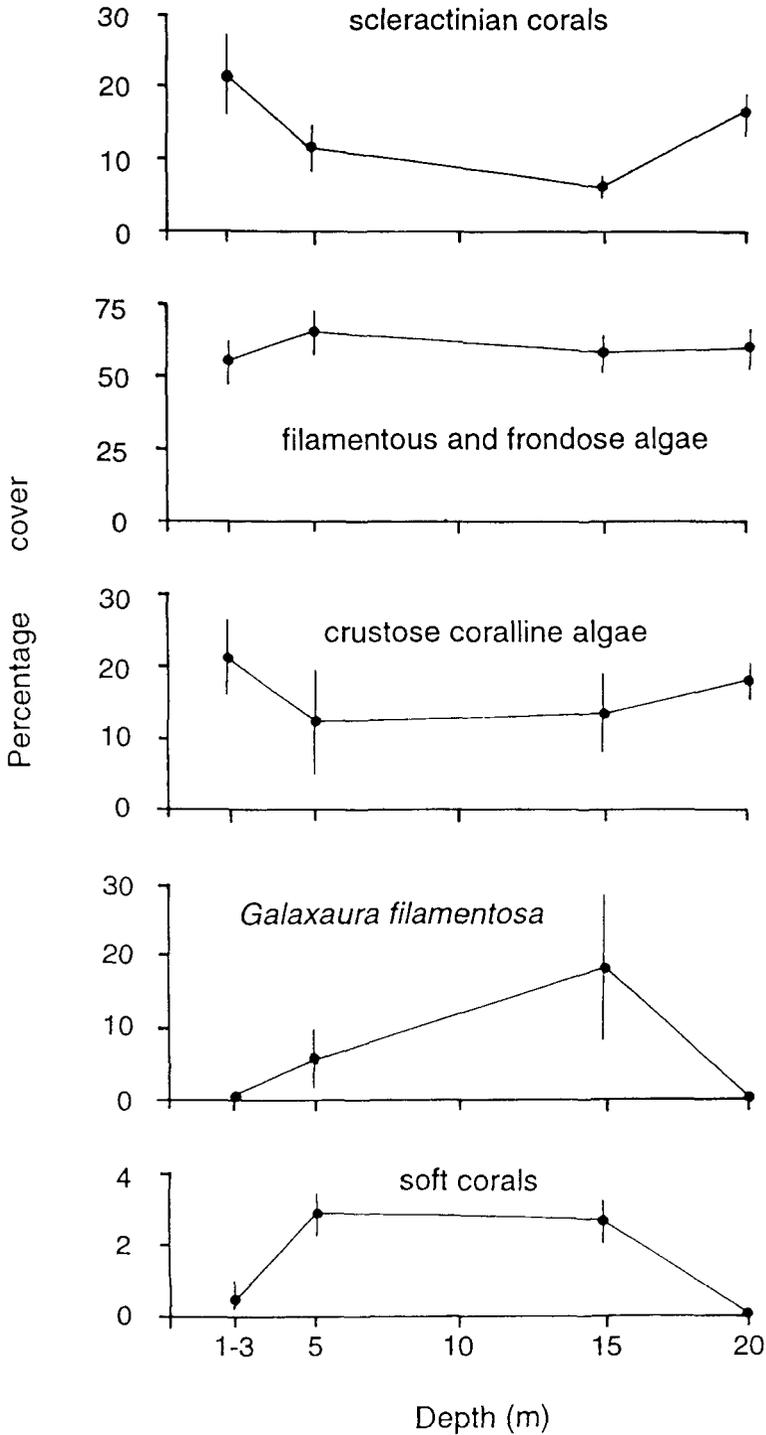
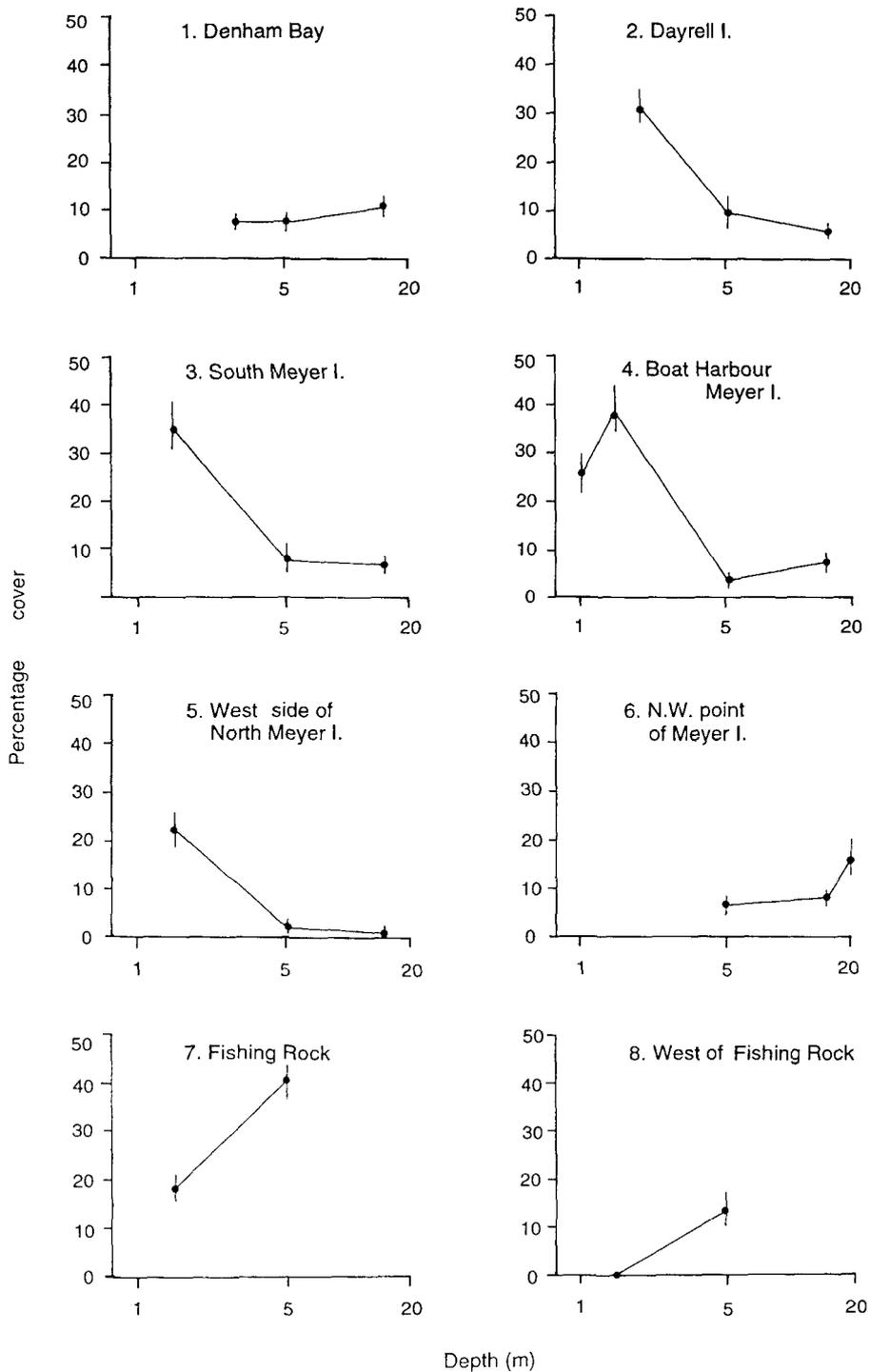


Fig. 4 Percentage benthic cover (mean  $\pm$  1 SE) of corals and algae on bedrock reefs at 1–3 m (7 sites), 5 m (8 sites), 15 m (7 sites) and 20 m (1 site) at locations 1–9 around Raoul and adjacent islands



**Fig. 5** Percentage benthic cover (mean  $\pm$  SE) of hermatypic corals at locations 1–8 around Raoul and adjacent islands.

locations Conversely, *Hydnophora pilosa* had highest cover at the sole 20 m site (location 6) The mean percent cover of four other species (*Cyphastrea serailia*, *Goniastrea australensis*, *Montipora capricornis*, *Turbinaria frondens*) showed no consistent trend with depth

The cluster analysis of similarity among hermatype faunas (Fig 7) identifies the following three site associations and one ungrouped site Site information is listed in Table 2

*Association A (sites 1a, 2a, 2b, 3a, 4a, 4b, 5a, 7a)*

Depth 1–5 m, mean coral cover 8–39%, Species number 3–8

Mostly low diversity faunas dominated by *Montastrea curta* (28–83% relative cover) and *Pocillopora damicornis* (5–18% relative cover), with locally common *Cyphastrea serailia*, *Leptastrea bewickensis*, *Montipora capricornis* and *Turbinaria radicalis*

*Association B (sites 2c, 3b, 3c, 4c, 5b, 6a, 6b, 6c, 9a)*

Depth 5–20 m, mean coral cover 2–17%, Species number 7–10

Moderately diverse faunas dominated by *Hydnophora pilosa* (34–80% relative cover) with locally common *Cyphastrea serailia*, *Goniastrea australensis*, *Montipora capricornis*, *Montipora spongodes*, *Plesiastrea versipora* and *Turbinaria frondens*

*Association C (sites 1b, 1c, 5c, 7b, 8b)*

Depth 5–15 m, mean coral cover 1–40%, Species number 7–11

Moderately diverse faunas dominated by *Cyphastrea serailia* (2–39% relative cover), *Goniastrea australensis* (7–31% relative cover), *Montipora capricornis* (2–27% relative cover) and *Turbinaria radicalis* (0–30% relative cover), with locally common *Coscinaraea columna*, *Leptastrea bewickensis*, *Montipora spongodes*, *Montastrea curta* and *Turbinaria frondens*

The site 5c fauna differed from others in the group in having very low coral cover and being dominated by *Plesiastrea versipora* (38% relative cover, comprising sparse large massive colonies) with relatively high *Hydnophora pilosa* cover (17%) In 1991 when this site was surveyed, living *Hydnophora pilosa* colonies were predominantly small juveniles but large, dead alga-encrusted coralla were common, indicating that the site had previously had an association B fauna

*Ungrouped (site 4d)*

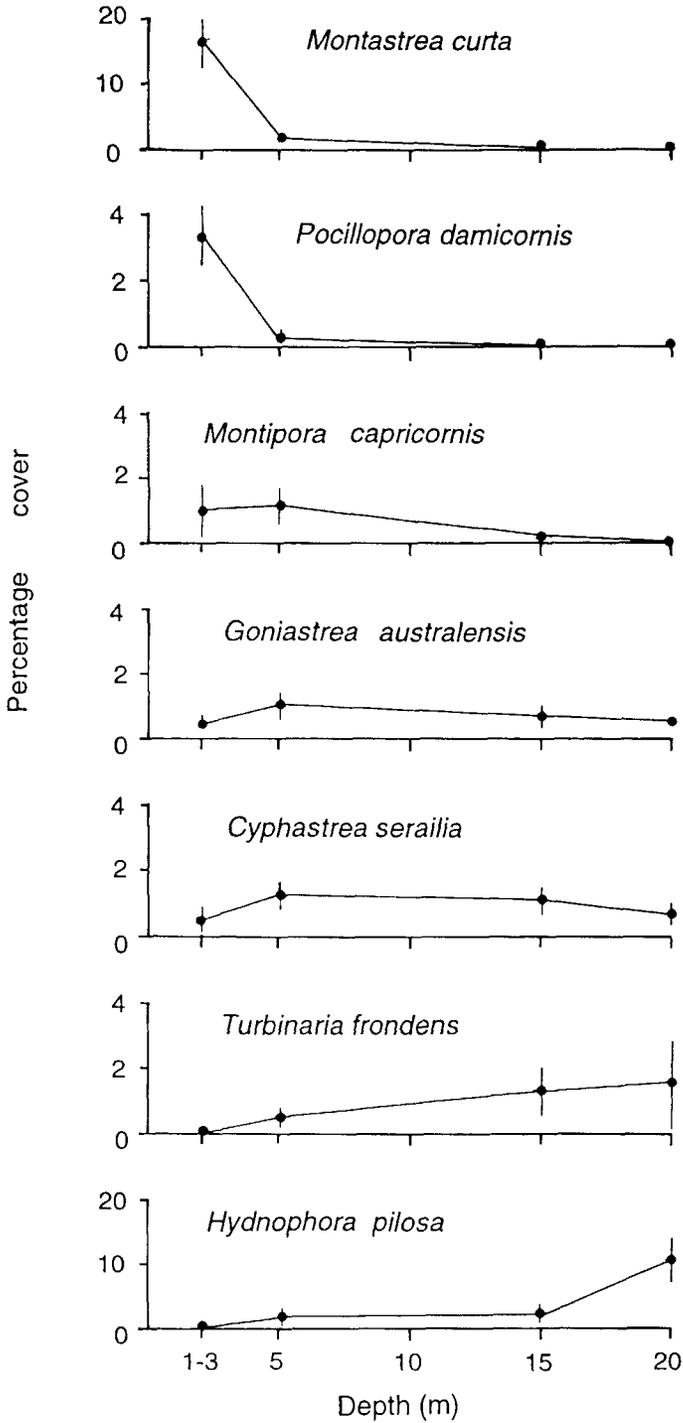
Depth 15 m, mean coral cover 7%, Species number 8

The fauna was dominated by large foliaceous *Turbinaria frondens* with

**Table 2** Coral associations (derived from cluster analysis) and summary of coral cover and species richness by site

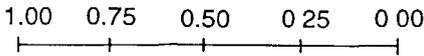
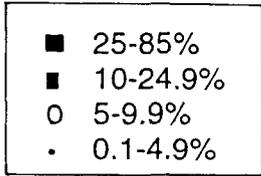
Association	Site	Mean percent		
		Depth (m)	coral cover	Species number
A	1a	3	7.7	5
A	2a	2	31.6	3
A	2b	5	9.8	8
A	3a	1.5	35.8	5
A	4a	1	25.7	7
A	4b	1.5	39.4	4
A	5a	1.5	22.4	3
A	7a	1.5	18.2	7
B	2c	15	5.9	7
B	3b	5	8.3	8
B	3c	15	7.0	8
B	4c	5	3.7	9
B	5b	5	2.0	8
B	6a	5	6.3	9
B	6b	15	8.3	8
B	6c	20	16.7	10
B	9a	15	2.7	8
C	1b	5	7.5	7
C	1c	15	10.4	9
C	5c	15	1.1	9
C	7b	5	40.5	11
C	8b	5	13.8	8
Ungrouped	4d	15	7.4	8

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**Fig. 6** Percentage benthic cover (mean  $\pm$  ISE) of hermatypic coral species on bedrock reefs at locations 1–9 around Raoul and adjacent islands. Depths and number of sites as in Fig. 4.

RELATIVE ABUNDANCE



*Montast.curta*  
*Poc.damicornis*  
*Hyd.pilosa*  
*Cyph.serailia*  
*Gon.australensis*  
*Montip.capricornis*  
*Cosc.columna*  
*Lept.bewickensis*  
*Montip.spongodes*  
*Ples.versipora*  
*Turb.frondens*  
*Turb.radicalis*

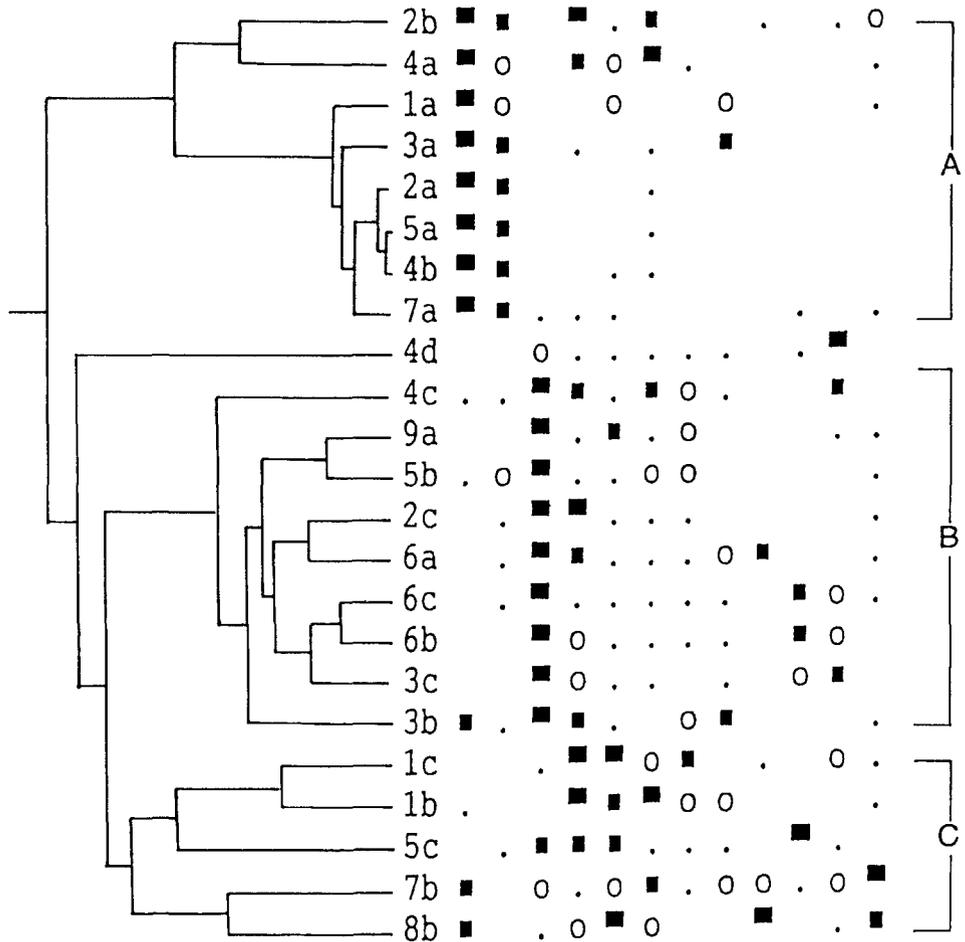


Fig. 7 Dendrogram classification of coral faunal associations produced by cluster analysis of percent relative cover data using Bray-Curtis distance

subdominant *Hydnophora pilosa* (81% and 9% relative cover respectively) Six other species (*Coscinaeraea columna*, *Cyphastrea serailia*, *Gomastrea australensis*, *Leptastrea bewickensis*, *Montipora capricornis*, *Plesiastrea versipora*) each contributed less than 5% relative cover The fauna at this site was most similar to some association B faunas, albeit with relative abundances of *Turbinaria frondens* and *Hydnophora pilosa* reversed

The following three depth-stratified coral zones are defined from the above classification, and from qualitative observations made around Raoul and adjacent islands.

- (1) Upper zone: Coral cover of approximately 8–40%, faunas typically with low species diversity and dominated by *Montastrea curta* and *Pocillopora damicornis* (i.e., association A of above). This coral zone was present on bedrock reefs immediately seawards of a benthic zone that straddled the mean low water datum, lacked corals and was dominated by filamentous, frondose and crustose algae and the large herbivorous gastropod *Patella kermadecensis* (see Morton & Miller 1973; Schiel et al. 1986). The upper coral zone extended to 4–5 m depth on exposed coasts but was shallower than 3 m at more sheltered sites. It was apparently absent from boulder coasts around Raoul.
- (2) Middle zone: This includes associations B, C and the ungrouped fauna (site 4d) described above. It was present on rocky reef and boulder substrata around Raoul and adjacent islands, from seawards of the upper coral zone to 30 m depth. The highest coral cover recorded was on rock patch-reefs surrounded by sandy seafloor at 3–6 m depth off Fishing Rock (i.e., 40%, location 7). Elsewhere coral cover was mostly less than 10%, but increased to approximately 15–25% at 18–25 m depth on some reefs (e.g., location 6; also Boat Cove: Schiel et al. 1986). Species richness within this zone was mostly higher than in the upper zone. Faunas were typically dominated by *Cyphastrea serailia* and/or *Hydnophora pilosa*, but *Coscinaraea columna*, *Goniastrea australensis*, *Leptastrea bewickensis*, *Montipora capricornis*, *Montipora spongodes*, *Plesiastrea versipora*, *Turbinaria frondens* and *Turbinaria radicalis* were locally common.
- (3) Lower zone: Found seawards of the middle zone, and comprised a sparse, low diversity fauna of *Coscinaraea columna* to at least 38 m and *Plesiastrea versipora* to beyond 45 m.

### **Benthic cover off the southern islands**

Hermatypic corals formed less than 1% of benthic cover on subtidal rocky reefs and boulder substrata around Macauley, Curtis and Cheeseman Is. and L'Esperance Rock, where sessile biotas were dominated by filamentous, frondose and crustose algae.

The shallowest hermatypes seen at Macauley I. were at approximately 7–8 m depth where the fauna included sparse *Montipora capricornis*, *Montastrea curta* and *Pocillopora damicornis*. The two last-named species were not seen any deeper. Coral faunas at 10–20 m were dominated by *Montipora capricornis*, *Montipora spongodes* and *Turbinaria radicalis* with rare *Goniastrea australensis*, *Hydnophora pilosa*, *Pavona explanulata* and *Plesiastrea versipora*. *Alveopora ?spongiosa* was the only hermatype seen below 20 m.

At Curtis and Cheeseman Is., *Montipora capricornis* and *Montipora spongodes* were present on steeply sloping rock faces at approximately 15–30 m. Although corals were sparse overall, they commonly had clumped dispersions and formed the dominant benthic cover over patches of several square metres extent at some sites. At L'Esperance Rock, *Montipora spongodes* was similarly sparse and patchily distributed at approximately 18–21 m depth on steeply sloping rock faces, and a single colony of *Alveopora ?spongiosa* was seen at 20 m.

### **Distribution of *Acanthaster planci***

The obligate coral predator *A. planci* was present at Raoul and Macauley Is. but has not been recorded from further south in the Kermadec chain (McKnight 1978; Francis et al. 1987; pers. obs.). The species was extremely rare at Macauley I. in 1988 and 1992 with no more than 1–2 individuals seen per dive. Hermatypic colonies damaged by predation were correspondingly rare. In contrast, *A. planci* was locally common around Raoul and adjacent islands from 1988 to 1995, and at some locations, including particularly the western side of Meyer I., a large number of corals that had recently been completely or partly eaten by the asteroid were observed during each of the respective visits. *A. planci* was most abundant

between about 3 m and 20 m depth around Raoul and adjacent islands, and the majority of eaten coral colonies were also within that depth range *A planci* and damaged corals were absent above about 3 m, and rare below 20 m

## Biogeography

### *Hermatype fauna*

All of the hermatypic coral species recorded from the Kermadec Islands except *Hydnophora pilosa* are present on the Great Barrier Reef of eastern Australia (9–24°S) and the majority, including *Pocillopora damicornis*, *Alveopora spongiosa*, *Coscinaraea columna*, *Psammocora haimeana*, *Leptoseris scabra*, *Pavona explanulata*, *Cycloseris vaughani*, *Cyphastrea serailia*, *Goniastrea australensis*, *Montastrea curta*, *Plesiastrea versipora* and *Turbinaria frondens* are widespread in the tropical and subtropical western and central Pacific Ocean (Veron 1986, 1993). Of the listed species, all except *Cycloseris vaughani* has been recorded at one or more of the other oceanic subtropical southwest Pacific Islands, namely Elizabeth and Middleton Reefs (29°3'S and 29°6'S), Lord Howe Island (31°3'S) and Norfolk Island (29°S) (Table 3). Proportionately fewer of the widely distributed species are shared with high latitude faunas on the northern New South Wales coast of southeastern Australia, or with Rapa Island (27°5'S), Pitcairn Group Islands (23°9–25°S) and Easter Island (27°S) in the central and eastern South Pacific (Table 3).

Five of the hermatype species represented in the Kermadec fauna have more limited distribution within the Pacific Ocean, and the Kermadec records are themselves the eastern-

**Table 3** Geographic distributions of Kermadec Islands hermatype species south of latitude 24°S off Eastern Australia and in the Southwestern (SWP) and Southeastern (SEP) Pacific Ocean. Locations and data sources: 1 Flinders Reef (Veron 1993), 2 Northern New South Wales Coast (Veron 1993, Harriott et al. in press), 3 Solitary Islands (Veron 1993, Harriott et al. 1994), 4 Elizabeth and Middleton reefs (Veron 1993), 5 Lord Howe Island (Veron 1993, Harriott et al. 1995), 6 Norfolk Island (F. J. Brook unpub. data), 7 Rapa Island (Faure 1985), 8 Pitcairn Group (Paulay 1989), 9 Easter Island (Wells 1972, Di Salvo et al. 1988).

	Eastern Australia			SWP Islands			SEP Islands		
	1	2	3	4	5	6	7	8	9
<i>Pocillopora damicornis</i>	x	x	x	x	x	x	x	x	x
<i>Montipora capricornis</i>									x
<i>Montipora spongodes</i>	x		x	x	x	x			
<i>Alveopora ?spongiosa</i>	x			x	x	x			
<i>Coscinaraea columna</i>	x		x	x	x	x	x		
<i>Psammocora haimeana</i>	x		x	x	x			x	
<i>Leptoseris scabra</i>				x	x		x		x
<i>Pavona explanulata</i>	x		x	x	x	x	x		
<i>Cycloseris vaughani</i>								x	x
<i>Hydnophora pilosa</i>			x	x	x	x			
<i>Cyphastrea serailia</i>	x		x	x	x	x	x	x	
<i>Goniastrea australensis</i>	x	x	x	x	x	x	x	x	
<i>Leptastrea bewickensis</i>	x			x	x				
<i>Montastrea curta</i>	x		x	x	x	x	x		
<i>Plesiastrea versipora</i>	x	x	x	x	x	x		x	
<i>Turbinaria frondens</i>	x	x	x	x	x	x			
<i>Turbinaria radicalis</i>	x	x	x	x	x	x			
<b>Totals</b>	<b>13</b>	<b>5</b>	<b>12</b>	<b>15</b>	<b>15</b>	<b>13</b>	<b>7</b>	<b>7</b>	<b>3</b>

most known in the South Pacific. Two species (*Montipora spongodes*, *Turbinaria radialis*) are widespread in the subtropical southwest Pacific, a further two (*Hydnophora pilosa*, *Leptastrea bewickensis*) are less so and *Montipora capricornis* is otherwise only recorded subtropically from Norfolk Island (Table 3).

The hermatypic coral diversity of the Kermadec Islands fauna is much lower than that of many other high latitude southwest Pacific faunas. For example, Flinders Reef (27°S), and the Solitary Islands group (30°S) off eastern Australia have recorded totals of 118 and 90 species respectively (Veron 1993; Veron et al. 1974; Harriott et al. 1994), Elizabeth and Middleton Reefs have a combined total of 118 species (Veron 1993), Lord Howe Island has 83 species (Veron 1993; Veron and Done 1979; Harriott et al. 1995) and Norfolk Island has at least 39 species (Brook 1990, unpub. data). Hermatype diversities at Raoul and Macauley Is. are comparable with those on the southeastern Australian mainland coast of New South Wales at 29.5–31°S (14 species: Veron 1974, 1993) and the offshore South West Rocks at 31°S (8 species: Harriott et al. in press), and with some southeast Pacific islands, including Easter Island at 27°S which has 10 species (Wells 1972; Di Salvo et al. 1988), Pitcairn Island at 25°S which has 17 species (Paulay 1989) and Oeno Atoll at 23.9°S which has 20 species (Paulay 1989). However, diversities are lower than at other islands in the Pitcairn Group (Paulay 1989) and at Rapa Island at 27.5°S in French Polynesia (60 species: Faure 1985). The hermatype diversity gradient along 2° of latitude within the Kermadec chain is comparable with that between northern New South Wales and Victoria on the southeastern Australian coast (i.e., from 29.5–39°S: see Cairns and Parker 1992; Veron 1993).

#### *Ahermatype fauna*

Four of the seven coastal ahermatypic coral species recorded from the Kermadec Islands, namely *Cladopsammia eguchii*, *Rhizopsammia* sp. cf. *R. verrilli*, *Tubastrea coccinea*, *Tubastrea diaphana*, are widely distributed in the tropical Pacific Ocean (Veron 1986; Cairns 1991). The three last-named species are also present at Lord Howe Island, and *Tubastrea diaphana* at Norfolk Island (pers. obs.). *Culicia rubeola* has been recorded from several tropical Pacific localities (e.g., Wells 1954, 1983; Di Salvo et al. 1988), but species classification within the genus is confused and those identifications may not be valid (Cairns 1991). If the Kermadec *Culicia* is in fact conspecific with the temperate New Zealand *Culicea rubeola*, it is the only shallow water coral species common to faunas of the two regions. Of the other two Kermadec species, *Dendrophyllia ijimai* is otherwise known only from Japan and the tropical western Indian Ocean (Cairns 1994; Cairns & Keller 1993), and *Coenocyathus brooki* is endemic to the Kermadec Islands (Cairns 1995).

All of the coastal ahermatype taxa recorded here from the Kermadecs are apparently restricted to inner to mid shelf depths around the islands (above). Distribution information in Cairns (1995) indicates that there is a marked faunistic break at approximately 100–150 m depth around the Kermadec Islands, as defined by the deepest limit of the coastal ahermatype taxa and the upper limit of a further 16 species restricted to outer shelf and upper slope depths (i.e., 100–1000 m). The latter group includes four species that are widespread in the tropical-subtropical Pacific but which do not extend as far south as New Zealand (*Caryophyllia rugosa*, *Caryophyllia hawaiiensis*, *Tethocyathus virgatus*, *Truncatoguymia irregularis*), eight species that are widespread in the tropical-subtropical Pacific and also range south to New Zealand (*Desmophyllum dianthus*, *Anomocora* sp. cf. *fecunda*, *Thrypticotrochus multilobatus*, *Gardineria hawaiiensis*, *Endopachys grayi*, *Eguchipsammia gaditana*, *Eguchipsammia japonica*, *Dendrophyllia alcocki*), three species that are apparently endemic to the subtropical southwestern Pacific (*Caryophyllia lamellifera*, *Crispatotrochus rugosus*, *Trochocyathus maculatus*), and one species that is known only from Japan and the Kermadec Islands

(*Truncatoflabellum phoenix*) The outer shelf – upper slope fauna thus differs from the coastal ahermatypic fauna in having a much higher proportion of widespread species that are shared with the New Zealand fauna

## DISCUSSION

Scleractinian coral faunas at the Kermadec Islands had the following characteristics

- 1 The hermatypic fauna was depauperate at the species level, and diversity within it and also within the coastal ahermatypic fauna attenuated markedly with increasing latitude along the island chain. Of particular interest was an 80% reduction in hermatypic diversity across the 35 km gap separating Macauley from Curtis and Cheesman Is.
- 2 Most hermatypic species at the Kermadecs had lower depth limits of between 20 m and 30 m, and adult *Pocillopora damicornis* and *Montastrea curta* were restricted to shallower than 8–10 m. The only species found deeper than 30 m were *Alveopora* ?*spongiosa*, *Coscinaria columnata* and *Plesiastrea versipora* (excluding the record of a single dead *Cyloseris vaughani* specimen at 33 m), and of those only *Plesiastrea versipora* extended deeper than 40 m. Around Raoul, hermatypic diversity was highest between 5 m and 20 m depth, and at Macauley it was highest at 20 m. The upper limit of hermatypes progressively deepened with increasing latitude along the island chain from intertidal around Raoul and adjacent islands, to approximately 7 m at Macauley I, 15 m at Curtis and Cheesman Is and 18 m at L'Esperance Rock.
- 3 Hermatypic coral cover on rocky reefs and boulder substrata was low and there were no biohermal fringing or patch reefs. Around Raoul, coral cover was commonly highest (up to 40%) at 1–6 m depth, and decreased rapidly below that to less than 10%, albeit with a further peak of 15–25% cover between 18 m and 25 m in some areas. Coral cover below 25–30 m depth was <1%. Around Macauley, Curtis and Cheesman Is and L'Esperance Rock, hermatypes formed less than 1% of benthic cover.
- 4 Most hermatypic species in the Kermadec fauna had encrusting to explanate growth form, commonly with mounds or columns on the upper surface of coralla. Three species that were predominantly encrusting (*Cyphastrea serailia*, *Goniastrea australensis*, *Montastrea curta*) also formed rare submassive coralla at shallow depths around Raoul (<6 m), and *Plesiastrea versipora* at Raoul generally had massive form at 10–25 m but was encrusting or submassive in shallower and deeper water. The only branching species (*Pocillopora damicornis*) formed low, compact, stoutly branched clumps, and *Turbinaria frondens* was the only foliaceous species present.
- 5 Most hermatypic species formed relatively small colonies at the Kermadecs, especially *Alveopora* ?*spongiosa* and *Psammocora haimeana*, which were consistently smaller than 10 cm diameter. Only two species at Raoul (*Plesiastrea versipora*, *Turbinaria frondens*) formed colonies larger than 1 m diameter. Further, colonies of several species (*Montastrea curta*, *Pavona explanulata*, *Hydnophora pilosa*, *Goniastrea australensis*, *Plesiastrea versipora*) were consistently much smaller at Macauley I than around Raoul and adjacent islands.
- 6 Most hermatypic species present at Raoul were reasonably common there, except *Leptoseris scabra* which is known only from a single freshly dead juvenile corallum (note that the abundance of *Cyloseris vaughani* is unknown, as sediment substrata were not surveyed). In contrast, seven (70%) of the hermatypic species at Macauley I (*Pocillopora damicornis*, *Alveopora* ?*spongiosa*, *Pavona explanulata*, *Hydnophora pilosa*, *Goniastrea australensis*, *Montastrea curta*, *Plesiastrea versipora*) were extremely rare, and *Alveopora* ?*spongiosa* was also very rare at L'Esperance Rock.

### Environmental influences

Some of the ecological features listed above are common to subtropical coral faunas elsewhere in the South Pacific and are, presumably, at least partly the result of physical environmental limitations on hermatype growth imposed by the high latitude location of the Kermadec Islands. They include the low overall species diversity and shallow lower depth limits of hermatypes compared with tropical faunas, and also the predominance of encrusting and explanate growth forms. Lower overall sea temperatures and irradiance in the subtropics compared with lower latitudes, coupled with greater seasonality, are likely controlling factors (Veron 1985a; Veron & Done 1979; Crossland 1988). The Kermadec hermatype fauna is much less diverse than those at other subtropical southwestern Pacific islands (see below) and that is probably the result, at least in part, of the relatively low diversity of subtidal habitats and, in particular, the absence of shallow sheltered rocky reefs and lagoons in the Kermadec group. However, the dwarfed size of some hermatype species at the Kermadecs (e.g., *Alveopora ?spongiosa*, *Psammocora haimeana*) and very shallow lower depth limits of adult *Pocillopora damicornis* and *Montastrea curta* compared with, for example, open coastal sites at Norfolk and Lord Howe Is. (pers. obs.), indicate that conditions for growth of those species are less favourable at the Kermadecs than at some other subtropical locations. Veron (1992) has shown that hermatype diversity and abundance in subtropical locations are strongly influenced by sea temperature: relatively small differences in temperature are correlated with large differences in coral species diversity and abundance. It is almost certain that some of the ecological differences between the Kermadec coral fauna and those at other subtropical southwestern Pacific locations are temperature-related, but at present there are insufficient hydrographic data to test that hypothesis.

Within the Kermadec group there is a latitudinal gradient in marine climate. Sea surface temperatures at Raoul I. are on average 1°C warmer than those at L'Esperance Rock (Francis et al. 1987). Island size and morphologic complexity also decrease from northeast to southwest within the group, with resultant parallel decreases in areal extent of shallow benthic habitats, bathymetric complexity, and diversity of substratum types and wave exposure regimes. Raoul I. has the greatest range of wave exposure settings, owing to both its large size, and to the presence of headlands, embayments, offshore islands and pinnacle reefs. In contrast, the small steep-sided southern islands (Curtis, Cheeseman, L'Esperance) are exposed to unrefracted oceanic swell and storm waves from every compass direction.

Those differences in sea temperature and habitat diversity presumably influence the composition and ecological structure of coral faunas at the various Kermadec Islands, as elsewhere. It is probable that the observed faunal attenuation and differences in species abundance and corallum size along the island chain are, at least partly, the results of both the latitudinal temperature gradient and differences in habitat diversity between islands. The shallowing of upper depth limits of hermatypic corals from southwest to northeast along the island chain is probably a reflection of species tolerances to the variation in wave exposure regimes between islands.

The overall shapes of depth-diversity curves for the hermatype faunas at Raoul and Macauley Is. (Fig. 3) are closely comparable with those for tropical reef slopes (Chappell 1980; Sheppard 1982) and some other subtropical open rocky coasts such as at Norfolk I. (pers. obs.). Chappell (1980) suggested that the curve shape reflects limitations imposed on hermatype species diversity by wave stress and illumination on shallow and deeper parts of reefs respectively.

Coral faunas at the Kermadec Islands are also undoubtedly influenced by biotic factors, including 'competition' with algae and predation. Algae form a high proportion of the benthic cover on shallow subtidal reefs and rubble substrata at the Kermadecs. Laminarian

and fuclean kelps other than the intertidal *Sargassum cristaefolium* are very rare (Nelson & Adams 1984, Schiel et al 1986, Cole et al 1992, this study), but the flora includes frondose, filamentous and tufted algal species that grow tall enough to overtop small coral colonies (e.g., *Dictyota* spp., *Dilophus intermedius*, *Galaxaura filamentosa*, *Delisea pulchra*), and which form lush, albeit patchy, subtidal swards. Hermatype recruitment and post-settlement survival are thus presumably influenced by patterns of distribution and abundance of algal species, both through availability of suitable settlement sites, and by shading and overgrowth of colonies by algae. The question of whether or not seasonal macroalgal blooms develop at the Kermadec Islands and, if so, how they affect coral recruitment and growth, is clearly an important area for future research. Similarly, although abundance and depth stratification of echinoid, herbivorous fish and mollusc species have been documented for the Kermadecs (Schiel et al 1986, Cole et al 1992), nothing is yet known about how benthic disturbance resulting from grazing indirectly influences coral species distribution and abundance, or whether facultative corallivory by grazers and omnivores has a significant effect on the coral communities.

However, circumstantial evidence from broad spatial correlations between hermatype abundance and the distribution of *Acanthaster planci* suggests that this species is a key modifier of hermatype communities around Raoul I. On most of the subtidal reefs surveyed around Raoul (i.e., excluding boulder coasts), coral cover was highest at immediate subtidal depths and declined to seawards. The transition from the upper to the middle zones identified above was defined by an abrupt decrease in coral cover and marked change in species dominance (e.g., at locations 2–5, 9). On some reefs there was another peak of coral abundance in deeper water between about 18 m and 25 m depth (e.g., location 6). In contrast, *A. planci* individuals and feeding traces were absent or extremely rare within the upper zone at those locations, but were locally common in the upper part of the middle zone down to about 20 m depth, and particularly so on the western side of Meyer I where densities of up to eight *A. planci* individuals per 1000 m<sup>2</sup> were observed in May 1995 (R. Babcock & F. Brook unpub. data). A rather different situation existed at Fishing Rock, where middle zone coral communities occupied a series of small rocky patch-reefs at 4–6 m depth (location 7). Those reefs are physically isolated from one another, and from a nearby intertidal rock platform, by wave-rippled coarse sand. No *A. planci* individuals or feeding traces were seen on the patch-reefs, and coral cover was substantially higher than in middle zone communities at similar depths at locations with *A. planci* present. That suggests that coral abundance in the middle zone was at least in part limited by *A. planci* predation, being highest at locations and depths where *A. planci* was absent or rare.

Further, there is evidence that the population structure of middle zone coral communities around Raoul was also influenced by *A. planci* predation. For example, as described above, in 1991 the hermatype fauna at 15 m depth at location 5 (off Meyer I) differed from those of nearby areas in having very low coral cover, a very low abundance of living *Hydnophora pilosa* constituting mostly small juveniles, and many large, *in situ* algal-covered *Hydnophora pilosa* skeletons. The localised nature of the *Hydnophora pilosa* die-off (extending over an area of several hundred square metres), lack of evidence of physical disturbance at the site, and presence of common *A. planci*, strongly implicates the asteroid as the agent of coral faunal change there.

Other obligate coral predators known from the Kermadec Islands include species of muricid, epitonid and phylidid molluscs (Brook 1998a) but their overall ecological influence on coral populations is unknown. Hermatype predators at Raoul included *Quoyola monodonta* (on *Pocillopora damicornis*), *Coralliphila bulbiformis* and *Coralliphila radula*, and ahermatype predators (on *Rhizopsammia* sp. cf. *R. verrilli* and *Tubastrea coccinea*) included

*Epitonium billeeana* and *Phestilla melanobranchia*. *Coralliophila bulbiformis* was also present at Macauley, Curtis and Cheesman Is. (pers. obs.).

### Biogeographic factors

The coastal coral fauna at the Kermadecs is dominated by widely-distributed tropical-subtropical species, but also includes a single endemic (*Coenocyathus brooki*) and one species possibly shared with mainland New Zealand coasts (*Culicea ?rubeola*). The majority of the tropical-subtropical species in the Raoul fauna are common there, have relatively high levels of recruitment judging by the abundance of juveniles, and probably form stable, self-maintaining populations. However, one hermatype species (*Leptoseris scabra*) is known only from a single juvenile that presumably resulted from propagule immigration from a source area outside the Kermadec region, and populations of dwarf *Alveopora ?spongiosa* and *Psammocora haimeana* at Raoul are possibly also augmented by or dependent on immigrant propagules from external source areas. Similarly, rare coral species at the southern Kermadec Islands (e.g., *Pocillopora damicornis*, *Alveopora ?spongiosa*, *Pavona explanulata*, *Hydnophora pilosa*, *Goniastrea australensis*, *Montastrea curta*, *Plesistrea versipora*) could have arrived by chance propagule dispersal from Raoul or further afield.

Oceanic circulation patterns in the southwestern Pacific define two possible source regions for immigrant propagules of tropical-subtropical coral species. The return flow of the subtropical gyre could carry propagules from sources to the west and northwest of the Kermadecs (i.e., New Caledonia, Coral Sea, Great Barrier Reef, Elizabeth and Middleton Reefs, Lord Howe Island, Norfolk Island). Of those localities, Norfolk Island is the most likely source of larvae because of its geographic position closest to the Kermadec Islands (1350 km). During summer months propagules could be carried to the northern Kermadec Islands in southward and southwestward-moving tropical watermasses associated with the Trade Wind Drift. Minerva Reefs (590 km north of the Kermadec Islands) and Tonga are the most likely source areas.

The geographic isolation of the Kermadec group suggests that levels of propagule immigration, and contemporary turnover of vagrant coral species, are probably both lower than at subtropical islands closer to potential larval source areas (cf., Harriott 1992; Harriott et al. 1994, 1995). However, marked differences in species composition between present-day and Early Pleistocene coral faunas at the northern Kermadec Islands (Brook 1998b) suggest a high long-term species turnover rate in the region during Quaternary time. In terms of overall species composition, the present-day coastal coral fauna at the Kermadec Islands has closest biogeographic affinities with other southwest Pacific Ocean faunas, including those of the Great Barrier Reef, Elizabeth and Middleton Reefs, Lord Howe Island and Norfolk Island. That, and the fact that hermatype diversity decreases eastwards from the Great Barrier Reef through Elizabeth and Middleton Reefs, Lord Howe and Norfolk Islands to the Kermadec Islands, suggests that eastward dispersal of propagules in watermasses of the subtropical gyre has been important in determining the origin of the Kermadec coral fauna (see also Marshall 1979; Francis 1993; Brook 1998a). The overall lower species diversity of the present-day hermatype fauna at the Kermadec Islands, compared with those at the other subtropical southwest Pacific islands, is probably as much a reflection of the greater biogeographic isolation of the Kermadecs as of differences in present-day environmental regimes.

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## APPENDIX 1. ANNOTATED LIST OF COASTAL SCLERACTINIAN CORALS OF THE KERMADEC ISLANDS

The following list includes species recorded from intertidal to 50 m depth around the Kermadec Is. New records are indicated by an asterisk, and previous records are given in square brackets. Numbers with an AK prefix refer to collections held at the Auckland War Memorial Museum and those with a K prefix to collections at the National Institute of Water and Atmospheric Research, Wellington

### FAMILY POCILLOPORIDAE

*Pocillopora damicornis* Linnaeus, 1758

[Vaughan 1917 – as *P bulbosa*, Kosmynin 1994] AK75804, AK75827, AK75829, AK75975, AK75979, AK76945

Intertidal rock pools and common on shallow subtidal reefs around Raoul and adjacent islets, rare at Macauley I. Compact, tightly branched coralla up to 300 mm across and 80 mm high with comparable robust form to those described elsewhere from wave-swept habitats (e.g., Veron and Pichon 1976, fig 58). Around Raoul this growth form reached a maximum depth of 8–10 m but small juveniles extended to 20 m. The Macauley record is based on a single specimen collected by M P Francis at 8 m depth, October 1985

### FAMILY ACROPORIDAE

*Montipora capricornis* Veron, 1985

[Vaughan 1917 – as *M calculata*, Kosmynin 1994 – as *M* sp cf *mullepora*] AK75803, AK75819, AK75825, AK76446, AK76447, AK76940

Intertidal rock pools, and common down to approximately 25 m depth on subtidal reefs and boulder substrata around Raoul and adjacent islands. Uncommon on reefs at 7–20 m depth at Macauley I and 15–30 m depth at Curtis and Cheeseman Is. Encrusting growth form, coralla from shallow water have the upper surface raised into closely spaced mounds 4–15 mm in diameter, whereas those from deeper

water have more widely spaced mounds. This species differs from the following in having larger and more closely spaced corallites, and a surface sculpture of mounds rather than columns.

\**Montipora spongodes* Bernard, 1897

AK75803, AK75819, AK75825, AK76446, AK76447, AK76940

Uncommon on subtidal reefs and boulder substrata. Present at all islands in the group, with a recorded depth range of approximately 3–25 m around Raoul, 12–20 m at Macauley, 15–30 m at Curtis and Cheeseman Is. and approximately 18–21 m at L'Esperance Rock. Encrusting growth form with finger-like columns projecting from the upper surface of the corallum.

FAMILY PORITIDAE

\**Alveopora ?spongiosa* Dana, 1846

AK75973, AK76439, AK76440

Uncommon to rare on subtidal reefs. Small nodular, hemispherical coralla (up to 40 mm diameter) at 24–33 m off Macauley I. and 12–20 m around Raoul, and a single corallum (60 mm greatest diameter) seen at 20 m off L'Esperance Rock.

FAMILY SIDERASTREIDAE

*Coscinaraea columna* (Dana 1846)

[Kosmynin 1994 – as *Leptoseris mycetoseroides*] AK75822, AK75976, AK75977, AK76941

Intertidal rock pools and common on subtidal reefs and boulder substrata down to 38 m depth around Raoul and adjacent islets. Predominantly encrusting growth form, but coralla with explanate form present on steeply sloping rock faces.

\**Psammocora haimeana* Edwards and Haime, 1851

AK139532

Uncommon on subtidal reefs at 3–25 m depth around Raoul and adjacent islets, small encrusting coralla up to 100 mm diameter.

FAMILY AGARICIIDAE

\**Leptoseris scabra* Vaughan, 1907

AK76055

Known from a single dead juvenile corallum (40 mm diameter) at 15 m depth on reef off western side of Meyer I, June 1991.

*Pavona explanulata* (Lamarck, 1816).

[Kosmynin 1994 – as *Leptoseris hawaiiensis*] AK75805, AK75970, AK76445, AK76450, AK76751, AK76948

Uncommon on subtidal reefs around Raoul and adjacent islets at 5–28 m depth; a single specimen collected at 20 m depth off Macauley I. by M.P. Francis, October 1985. Encrusting to explanate coralla, including some with stumpy columns projecting from upper surface.

FAMILY FUNGIIDAE

\**Cycloseris vaughani* (Boschma, 1923)

AK76054

Known from a single dead juvenile corallum (20 mm diameter) collected amongst coral rubble at 33 m depth west of Meyer I., June 1991.

FAMILY MERULINIDAE

*Hydnophora pilosa* Veron, 1986

[Kosmynin 1994 – as *H. exesa*] AK75807, AK75961, AK75972

Common on subtidal reefs and boulder substrata from immediate subtidal to 30 m depth around Raoul and adjacent islets; rare at 10–15 m depth on reefs off Macauley I. Encrusting to explanate growth form, commonly with stout columns projecting from upper surface.

FAMILY FAVIIDAE

*Cyphastrea serailia* (Forsk., 1775)

[Vaughan 1917; Kosmynin 1994] AK75818, AK75978, AK76944

Intertidal rock pools and common on subtidal reefs and boulder substrata to at least 30 m depth around Raoul and adjacent islets. Predominantly encrusting growth form, but coralla with explanate form present on steeply sloping rock faces and rare submassive to columnar coralla present locally in shallow water.

*Gonastrea australensis* (Edwards and Haime, 1857)

[Vaughan 1917 – as *G. benhami*; Veron et al. 1977; Kosmynin 1994] AK75782, AK75801, AK75823, AK75826, AK75828, AK75965, AK75966, AK76444

Intertidal rock pools and common on subtidal reefs and boulder substrata to 27 m depth around Raoul and adjacent islets; uncommon at approximately 10–20 m depth at Macauley I. Predominantly encrusting

growth form, but explanate coralla present on steeply sloping rock faces and rare submassive coralla present locally in shallow water around Raoul

\**Leptastrea bewickensis* Veron, Pichon and Wijnsman – Best, 1977

AK75964, AK76004, AK76939, AK76947

Intertidal rock pools and locally common on subtidal reefs and boulder substrata to 22 m depth around Raoul and adjacent islets Encrusting growth form

*Montastrea curta* (Dana, 1846)

[Vaughan 1917 – in *Orbicella*, Kosmynin 1994] AK75808, AK75831, AK75832, AK75968, AK75974

Intertidal rock pools and common on subtidal reefs to 10 m depth around Raoul and adjacent islets, rare on subtidal reefs at approximately 7–8 m depth at Macauley I Predominantly encrusting growth form, but rare submassive coralla present locally around Raoul

\**Plesiastrea versipora* (Lamarck, 1816)

AK75802, AK75969, AK76747, AK76749

Common on reefs and boulder substrata around Raoul and adjacent islets from immediate subtidal to >45 m depth, rare at Macauley I on reefs at approximately 20 m depth Growth form at Raoul varies with depth, coralla shallower than 10 m mostly encrusting sheets, those between 10 m and 20–25 m massive, commonly with stout columns projecting from upper surface, and coralla below 20–25 m submassive to encrusting Macauley I colonies a few centimetres in diameter with hemispherical growth form

#### FAMILY RHIZANGIIDAE

\**Culicia ?rubeola* (Quoy and Gaimard, 1833)

AK75813, AK75962, AK75963, AK76442, AK76443, K851

Uncommon on overhangs and in crevices on reefs from 6 m to at least 35 m depth, and recorded from a gravel substratum at 104–106 m depth (K851) Present at all islands in the Kermadec group Encrusting reptoid coralla up to 50 mm across

#### FAMILY CARYOPHYLLIIDAE

*Coenocyathus brooki* Cairns, 1995

AK75814, AK75981, AK75982, AK75983, AK76049, AK76050, AK76441, AK76950, K820

Locally common in caves and under overhangs on reefs from 6 m to at least 40 m depth, and recorded from a gravel substratum at 95–122 m depth (K820) Present at all islands in the Kermadec group

#### FAMILY DENDROPHYLLIIDAE

*Cladopsammia eguchii* (Wells, 1982)

[Cairns 1995] AK76949

Common on roof of a submarine cave at 6–8 m depth off western side of Meyer I, but not seen elsewhere at the Kermadec Islands

\**Dendrophyllia ijimai* Yabe and Eguchi, 1934

AK76752

Common on overhanging rock face at 22–24 m depth on submarine pinnacle off Nugent I, but not seen elsewhere at the Kermadec Is Arborescent growth form, irregularly branched, up to 80 mm tall Main branches up to 9 mm in diameter, axial corallites up to 20 mm long and 6 mm in greatest calicular diameter Polyps orange

\**Rhizopsammia* sp. cf. *R. verrilli* van der Horst, 1922

AK75816, AK76047, AK76052, AK76053

Common in caves and under rock overhangs from 6 m to at least 45 m depth around Raoul and adjacent islets Growth form varies from single corallites or a few well-spaced corallites connected by basal stolons through to small subphaceloid or arborescent coralla Individual corallites cylindrical, up to 70 mm tall and 9 mm in greatest calicular diameter Polyps orange to pink

\**Tubastrea coccinea* Lesson, 1829

AK75984, AK76750, AK76754

Locally common under rock overhangs at 8–24 m depth around Raoul and adjacent islets Low, compact coralla up to 90 mm across and 50 mm tall

\**Tubastrea diaphana* Dana, 1846

AK75809, AK75817, AK75824, AK75830, AK76048, AK76451, AK76753

Locally common in caves and under rock overhangs between 8 m and 30 m depth around Curtis and Cheeseman Is, Macauley I and Raoul and adjacent islets Arborescent dendroid coralla up to 150 mm tall and 140 mm across

*Turbinaria frondens* (Dana, 1846)

[Vaughan 1917 – as *T. crater*, Kosmynin 1994 – as *T. bifrons*]

AK75820, AK75821, AK75967, AK76748

Common on subtidal reefs and boulder substrata at 2–30 m depth around Raoul and adjacent islets. Encrusting to vasiform in shallow water, foliaceous with nested whorls at approximately 8–25 m depth, and crateriform in deeper water.

*Turbinaria radicalis* Bernard, 1896

[Kosmynin 1994] AK75783, AK75806, AK75971, AK76452, AK76943

Common on subtidal reefs and boulder substrata at 1–25 m depth around Raoul and adjacent islets; uncommon at approximately 20 m depth on reefs off Macauley I. Encrusting growth form.