Journal of the Royal Society of Western Australia, 94: 267–284, 2011

Patterns in marine community assemblages on continental margins: a faunal and floral synthesis from northern Western Australian atolls

A Sampey [1] & J Fromont [2]

[1] Aquatic Zoology, Western Australian Museum, Locked Bag 49, Welshpool DC, WA 6986
✉ alison.sampey@museum.wa.gov.au

[2] Aquatic Zoology, Western Australian Museum, Locked Bag 49, Welshpool DC, WA 6986
✉ jane.fromont@museum.wa.gov.au

Manuscript received November 2010; accepted January 2011

Abstract

Corals and fishes are the most visually apparent fauna on coral reefs and the most often monitored groups to detect change. In comparison, data on noncoral benthic invertebrates and marine plants is sparse. Whether patterns in diversity and distribution for other taxonomic groups align with those detected in corals and fishes is largely unknown. Four shelf-edge atolls in the Kimberley region of Western Australia were surveyed for marine plants, sponges, scleractinian corals, crustaceans, molluscs, echinoderms and fishes in 2006, with a consequent 1521 species reported. Here, we provide the first community level assessment of the biodiversity of these atolls based on these taxonomic groups. Four habitats were surveyed and each was found to have a characteristic community assemblage. Different species assemblages were found among atolls and within each habitat, particularly in the lagoon and reef flat environments. In some habitats we found the common taxa groups (fishes and corals) provide adequate information for community assemblages, but in other cases, for example in the intertidal reef flats, these commonly targeted groups are far less useful in reflecting overall community patterns.

Keywords: biodiversity, marine communities, species turnover, Mermaid Reef, Rowley Shoals, Scott Reef, Seringapatam Reef

Introduction

Describing patterns of species diversity and distribution is important for detecting changes to community assemblages; yet marine community assemblage data are rare. Studies on coral reefs have tended to focus on corals and fishes, and less on noncoral benthic invertebrates (Przeslawski *et al.* 2008). While corals and fishes can be the most visually apparent faunal taxa on tropical reefs, there is significantly less information available on other taxonomic groups, even though they may be providing crucial ecosystem services, including nutrient cycling, water quality maintenance and herbivory (Przeslawski *et al.* 2008).

Most of our knowledge about the diversity, distribution and ecosystem function of tropical ecosystems is based on corals and fishes (Przeslawski *et al.* 2008). Some authors question whether diversity patterns derived from well known taxa can be used to describe whole community patterns (Purvis & Hector 2000). Moreover, in the majority of marine and terrestrial communities most species occur in relatively low abundance (Gray *et al.* 2005), but much of the literature on the contribution of biodiversity to ecosystem function is based on common species (Lyons *et al.* 2005). However, if whole community data are available, the information on rare species and poorly studied taxa could be used to test whether patterns in diversity, distribution and abundance suggested by the more common species reflect overall community patterns (Ferrier & Guisan 2006).

Comparative quantitative baseline data that can be used to detect change are particularly important in the context of global climate change (Przeslawski *et al.* 2008). The diversity-stability hypothesis suggests that biodiverse systems provide a buffer against major changes in an ecosystem in response to environmental change (Chapin III *et al.* 2000). This suggestion highlights the need to assess community diversity for general patterns, where community data are available.

Spatial heterogeneity in species richness and composition is an obvious feature of the natural world (Gaston 2000). Along the northern Western Australian coast species richness and composition may vary with latitude (fishes, Hutchins 2001; Travers *et al.* 2006) and can also vary with habitat (sponges and fishes, Fromont *et al.* 2006; Travers *et al.* 2006). A gradient in species composition and diversity has been discussed for northern Western Australia with high diversity of tropical species in lower latitudes near the coral triangle and decreasing southward (Wilson & Allen 1987; Wells & Allen 2005). To date these findings have been restricted to certain better known taxonomic groups such as corals (Veron & Marsh 1988; Veron 1993; Greenstein & Pandolfi 2008), echinoderms (Marsh & Marshall 1983), molluscs (Wells 1986, 1990) and fishes (Allen 1997; Hutchins 1999).

The atolls of the Sahul Shelf in northern Western Australia are emergent oceanic reef systems at the edge of the Australian continental shelf (Fig. 1), Mermaid, Scott (South and North), and Seringapatam Reefs are four

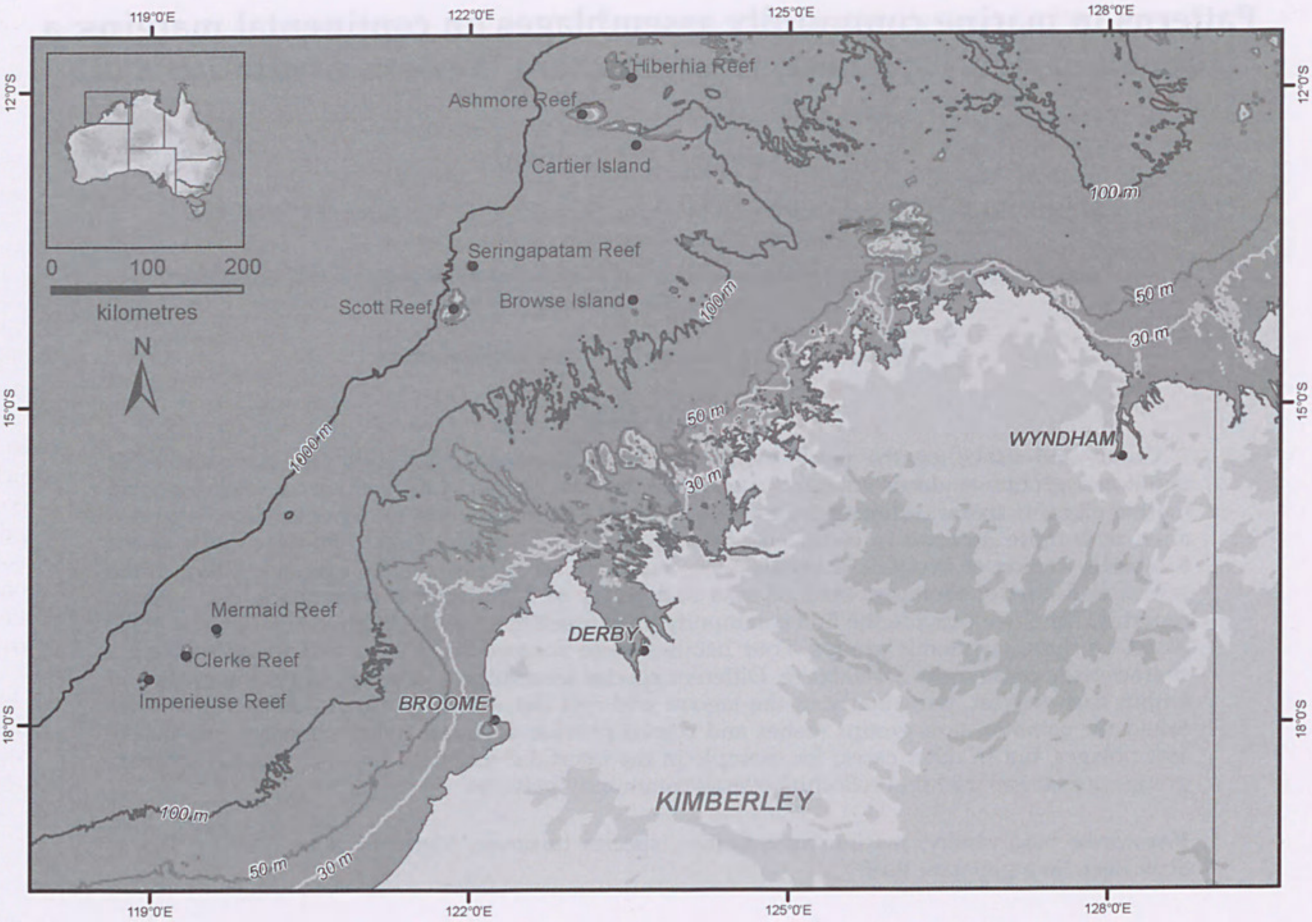


Figure 1. Map of northern Western Australian atolls.

of these. These atolls are thought to have formed some 5–6 million years ago (Anon 2008). The waters in and around the atolls are typical of the Timor Sea and the north eastern Indian Ocean, being warm, clear and oligotrophic. Surface currents in some channels within the atolls can reach up to 2 knots during spring tides. At 9 metres depth at South Scott Reef the mean water temperature range is 25–31 °C (Gilmour *et al.* 2009). These atolls occur in one of the most cyclone-prone regions in the world; in 2004 a category 5 cyclone passed directly over South Scott and North Scott Reefs (Gilmour *et al.* 2009). The intensity of storm events is predicted to increase with global climate change (Solomon *et al.* 2007) and consequent damage will depend on the wind speed, and the direction and duration of the event (Puotinen 2007). There is currently little knowledge of how an increase in the occurrence of extreme events will affect tropical benthic invertebrates, or how community assemblages may change as a consequence (Przeslawski *et al.* 2008).

Realising conservation goals requires strategies for managing entire systems, including areas identified as important to both production and protection (Margules & Pressey 2000). Three of the atolls (South Scott, North Scott and Seringapatam Reefs) discussed in this paper are presently unprotected and subject to fishing pressure and increased shipping, which may introduce non-native species.

The study atolls have been the subject of previous investigations. In 1982 and 1984 the Western Australian Museum undertook species inventories of taxonomic groups including molluscs, corals, echinoderms and fishes at Mermaid, Clerke, South Scott, North Scott, and Seringapatam Reefs (Berry 1986). The three northern atolls, South Scott, North Scott, and Seringapatam Reefs, have been the subject of intensive recent study as a result of the presence of a major gas reserve beneath and adjacent to them. Heyward *et al.* (2007) established baseline monitoring of fishes and corals, while Smith *et al.* (2008) examined coral mortality and recovery after a mass bleaching event that affected the atolls in 1998. Underwood *et al.* (2007) examined genetic connectivity in a brooding coral species, *Seriatopora hystrix*, in part to establish the role of dispersal in maintaining populations at these atolls.

In 2006 the Western Australian Museum surveyed four of these atolls (Mermaid, South Scott, North Scott, and Seringapatam Reefs and the diversity and distributions of seven taxa were documented (Bryce 2009 and papers therein). Results were presented for each taxonomic group, with varying levels of analyses, and there was no synthesis of results across all taxa. For a number of taxa it was observed that there were differences in species richness and composition within the different habitats and atolls. A number of factors were discussed as potentially affecting assemblage patterns between atoll and habitat, including atoll separation distance, habitat, and exposure but none of these were specifically analysed.

Here, we present a community-level analysis of the biodiversity of these atolls using the 2006 survey data. This is the first assessment to be undertaken on the combined marine flora and fauna of the atolls in this region and the results will thus contribute to a greater understanding of current species richness (diversity) patterns, and community assemblage structure of these atolls. As very little is known about the factors that influence the distribution of these community assemblages, our analyses focused on exploring whether communities differed in terms of diversity and composition among the atolls and the habitats represented. We also assessed the potential role of abiotic environmental factors on community structure and explored the possibility that the distributions of the various taxa comprising the communities were correlated.

Methods

Field collection

During the 2006 survey a total of 45 stations were sampled encompassing four main habitat types (reef flat, tidal channel, reef front and lagoon; Table 1). The reef flat habitat was in the intertidal zone, whereas the other three habitats were subtidal. The tidal channel habitat was only present at Mermaid and North Scott Reefs. The stations sampled encompassed a range of substrates (rock, rubble and sand), exposures (e.g. to desiccation i.e. intertidal vs. subtidal, and exposed vs. protected from prevailing currents and cyclones), depths (0 to 20 m), and atoll separation distances (35 to 500 km).

Seven taxonomic groups were surveyed: marine plants (algae and seagrasses, Huisman *et al.* 2009), sponges (Fromont & Vanderklift 2009), corals (McKinney 2009), macromolluscs (≥ 10 mm, Bryce & Whisson 2009), crustaceans (decapods and stomatopods only, Titelius *et al.* 2009), echinoderms (except crinoids, Bryce & Marsh 2009) and fishes (Moore & Morrison 2009). Methodology varied among taxonomic groups and differed in some habitats, with full details provided in Bryce (2009), and papers within. Briefly, marine plants and crustaceans were recorded as presence-absence, sponges, corals, molluscs and echinoderms were counted, and fish numbers were recorded on a semi-quantitative log abundance scale (Moore & Morrison 2009). The sampling effort within taxa for each station within a habitat was generally comparable. The intertidal reef flat was sampled as reef walks (rotenone stations in rock pools for fishes) and the area was searched for each taxa to generate a qualitative species list for all groups except sponges, which were always sampled quantitatively along transects. The reef flat station at Mermaid Reef was covered with flowing water so no rotenone station was surveyed for fishes. Instead fishes were surveyed by snorkel (Table 1) towards the reef front, so they were in a subtidal habitat different from the remaining taxa, which were sampled intertidally. The reef front and lagoon stations were all sampled using quantitative methods along transects (either tape or compass bearing) on SCUBA with comparable effort except for one lagoon station at Mermaid Reef, which was surveyed on snorkel, and a lagoon station at Seringapatam Reef, which was sampled qualitatively (Table 1). The tidal channel stations were qualitatively sampled on drift dives (Table 1). The lagoon and reef front subtidal habitats were videoed and analysed for percent cover at the quantitatively sampled stations (Morrison 2009).

Data analyses

Data analyses were based on a matrix of 1521 marine floral and faunal species from 45 stations. All analyses were undertaken in PRIMER v6.1.11 (Clarke & Warwick 2001; Clarke & Gorley 2006). Although, as mentioned previously, a few stations had non standard effort, this did not greatly affect the overall patterns in community structure and the relationships found among habitats and atolls. Data was examined for each taxonomic group (both abundance and presence-absence) in various combinations, i.e. motile vs. sessile vs. fishes, and with and without outliers to examine station groupings. The Mermaid reef flat station was removed from any further analysis as the community sampled at this station was not comparable, with fish surveyed on snorkel in a different depth to the remaining taxa (Table 1).

Table 1

Summary of the sampling methods and number of stations for each habitat and atoll. The same method was used for all stations within a habitat except where indicated by superscript. Sponges were sampled quantitatively along transects[1], Fish were sampled on snorkel[f], one station was sampled qualitatively[*].

	Habitat				
	Reef Flat	**TidalChannel**	**Reef Front**	**Lagoon**	
Method	reef walk, rotonone	drift dive	SCUBA Transects	SCUBA Transects	
Data	qualitative[1]	qualitative	quantitative	quantitative	
Atoll					**Total**
Mermaid Reef	1[f]	2	5	8[*]	**16**
South Scott Reef	3	–	6	5	**14**
North Scott Reef	3	1	3	3	**10**
Seringapatam Reef	1	–	2	2[*]	**5**
Habitat Total	**8**	**3**	**16**	**18**	**45**

The overall structure in the community was explored using non-metric multidimensional scaling (nMDS) and cluster analysis using complete linkage, based on a Bray-Curtis dissimilarity matrix of presence-absence data. Presence-absence data was used to standardise the varying methods of quantification (presence-absence, counts, log-abundance) that were applied across the taxonomic groups. The similarity profiles (SIMPROF) test (Clarke *et al.* 2008) was used to determine if there was significant structure in the observed station groupings in the nMDS and cluster analyses. These analyses were done firstly on all stations (except the reef flat station at Mermaid Reef) to explore the broad groupings for the four main habitat types, and secondly on a subset of the data from the subtidal quantitative stations, to examine the lagoon and reef front communities in more detail. Analysis of similarity (ANOSIM) was used to test for differences in the community due to atoll and habitat. We did this firstly, with habitat nested in atoll as the tidal channel habitat was not sampled at all atolls and the reef flat data at Mermaid Reef was not analysed, and secondly as a crossed test of atoll and habitat for the lagoon and reef front communities.

Similarity percentages (SIMPER) were used to identify species that were consistently present in a habitat or atoll (typifying species), and those that discriminated between habitats or atolls, that is consistently present in one habitat or atoll but absent from others (discriminating species). Typifying species had a high average presence across stations within a habitat or atoll and a high similarity to SD ratio of approximately one. Discriminating species were those that had a higher average presence (~1) in one habitat or atoll and a high dissimilarity/SD ratio (~1). These analyses were undertaken firstly on the entire dataset to look for typifying and discriminating species for each habitat, and then repeated for the quantitative subtidal stations in the lagoon and reef front habitats to determine typifying and discriminating species for each atoll in these habitats only.

To explore whether the structure in the biotic communities could be explained by abiotic environmental variables, the stations were coded for a range of physical factors that could have an influence on the biological communities. Due to the variation in methods among habitats, these analyses were only undertaken on the communities at the quantitative subtidal stations (lagoon and reef front, Table 1). Seven abiotic environmental variables were used: percent rock, percent rubble, percent sand, geomorphic zone (1: lagoon, 2: reef front), direction quadrant, depth, and atoll separation distance. Percent rock, rubble, and sand were calculated from the video transects at each station (values used were an average of the replicate transects per station) and were examined because species are usually associated with different substrates. A measure of exposure to prevailing winds and currents was estimated (direction quadrant) by placing a compass rose on the map of each atoll and coding the stations for the exposure quadrant they occurred in (1: NNE, 2: NE, 3: SE, 4: SSE, 5: SSW, 6: SW, 7: NW, 8: NNW). The maximum depth recorded from each station was used. The atolls in this study were varying distances apart, which has implications for population connectivity between atolls. Atoll separation distance is the approximate distance in kilometres of each atoll from the northernmost atoll (Seringapatam – 0, North Scott – 35, South Scott – 55, Mermaid – 500). This abiotic dataset was normalised and nMDS and cluster analyses were performed using Euclidean distance. The BEST procedure was employed as a global test to determine if there was biotic structure that could be explained with the abiotic variables, and this was further explored using the LINKTREE analysis (Clarke & Gorley 2006; Clarke *et al.* 2008) to identify which factors may have influenced biota.

Finally, we used a 2nd stage MDS to correlate the resemblance matrixes for each taxonomic assemblage, to determine how similar their multivariate pattern was, and if each taxonomic group provided the same information about the interrelationships of atolls and habitats.

Results

Patterns in species richness among habitats and atolls

The intertidal reef flat communities had lower species richness (mean across all atolls of 181.5 species) than the subtidal habitats of tidal channel ($\bar{x}$ = 268), reef front ($\bar{x}$ = 548.5) and lagoon ($\bar{x}$ = 530). South Scott consistently had highest species richness of the atolls sampled in all habitats and Seringapatam had lowest species richness, but this atoll also had the lowest sampling effort.

Mean species diversity varied for each taxonomic group and no general trends were apparent. For example, mean species richness of molluscs was highest at South Scott Reef on the reef flat, Mermaid Reef in the tidal channel, and North Scott Reef on the reef front, whereas fishes had highest species richness at South Scott Reef on the reef front and lagoon, and North Scott Reef and Seringapatam on the reef front (Fig. 2).

All taxonomic groups were found in all habitats but their proportional contribution to species richness within habitats differed. Species richness in the reef flat habitat was dominated by molluscs, fishes dominated in tidal channels and on reef fronts and corals had high species richness on reef fronts and in lagoons. The remaining taxa, marine plants, sponges, crustaceans and echinoderms, had lower species richness than the other groups, but their mean species richness was similar across all habitats (Fig. 2). The unusually high coral diversity on the reef flat at Mermaid Reef was partly due to only one station being sampled and the different sampling effort that was applied at this station (qualitative rather than quantitative). Species richness of the subtidal habitats (lagoon, reef front and tidal channel) was dominated by corals and fishes (Fig. 2).

Differences in the floral and faunal communities among habitats

The intertidal reef flat community significantly differed from the communities at the three subtidal habitats (Fig. 3). Within each habitat group there was clear structuring due to atolls, with Mermaid Reef separating from the northern atolls of Scott (North and South) and Seringapatam Reefs (Fig. 3). The SIMPROF

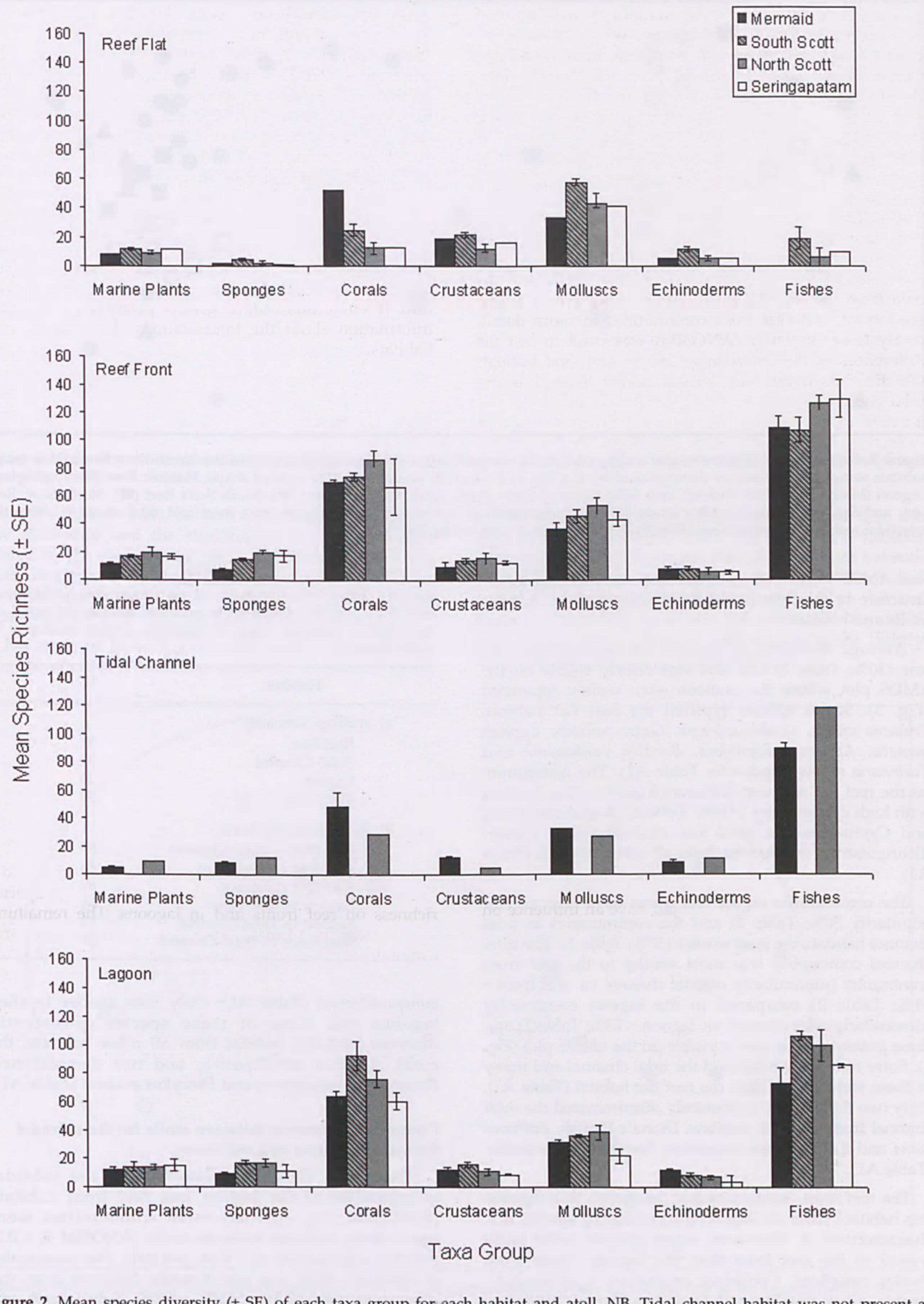


Figure 2. Mean species diversity (± SE) of each taxa group for each habitat and atoll. NB. Tidal channel habitat was not present at South Scott or Seringapatam Reefs and no fishes were surveyed on the reef flat at Mermaid Reef.

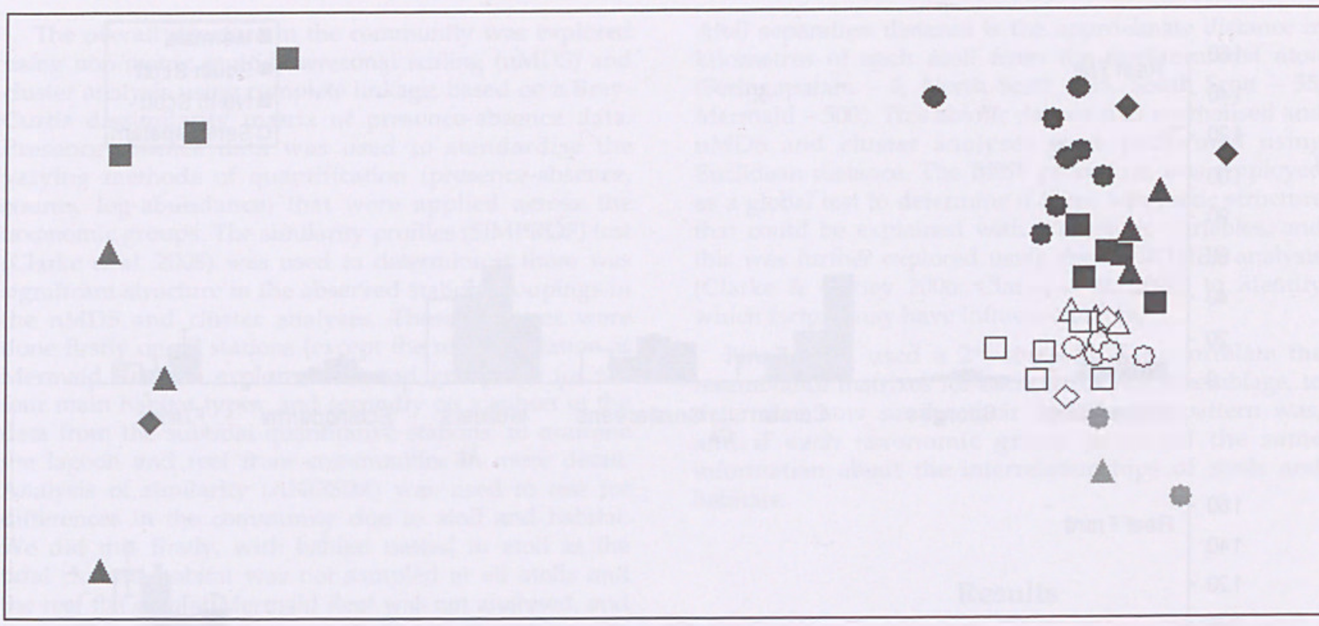


Figure 3. Non-metric multidimensional scaling plot of the marine floral and faunal communities of the North-West Shelf atolls for all habitats sampled. Habitats are distinguished by shading and the atolls are indicated by symbol shape. Habitat: Reef Flat (dark grey), Lagoon (black), Reef Front (white), and Tidal Channel (light grey). Atoll: Mermaid Reef (●), South Scott Reef (■), North Scott Reef (▲), and Seringapatam Reef (◆). Stress 0.08. The separation of subtidal habitats (lagoon, reef front and tidal channel), from the intertidal reef flat was significant (SIMPROF $p<0.05$, Bray-Curtis Similarity, 15%)

and ANOSIM ($R= 0.8$, $p<0.001$) tests showed significant structure in the faunal and floral communities of these atolls and habitats.

Average similarity of the reef flat communities was low (30%; Table 2) and this was clearly visible on the nMDS plot where the stations were widely separated (Fig. 3). Seven species typified the reef flat habitat, *Tridacna crocea, Lambis chiragra, Conus miliaris, Cypraea moneta, Acropora digitifera, Boodlea vanbosseae* and *Turbinaria ornata* (Appendix Table A1). The community on the reef flat was very different from all other habitats with high dissimilarity (~90%; Table 2). *Boodlea vanbosseae* and *Cypraea moneta* were key discriminating species distinguishing this habitat from all other habitats (Table A1).

The communities on the reef fronts were most similar (similarity 50%; Table 2) and the communities in tidal channel habitats the least similar (37%; Table 2). The tidal channel community was most similar to the reef front community (dissimilarity of tidal channel vs. reef front = 61%; Table 2) compared to the lagoon community (dissimilarly tidal channel vs. lagoon = 73%; Table 2) and these patterns were clearly visible on the nMDS plot (Fig. 3). Forty four species typified the tidal channel and many of these were absent from the reef flat habitat (Table A1). Only two fish species consistently discriminated the tidal channel from all other habitats, Diana's Pigfish, *Bodianus diana* and the Emperor Angelfish, *Pomacanthus imperator* (Table A1).

The reef front community had 58 species that typified this habitat (Table A1) but no discriminating species that characterised it. However, eight species were more typical of the reef front than the lagoon. These were *Porites vaughani, Cerithium echinatum, Cephalopholis urodeta, Chaetodon punctatofasciatus, Chromis xanthura, Forcipiger flavissimus, Naso caesius, and Thalassoma quinquevittatum* (Table A1). Only nine species typified lagoons and three of these species consistently discriminated this habitat from all other habitats: the coral, *Acropora abrolhosensis*, and two damselfishes, *Pomacentrus moluccensis* and *Dascyllus aruanus* (Table A1).

Table 2

Average Bray-Curtis similarity of the community within each habitat (a) and the dissimilarity between habitats (b) based on the SIMPER analysis. High % indicated greater similarity or dissimilarity.

Habitat	%
a) Average similarity	
Reef Flat	30
Tidal Channel	37
Lagoon	40
Reef Front	50
b) Average dissimilarity	
Reef Flat vs Tidal Channel	89
Reef Flat vs Reef Front	86
Reef Flat vs Lagoon	87
Lagoon vs Reef Front	65
Lagoon vs Tidal Channel	73
Reef Front vs Tidal Channel	61

Community turnover between atolls for the subtidal habitats of lagoon and reef front

There was significant structure in the subtidal communities of the lagoon and reef front habitats (SIMPROF, Fig. 4), and these communities were significantly different between atolls (ANOSIM $R = 0.7$, $p<0.001$) and habitats ($R = 0.86$, $p<0.001$). The community at Mermaid Reef was significantly different from the other atolls ($R = 0.85 - 0.95$, $p<0.05$). South Scott and North Scott Reefs were significantly different from each

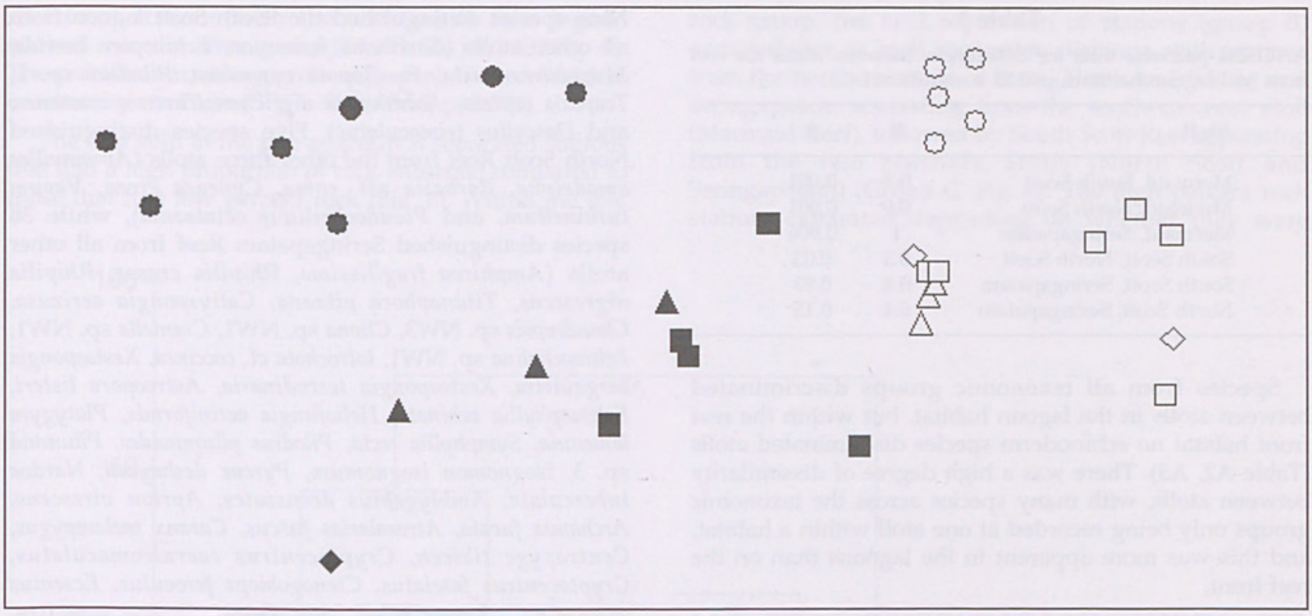


Figure 4. Non-metric multidimensional scaling plot of the marine floral and faunal communities in the lagoon and on the reef front. Symbols as in Figure 3. Stress 0.11.

other (R = 0.34, $p < 0.05$), but had a low R value indicating low difference and the significance p value is likely related to the larger number of replicates at these two reefs compared to Seringapatam Reef which was similar to both North and South Scott Reefs with a non significant low R (R = 0.4, $p > 0.05$; Table 3, Fig. 4).

For each of these habitats the atolls had a similar average similarity, with the similarity of the reef front habitat (52–59 %; Table 4) being slightly higher than the lagoon habitat (48–53 %; Table 4). The lagoon habitats were slightly more dissimilar than the reef front habitats for each atoll pair, indicating more unique floral and faunal components in the lagoons compared to the reef front habitats (Table 4). This is also evident on the nMDS plot, where the reef front stations are more tightly clustered than the lagoon stations (Fig. 3).

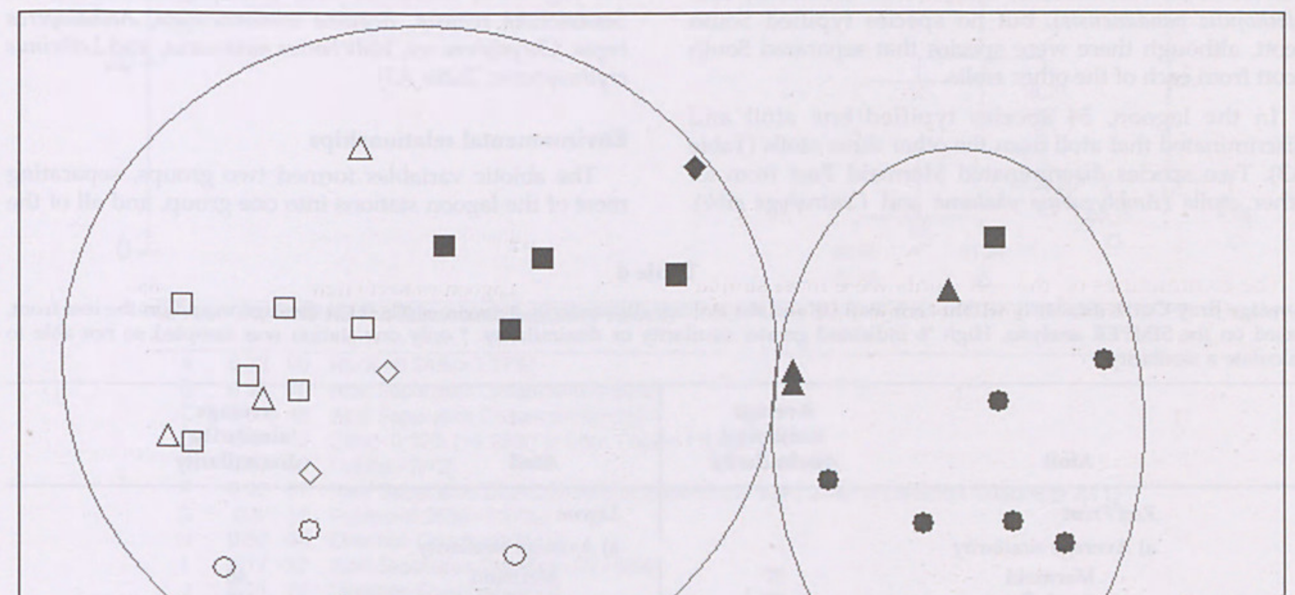


Figure 5. Non-metric multidimensional scaling plot of the abiotic environmental factors for the stations in the lagoons and on the reef front. Cluster groups are significant with SIMPROF, $p < 0.05$ and there was no significant grouping below this level. Symbols as in Figure 3. Stress 0.15.

Table 3

ANOSIM pairwise tests for differences between atolls for reef front and lagoon habitats, p<0.05 is significant.

Atoll	R	p
Mermaid, South Scott	0.9	0.001
Mermaid, North Scott	0.9	0.001
Mermaid, Seringapatam	1	0.006
South Scott, North Scott	0.3	0.03
South Scott, Seringapatam	0.4	0.83
North Scott, Seringapatam	0.4	0.15

Species from all taxonomic groups discriminated between atolls in the lagoon habitat, but within the reef front habitat no echinoderm species discriminated atolls (Table A2, A3). There was a high degree of dissimilarity between atolls, with many species across the taxonomic groups only being recorded at one atoll within a habitat, and this was more apparent in the lagoons than on the reef front.

Overall, 17 species found in reef front habitats typified one of the atolls and discriminated that atoll from the other three (Table A2). For example, four species (*Morula uva, Chaetodon adiergastos, Chaetodon unimaculatus* and *Lutjanus rivulatus*) discriminated the reef fronts at Mermaid Reef from the reef fronts at all other atolls. Nine species discriminated North Scott from all other atolls (*Niphates* sp. NW4, *Acanthastrea brevis, Ctenactis echinata, Barbatia* aff. *coma, Chicoreus brunneus, Lioconcha castrensis, Pinna bicolour, Cheilodipterus quinquelineatus*, and *Pomacentrus amboinensis*). Four species discriminated Seringapatam from all other atolls (*Haloplegma duperreyi, Pterocladiella caerulescens, Halichoeres nebulosus*, and *Stethojulis bandanensis*), but no species typified South Scott, although there were species that separated South Scott from each of the other atolls.

In the lagoon, 54 species typified one atoll and discriminated that atoll from the other three atolls (Table A3). Two species discriminated Mermaid Reef from all other atolls (*Amblygobius phalaena* and *Centropyge eibli*). Nine species distinguished the South Scott lagoon from all other atolls (*Ganonema farinosum, Echinopora horrida, Montastrea curta, Pocillopora verrucosa, Pilodius* sp. 1, *Trapezia septata, Acanthurus nigricans, Chromis xanthura*, and *Dascyllus trimaculatus*). Five species distinguished North Scott Reef from the other three atolls (*Avrainvillea amadelpha, Barbatia* aff. *coma, Cypraea erosa, Vasum turbinellum*, and *Pseudocheilinus octotaenia*), while 38 species distinguished Seringapatam Reef from all other atolls (*Amphiroa fragilissima, Rhipilia crassa, Rhipilia nigrescens, Titanophora pikeana, Callyspongia aerizusa, Chondropsis* sp. NW3, *Cliona* sp. NW1, *Craniella* sp. NW1, *Echinochalina* sp. NW1, *Iotrochota* cf. *coccinea, Xestospongia bergquistia, Xestospongia testudinaria, Astreopora listeri, Echinophyllia echinata, Heliofungia actiniformis, Platygyra lamellina, Symphyllia recta, Pilodius pilumnoides, Pilumnid* sp. 3, *Isognomon isognomum, Pyrene deshayesii, Nardoa tuberculata, Amblygobius decussates, Aprion virescens, Archamia fucata, Atrosalarias fuscus, Caranx melampygus, Centropyge tibicen, Cryptocentrus caeruleomaculatus, Cryptocentrus fasciatus, Ctenogobiops feroculus, Ecsenius schroederi, Epinephelus maculates, Eviota prasites, Gnatholepis anjerensis, Halichoeres prosopeion, Pterocaesio pisang*, and *Scolopsis affinis*).

The separation of Mermaid Reef from the three northern atolls was apparent for both lagoon and reef front habitats. Eight species discriminated the reef front at the three northern atolls (South Scott, North Scott and Seringapatam Reefs) from Mermaid Reef (*Plakortis nigra, Favites stylifera, Pocillopora damicornis, Tetralia* sp. 1, *Cheilinus trilobatus, Chrysiptera rex, Nemateleotris magnifica*, and *Pomacentrus lepidogenys*; Table A2). Seven species discriminated the lagoon at the northern three atolls from the lagoon at Mermaid Reef (*Lithophyllon undulatum, Sandalolitha robusta, Beguina semiorbiculata, Aethaloperca rogaa, Chrysiptera rex, Halichoeres melanurus*, and *Lethrinus erythropterus*; Table A3).

Environmental relationships

The abiotic variables formed two groups, separating most of the lagoon stations into one group, and all of the

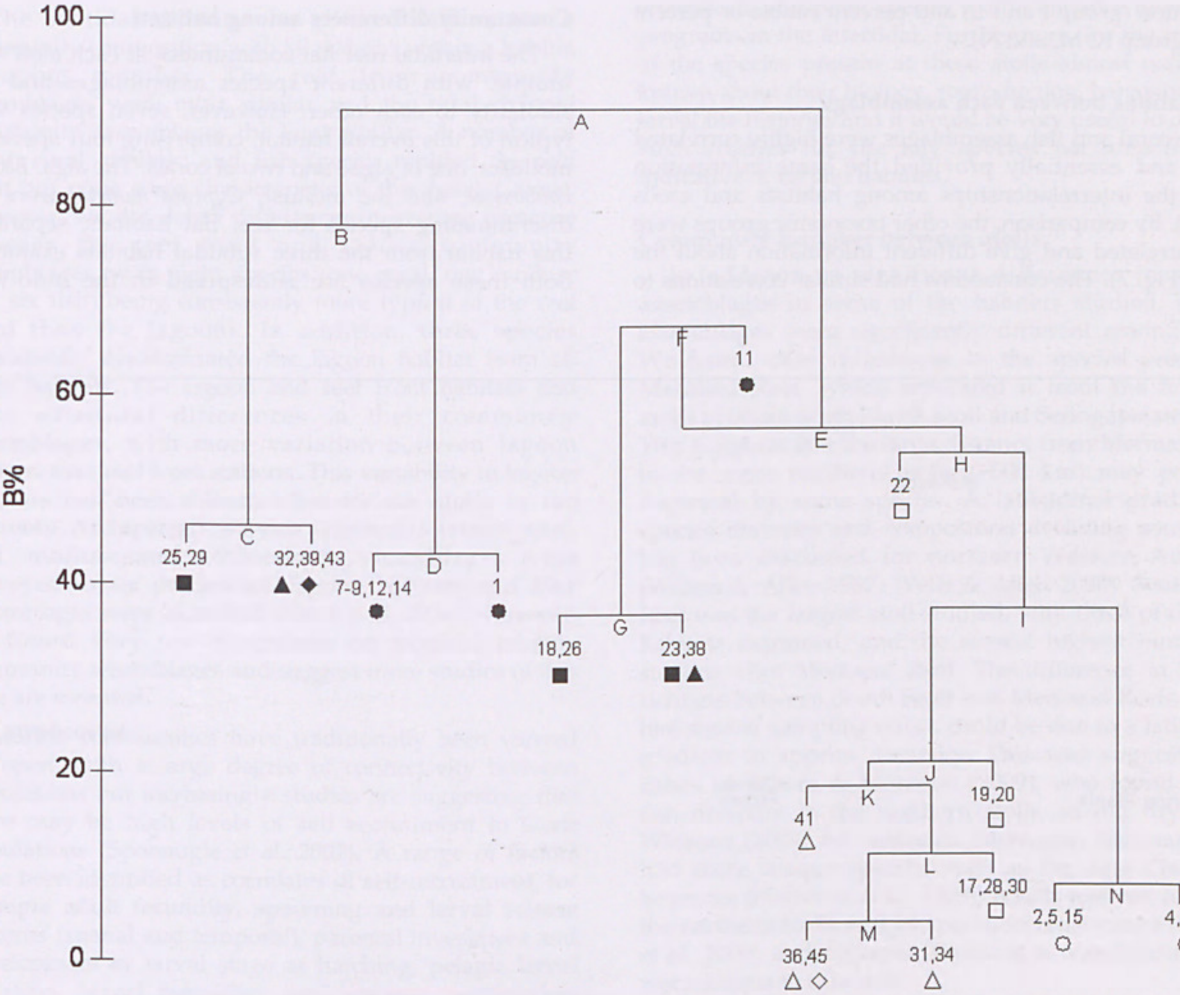
Table 4

Average Bray-Curtis similarity within each atoll (a) and the average dissimilarity between atolls (b) in the lagoon and on the reef front, based on the SIMPER analysis. High % indicated greater similarity or dissimilarity. * only one station was sampled so not able to calculate a similarity.

Atoll	Average similarity/ dissimilarity	Atoll	Average similarity/ dissimilarity
Reef Front		*Lagoon*	
a) Average similarity		a) Average similarity	
Mermaid	57	Mermaid	48
South Scott	52	South Scott	49
North Scott	59	North Scott	53
Seringapatam	50	Seringapatam	*
b) Average dissimilarity		b) Average dissimilarity	
Mermaid, South Scott	54	Mermaid, South Scott	62
Mermaid, North Scott	54	Mermaid, North Scott	59
Mermaid, Seringapatam	54	Mermaid, Seringapatam	66
South Scott, North Scott	49	South Scott, North Scott	54
South Scott, Seringapatam	49	South Scott, Seringapatam	62
North Scott, Seringapatam	45	North Scott, Seringapatam	54

reef front stations with the addition of four lagoon stations into the other group (18, 23, 26, and 43, Fig. 4). These abiotic variables significantly explain the biological community structure (BEST, Rho = 0.58, p<0.001).

The first split in the tree at group A separated stations that had a high proportion of rock substrate compared to those that had low percent rock (Fig. 6). Within the low rock group, the next separation of stations (group B) occurred due to atoll separation distance, with stations from the northern atolls of Scott (North and South) and Seringapatam separating from the southern most atoll (Mermaid Reef), followed by South Scott Reef separating from the two northern atolls (North Scott and Seringapatam) (Group C, Fig. 6). The high percent rock stations separated depending on whether they were



Group	R	B%	Abiotic factor and inequality values
A	0.72	90	Rock <0.24%(>0.27%)
B	0.93	78	Atoll Separation Distance<55(>500)
C	0.67	46	Atoll Separation Distance>55(<35)
D	0.8	43	Sand<0.19% (>0.23%) or Max. Depth>11(<10.5)
E	0.57	56	Habitat<1(>2)
F	0.92	67	Reef Separation Dist<55(>500) or Sand<0.097%(>0.23%) or Direction Quadrant>2(<1)
G	0.5	37	Rubble<0.25%(>0.27%)
H	0.67	54	Direction Quadrant>8(<7)
I	0.77	37	Atoll Separation Distance<55(>500)
J	0.51	21	Direction Quadrant<5(>7)
K	0.61	18	Rubble>0.35%(<0.17%)
L	0.37	11	Atoll Separation Distance<35(>55)
M	0.25	4	Sand<0.027%(>0.077%) or Direction Quadrant<2(>3) or Rubble<0.007%(>0.04%)
N	0.58	8	Direction Quadrant<2(>4) or Rubble<0%(>0.14%)

Figure 6. LINKTREE analysis showing the divisive clustering of the stations based on the biotic community and constrained by the inequalities of one or more abiotic factors. Symbols as in Figure 3. For each split in the tree the ANOSIM R value (relative subgroup separation) and B% (absolute subgroup separation, scaled to maximum of first division) is given. The abiotic factor contributing to the split is listed with the first inequality defining the group to the left of the split and the value in brackets defining the group to the right. Habitat: 1 – lagoon, 2 – reef front; atoll separation distance (km): Seringapatam – 0, North Scott – 35, South Scott – 55, Mermaid – 500; direction quadrant: 1 – NNE, 2 – NE, 3 – SE, 4 – SSE, 5 – SSW, 6 – SW, 7 – NW, 8 – NNW.

associated with either the lagoon habitat or the reef front (group E, Fig. 6). There was a reversal, indicating that an explanatory environmental variable is missing, in the tree at group F that appeared to have been caused by the community at station 11 in Mermaid Reef lagoon. Group G consisted of lagoon stations from Scott Reef splitting into two groups based on the amount of rubble at the stations. The reef front stations showed partitioning due to exposure (direction quadrant, Group H, J and N), atoll separation (group I and L) and percent rubble or percent sand (group K, M, and N).

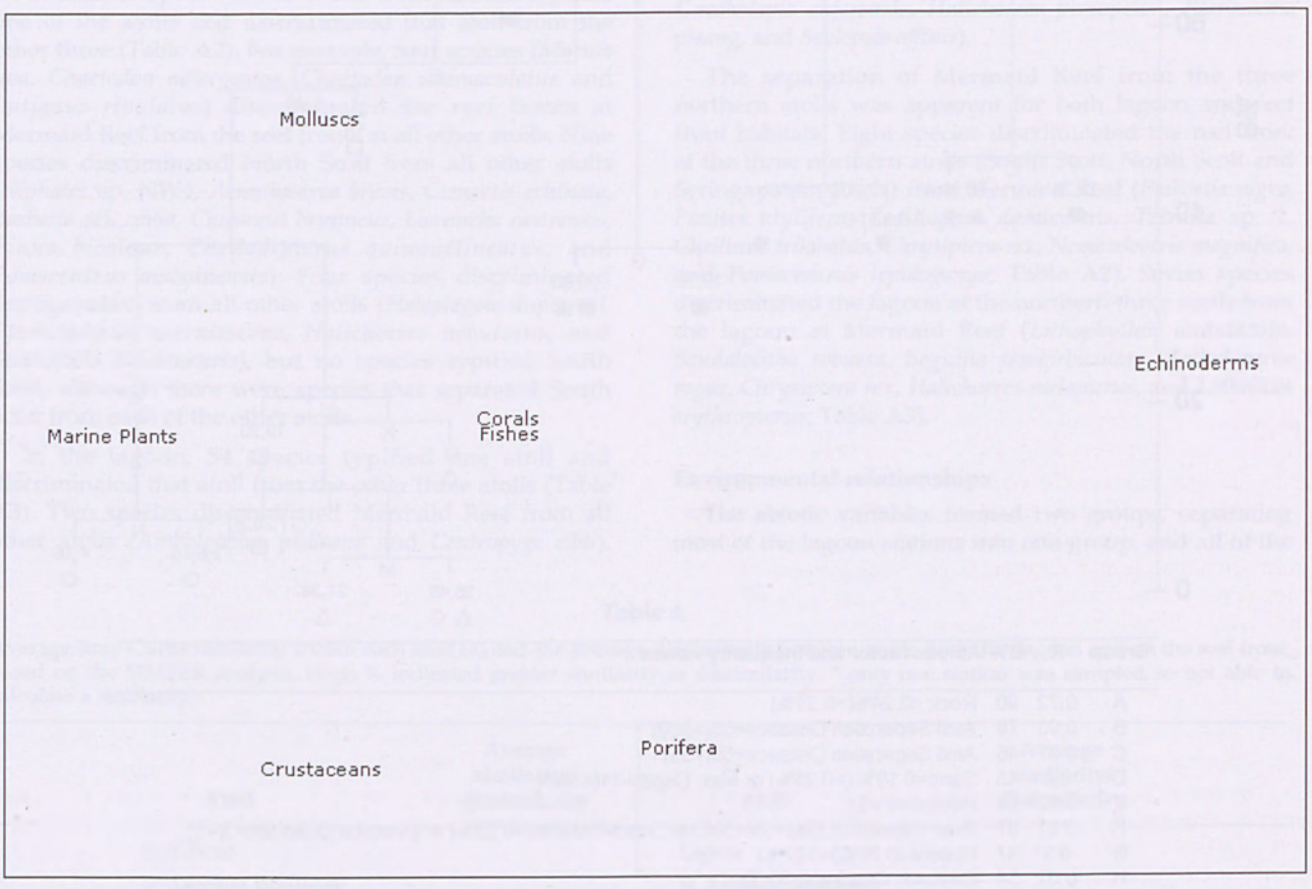
Correlations between each assemblage

The coral and fish assemblages were highly correlated (0.79) and essentially provided the same information about the interrelationships among habitats and atolls (Fig. 7). By comparison, the other taxonomic groups were less correlated and give different information about the atolls (Fig. 7). The crustaceans had similar correlations to marine plants, corals and sponges (~ 0.5), while echinoderms had low correlations with all the taxonomic groups examined (range 0.18 to marine plants to 0.41 with corals). Marine plants had similar correlations to fishes and molluscs (0.52).

Discussion

Community differences among habitats

The intertidal reef flat communities at each atoll were unique, with different species assemblages and low similarity to each other. However, seven species were typical of this overall habitat, comprising four species of molluscs, one of algae and two of corals. The alga, *Boodlea vanbosseae*, and the mollusc, *Cypraea moneta*, were key discriminating species for reef flat habitats, separating this habitat from the three subtidal habitats examined. Both these species are widespread in the Indo-West



TaxaGroup	Porifera	Fishes	Crustaceans	Molluscs	Echinoderms	Corals
Fishes	0.66					
Crustaceans	0.44	0.55				
Molluscs	0.36	0.59	0.35			
Echinoderms	0.28	0.30	0.26	0.23		
Corals	0.53	0.79	0.59	0.59	0.41	
Marine Plants	0.39	0.52	0.47	0.52	0.18	0.59

Figure 7. Second stage nMDS plot for each floral and faunal assemblage and the Spearman correlations underlying the nMDS plot. Stress 0.03.

Pacific and known inhabitants of the intertidal zone. Intertidal species may be more vulnerable to climate change than subtidal species as they are already likely to be living at their physiological limits (Harley *et al.* 2006). In these isolated atolls possibly subject to increasing cyclone events, significant changes in intertidal species assemblages should be anticipated and monitoring of these key species could aid in early detection of change in these assemblages.

The subtidal habitats also showed differences in community composition with all stations within a habitat grouping together. The reef front community assemblages were most similar and the tidal channel community assemblages the least similar. A number of plant, coral, mollusc and fish species typified the reef front but none were characteristic of this habitat alone. However, we did detect differences in average presence between the reef front and lagoon community assemblages, with eight species (one coral, one mollusc and six fish) being consistently more typical of the reef front than the lagoons. In addition, three species consistently discriminated the lagoon habitat from all other habitats. The lagoon and reef front habitats had clear structural differences in their community assemblages, with more variation between lagoon stations than reef front stations. This variability in lagoon habitats has been documented for six atolls in the Tuamotu Archipelago (French Polynesia) where coral, fish, mollusc and echinoderm assemblages were surveyed in six predefined lagoon habitats and four assemblages were identified (Pante *et al.* 2006). However, we found very few references on tropical marine community assemblages and suggest more studies of this type are essential.

Marine communities have traditionally been viewed as 'open' with a large degree of connectivity between populations but increasingly studies are suggesting that there may be high levels of self recruitment in some populations (Sponaugle *et al.* 2002). A range of factors have been identified as correlates of self-recruitment, for example adult fecundity, spawning and larval release patterns (spatial and temporal), parental investment and development of larval stage at hatching, pelagic larval duration, larval behaviour and sensory capabilities, geographic site isolation, flow variability and water column stratification (Sponaugle *et al.* 2002). In particular some studies have shown that atoll lagoons may have higher levels of self-recruitment than some other habitats such as the reef front. This idea has found support in studies on west Pacific atolls examining the distribution and size structure (Leis 1994; Leis *et al.* 1998) and genetics (Planes *et al.* 1998) of larval fishes, and corals on the Great Barrier Reef (see Ayre and Duffy 1994 in Underwood *et al.* 2007). We found the lagoon community assemblages on the northern Western Australian atolls had a higher number of unique species than the reef front habitats, in particular in Mermaid Reef lagoon. Therefore, enclosed lagoon habitats at these atolls may pose more of a barrier to dispersal than the reef front environments, and preclude dispersal of species with short-lived or non pelagic larvae. Genetic studies on a wide range of taxa with a variety of reproductive strategies that reside in these lagoons could test this hypothesis.

In this study, we have highlighted some species associated with particular habitats that could serve as sentinels of change. Although the key discriminating species were largely fishes and corals in the subtidal habitats examined in this study, this was not the case for the intertidal habitat. Consequently, the baseline monitoring of fishes and corals at the three northern atolls of South Scott, North Scott and Seringapatam Reefs (Heyward *et al.* 2007) would seem appropriate for the subtidal habitats, but the inclusion of some mollusc, crustacean, and plant species would enhance monitoring programs in the intertidal. Furthermore, for the majority of the species present at these atolls almost nothing is known about their biology, reproduction, behaviour, and larval life histories and it would be very useful to conduct such studies for the key species we identified as indicative of certain habitats.

Community turnover between atolls

In addition to significant differences in species assemblages in some of the habitats studied, species assemblages were significantly different among atolls. We found clear differences in the species present at Mermaid Reef, which separated it from the northern atolls of South Scott, North Scott and Seringapatam Reefs. This suggests that the large distance from Mermaid Reef to the more northern atolls (~500 km) may preclude dispersal by some species. A latitudinal gradient of species diversity and composition declining southward has been discussed for northern Western Australia (Wilson & Allen 1987; Wells & Allen 2005). South Scott Reef was the largest atoll studied, with three of the four habitats examined, and the second highest number of stations after Mermaid Reef. The difference in species richness between South Scott and Mermaid Reefs, which had similar sampling effort, could be due to a latitudinal gradient in species diversity. This was suggested for fishes by Moore & Morrison (2009), who found higher fish diversity in the northern atolls, as did Bryce and Whisson (2009) for molluscs. Moreover, Mermaid Reef had more unique species, such as the alga *Cladophora herpestica* (Huisman *et al.* 2009), which was not found in the northern atolls and 24 species of crustaceans (Titelius *et al.* 2009) and sponges (Fromont & Vanderklift 2009) were unique to this atoll.

All the atolls, except South Scott Reef appeared to have distinct species assemblages. Distinct sponge communities have been previously reported for other nearby atolls such as Ashmore, Cartier and Hibernia Reefs (Hooper 1994), and our results suggest that for many taxa groups, distinct species assemblages are characteristic of these offshore atolls. Distinct assemblages at different atolls have also been documented in French Polynesia and indicates that marine reserve design based solely on representativeness would require the protection of the majority of atolls and habitats (Pante *et al.* 2006).

The scientists involved in this study in some instances reported on numerous rare species; for example, 169 species of corals were reported from fewer than 10 of the 45 stations sampled, with only 22 species being abundant (found at more than 25 stations), (McKinney 2009), 79 species of sponges were found only at one of the atolls, and only 14 species could be considered widespread and common (Fromont & Vanderklift 2009), and the majority of the crustacean species were rare with most recorded from fewer than three stations (Titelius *et al.* 2009). Although 124 mollusc species were common to all four atolls studied, many species were found only at one of the atolls (Bryce & Whisson 2009). These findings of a large number of rare species gives support to what is already known for terrestrial environments (Rabinowitz *et al.* 1986; Howe 1999) and which is being increasingly reported in marine environments (Gray *et al.* 2005; Fromont *et al.* 2006 and references therein). Echinoderms were rare and frequently sparse in the environments surveyed. However, they were collected in conjunction with molluscs and consequently received a much lower sampling effort than the other taxonomic groups, which may in part account for this rarity and low abundance.

Environmental drivers and assemblage correlations.

Cross-shelf differences in both species richness and community composition have been commented on for the Kimberley region (Marsh & Marshall 1983; Hutchins 1999; Hutchins 2001; Huisman *et al.* 2009; Moore & Morrison 2009). Faunal species richness on the atolls was higher than on the coastal Kimberley reefs and different species occurred on the atolls compared to the Kimberley coast, both for echinoderms (Marsh & Marshall 1983) and fishes (Hutchins 1999; Hutchins 2001). In contrast, this pattern was reversed for algae, with higher species richness along the coast compared to the atolls (Huisman *et al.* 2009). However, these comparisons were based on total species richness and were not partitioned by habitat or adjusted species richness calculations for unequal sampling effort. New species richness assessments of this data (with unequal sampling effort addressed) suggest that some taxa groups are more diverse in subtidal habitats on the offshore atolls than on the Kimberley coast but diversity is more variable in the intertidal and may not follow the same trend (Sampey *et al.* unpublished data). Compared to the oligotrophic environment of the offshore atolls, the Kimberley coast can have high nutrient, sediment and freshwater flows, and as a result the waters are turbid with high levels of flocculating silt on the reefs. The differences in species richness and community assemblages found among the same habitats on the atolls compared to the coast suggest that different abiotic factors contribute to the maintenance of assemblages. These are likely to be environmental aspects (such as degree of turbidity, siltation, tolerance to freshwater, and desiccation exposure) and differences in the tolerances, recruitment and survivorship of the different taxonomic groups to such environmental conditions.

In the north-west atolls study, the authors detected differences in species assemblages (sponges, Fromont & Vanderklift 2009, corals, McKinney 2009, molluscs, Bryce & Whisson 2009, crustaceans, Titelius *et al.* 2009 and fishes, Moore & Morrison 2009) and suggested these differences could be attributed to a number of factors: habitat requirements (reef flat vs. lagoon vs. tidal channel vs. reef front as well as microhabitats) (Bryce & Whisson 2009; Fromont & Vanderklift 2009; McKinney 2009; Moore & Morrison 2009; Titelius *et al.* 2009), latitudinal gradients in species richness (Bryce & Whisson 2009; Fromont & Vanderklift 2009; McKinney 2009; Moore & Morrison 2009; Titelius *et al.* 2009), and influences of cyclonic activity (i.e. exposure) (Bryce & Whisson 2009; Moore & Morrison 2009; Titelius *et al.* 2009). However, none of these factors were previously explicitly explored except for corals. In this study, our analyses have explored the link between the biotic community and abiotic environmental factors. We detected that substrate type was the principal abiotic variable influencing the biotic community assemblages, and atoll separation distance was also important for assemblages where percent of hard substrate was low, as was habitat type (lagoon vs. reef front) for assemblages where percent of hard substrate was high. These results are not surprising as many species will have a substrate preference such as corals and sponges that require a hard substrate as an attachment point, and other species which live amongst rubble or sand. Within the lagoon habitat there was high substrate variability, as the area sampled might have been on a lagoon bommie, slope or sand flat with varying amounts of fracturing of the reef and incursions of sand (Bryce, 2009). These factors will influence the species assemblages that can occur there.

Coral and fish species are the most studied taxa in tropical ecosystems (Przeslawski *et al.* 2008), yet our data found that the interrelationships of habitat and atolls for these two assemblages were highly correlated. By contrast, the other taxonomic groups had varying correlations with corals, fishes and each other, and thus provide additional information about these habitats and atolls. For example, crustaceans had similar correlations to marine plants, corals and sponges, which may be due to some crustacean species being associated with one of the sessile taxonomic groups, such as species of *Tetralia* that are associated with acroporid corals and species of pilumnid crabs that are associated with sponges (Titelius *et al.* 2009). This has important implications for management and monitoring of change at these atolls and implies that using corals and fishes as surrogates for other taxonomic groups is insufficient.

Conclusions

In this study, we focussed on exploring differences in community composition among habitats and atolls using presence absence data in a non-parametric framework with a view to providing useful insights into the communities that occur there. It would be useful in future surveys to sample with a standardised methodology and a balanced sample design to enable more rigorous comparisons.

Overall, this synthesis study has presented a sound baseline dataset of species assemblages occurring at these atolls. We have clearly demonstrated that habitats have characteristic community assemblages and that atolls have different species assemblages in some of these habitats, particularly in the lagoon and reef flat environments. In some habitats the common taxa groups (fishes and corals) may provide adequate information for the overall species assemblages and can be used as surrogates, but in other cases, e.g. in the intertidal, these commonly targeted groups are far less useful in reflecting overall community patterns.

Acknowledgements: We are extremely grateful to our taxonomic colleagues for allowing us to use their datasets to generate this study: Clay Bryce (molluscs & echinoderms), Christine Hass (crustaceans), John Huisman (marine plants), Dave McKinney (corals), Loisette Marsh (echinoderms), Glenn Moore (fishes), Sue Morrison (fishes), Peter Morrison (habitat video), Melissa Titelius (crustaceans), and Corey Whisson (molluscs). Their collections, taxonomic identifications and expert knowledge made this paper possible. We thank Diana Jones for encouraging our efforts to produce this synthesis paper. Many thanks to Stacey Osborne for assistance with sourcing and formatting some of the references. We gratefully acknowledge the support of Woodside Energy Ltd for funding the northern Western Australian atolls survey in 2006. Thanks to Akeal Hayek and Gaia Resources for providing the map. Many thanks to Diana Jones, David Sutton, Corey Whisson and two reviewers for comments on the manuscript.

References

Allen G 1997 The Marine Fishes of Tropical Australia and South-East Asia. Perth, Australia, Western Australian Museum. 292 p.

Anon 2008 Scott Reef Status Report 2008. 1–28 p.

Berry P (ed) 1986 Faunal Survey of the Rowley Shoals, Scott Reef and Seringapatam Reef North-Western Australia. Supplement No. 25: i–vi, 1–106. Perth, Western Australia, Western Australian Museum.

Bryce C (ed) 2009 Marine Biodiversity Survey of Mermaid Reef (Rowley Shoals), Scott and Seringapatam Reef. Supplement No. 77: i–xv, 1–256. Perth, Western Australia, Western Australian Museum.

Bryce C & Marsh L 2009 Echinodermata (Asteroidea, Echinoidea and Holothuroidea) of Mermaid (Rowley Shoals), Scott and Seringapatam Reefs, Western Australia. Records of the Western Australian Museum Supplement 77: 209–220.

Bryce C & Whisson C 2009 The macromolluscs of Mermaid (Rowley Shoals), Scott and Seringapatam Reefs, Western Australia. Records of the Western Australian Museum Supplement 77: 177–208.

Chapin III FS, Zavaleta ES, Eviner VT, Naylor RL, Vitousek PM, Reynolds HL, Hooper DU, Lavorel S, Sala OE & Hobbie SE 2000 Consequences of changing biodiversity. Nature 405(6783): 234–242.

Clarke K & Warwick R 2001 Change in Marine Communities: An Approach to Statistical Analysis and Interpretation. 2nd edition. 173 p.

Clarke K & Gorley R 2006 PRIMER v6: User Manual/Tutorial. 190 p.

Clarke K, Somerfield P & Gorley R 2008 Testing of null hypotheses in exploratory community analyses: similarity profiles and biota-environment linkage. Journal of Experimental Marine Biology and Ecology 366(1–2): 56–69.

Ferrier S & Guisan A 2006 Spatial modelling of biodiversity at the community level. Journal of Applied Ecology 43(3): 393–404.

Fromont J & Vanderklift M 2009 Porifera (sponges) of Mermaid, Scott and Seringapatam Reefs, north Western Australia. Records of the Western Australian Museum Supplement 77: 89–104.

Fromont J, Vanderklift M & Kendrick GA 2006 Marine Sponges of the Dampier Archipelago, Western Australia: patterns of species distributions, abundance and diversity. Biodiversity and Conservation 15: 3731–3750.

Gaston K J 2000 Global patterns in biodiversity. Nature 405(6783): 220–227.

Gilmour J P, Smith L D & Brinkman R M 2009 Biannual spawning, rapid larval development and evidence of self-seeding for scleractinian corals at an isolated system of reefs. Marine Biology 156: 1297–1309.

Gray J S, Bjoergesaeter A & Ugland K I 2005 The impact of rare species on natural assemblages. Journal of Animal Ecology 74(6): 1131–1139.

Greenstein B J & Pandolfi J M 2008 Escaping the heat: range shifts of reef coral taxa in coastal Western Australia. Global Change Biology 14(3): 513–528.

Harley C D G, Randall Hughes A, Hultgren K M, Miner B G, Sorte C J B, Thornber C S, Rodriguez L F, Tomanek L & Williams S L 2006 The impacts of climate change in coastal marine systems. Ecology Letters 9(2): 228–241.

Heyward A, Halford A, Smith L & Williams D M 2007 Coral Reefs of North West Australia: Baseline Monitoring of an Oceanic Reef Ecosystem. Proceedings of the 8th International Coral Reef Symposium 1: 289–294.

Hooper J N A 1994 Coral reef sponges of the Sahul Shelf- a case for habitat preservation. Memoirs of the Queensland Museum. Brisbane 36(1): 93–106.

Howe H F 1999 Dominance, diversity and grazing in tallgrass restoration. Ecological Restoration 17(1&2): 59–66.

Huisman J, Leliaert F, Verbruggen H & Townsend R 2009 Marine Benthic Plants of Western Australia's shelf-Edge atolls. Records of the Western Australian Museum Supplement 77: 50–88.

Hutchins J 1999 Biogeography of the nearshore marine fish fauna of the Kimberley, Western Australia. In: B S, Sire J-Y ed. Proceedings of the 5th Indo-Pacific Fish Conference. Pp. 99–108.

Hutchins J B 2001 Biodiversity of shallow reef fish assemblages in Western Australia using a rapid censusing technique. Records of the Western Australian Museum 20(3): 247–270.

Leis J M 1994 Coral sea atoll lagoons: closed nurseries for the larvae of a few coral reef fishes. Bulletin of Marine Science 54(1): 206–227.

Leis J M, Trnski T, Doherty P J & Dufour V 1998 Replenishment of fish populations in the enclosed lagoon of Taiaro Atoll:(Tuamotu Archipelago, French Polynesia) evidence from eggs and larvae. Coral Reefs 17(1): 1–8.

Lyons K G, Brigham C A, Traut B H & Schwartz M W 2005 Rare species and ecosystem functioning. Conservation Biology 19(4): 1019–1024.

Margules C R & Pressey R L 2000 Systematic conservation planning. 405(6783): 243–253.

Marsh L M & Marshall J I 1983 Some aspects of the zoogeography of northwestern Australian echinoderms (other than holothurians). Bulletin of Marine Science 33(3): 671–687.

McKinney D 2009 A survey of the scleractinian corals at Mermaid, Scott and Seringapatam Reefs, Western Australia. Records of the Western Australian Museum Supplement 77: 105–144.

Moore G & Morrison S 2009 Fishes of three North West Shelf atolls off Western Australia: Mermaid (Rowley Shoals), Scott and Seringapatam Reefs Records of the Western Australian Museum Supplement 77: 221–255.

Morrison P 2009 Subtidal Habitats of Mermaid Reef (Rowley Shoals), Scott and Seringapatam Reefs, Western Australia. Records of the Western Australian Museum Supplement 77: 29–49.

Pante E, Adjeroud M, Dustan P, Penin L & Schrimm M 2006 Spatial patterns of benthic invertebrate assemblages within atoll lagoons: importance of habitat heterogeneity and considerations for marine protected area design in French Polynesia. Aquatic Living Resources 19(3): 207–217.

Planes S, Romans P & Lecomte-Finiger R 1998 Genetic evidence of closed life-cycles for some coral reef fishes within Taiaro Lagoon (Tuamotu Archipelago, French Polynesia). Coral Reefs 17(1): 9–14.

Przeslawski R, Ahyong S, Byrne M, WoeRheide G & Hutchings P 2008 Beyond corals and fish: the effects of climate change on noncoral benthic invertebrates of tropical reefs. Global Change Biology 14(12): 2773–2795.

Puotinen M P 2007 Modelling the risk of cyclone wave damage to coral reefs using GIS: a case study of the Great Barrier

Reef, 1969–2003. International Journal of Geographical Information Science 21: 97–120.

Purvis A & Hector A 2000 Getting the measure of biodiversity. Nature 405(6783): 212–219.

Rabinowitz D, Cairns S & Dillon T 1986. Seven forms of rarity and their frequency in the flora of the British Isles In: Soule ME ed. Conservation Biology: The science of scarcity and diversity. Sunderland, Massachusetts, Sinauer. Pp. 182–204.

Smith L, Gilmour J & Heyward A 2008 Resilience of coral communities on an isolated system of reefs following catastrophic mass-bleaching. Coral Reefs 27(1): 197–205.

Solomon S, Qin D, Manning M, Marquis M, Averyt K, Tignor M, Miller J, HLR, Chen Z 2007 Climate Change 2007: The Physical Science Basis: Contribution of Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change. Cambridge, Cambridge University Press. 996 p.

Sponaugle S, Cowen R K, Shanks A, Morgan S G, Leis J M, Pineda J, Boehlert G W, Kingsford M J, Lindeman K C & Grimes C 2002 Predicting self-recruitment in marine populations: biophysical correlates and mechanisms. Bulletin of Marine Science 70(Supplement 1): 341–375.

Titelius M, Sampey A & Hass C 2009 Crustaceans of Mermaid (Rowley Shoals), Scott and Seringapatam Reefs, north Western Australia. Records of the Western Australian Museum Supplement 77: 145–176.

Travers M, Newman S & Potter I 2006 Influence of latitude, water depth, day v. night and wet v. dry periods on the species composition of reef fish communities in tropical Western Australia. Journal of Fish Biology 69(4): 987–1017.

Underwood J, Smith L, Van Oppen M & Gilmour J 2007 Multiple scales of genetic connectivity in a brooding coral on isolated reefs following catastrophic bleaching. Molecular ecology 16(4): 771–784.

Veron J E N 1993 A biogeographic database of hermatypic corals: species of the Central Indo-Pacific genera of the world. Townsville, Australian Institute of Marine Science. 433 p.

Veron J E N & Marsh L M 1988 Hermatypic corals of Western Australia: records and annotated species list. Records of the Western Australian Museum Supplement No. 29: i–v, 1–136.

Wells F 1986 Zoogeographic affinities of prosobranch gastropods of offshore coral reefs in northwestern Australia. The Veliger 29(2): 191–199.

Wells F 1990 Comparative zoogeography of marine molluscs from Northern Australia, New Guinea, and Indonesia. The Veliger 33(2): 140–144.

Wells F E & Allen G R 2005 Marine biodiversity on offshore coral reefs in north-western Australia. The Beagle, Records of the Museums and Art Galleries of the Northern Territory Supplement 1: 43–50.

Wilson B & Allen G 1987. Major Components and Distribution of Marine Fauna In: Dyne G, Walton D ed. Fauna of Australia. General Articles. Canberra, Australian Government Publishing Service. Pp. 43–68.

Appendix

The typifying and discriminating species identified with the SIMPER analyses are presented here. Species from all taxonomic groups were restricted to certain habitats (Table A1). Within the lagoon (Table A2) and reef front (Table A3) habitats some species were restricted to certain atolls and there were more unique species at an atoll in the lagoon habitat than the reef front habitats.

Table A1

Typifying (T) and discriminating (D) species for each habitat.
The habitat that a species typifies (Average presence of ~1, i.e. present in most stations from that habitat) is listed first and then the habitats that it discriminates from are listed in brackets (Dissimilarity/SD ratio of ~ 1; i.e. absent from that habitat). Habitats: Fl – reef flat, TC – tidal channel, Fr – reef front, L – lagoon.

Species	T (D)	Species	T (D)
Marine Plants		Fishes	
Boodlea vanbosseae	Fl (TC, Fr, L)	*Acanthurus nigricans*	TC, Fr (Fl, L)
Halimeda minima	Fr, L (Fl, TC)	*Acanthurus olivaceus*	TC (Fl, L)
Hydrolithon onkodes	Fr (Fl, L)	*Aethaloperca rogaa*	TC (Fl)
Turbinaria ornata	Fl (TC, Fr)	*Balistapus undulatus*	TC, Fr (Fl)
Valonia ventricosa	Fr (Fl, TC)	*Bodianus axillaris*	TC (Fl, L)
Sponges		*Bodianus diana*	TC (Fl, Fr, L)
Cliona orientalis	TC (Fl, L)	*Cephalopholis argus*	TC, Fr (Fl)
Lamellodysidea herbacea	TC, Fr (Fl)	*Cephalopholis urodeta*	Fr (L)
Jaspis splendens	TC (Fl)	*Chaetodon auriga*	TC, L (Fl)
Corals		*Chaetodon citrinellus*	TC (Fl, L)
Acropora abrolhosensis	L (Fl, TC, Fr)	*Chaetodon ephippium*	TC (Fl)
Acropora digitifera	Fl (TC, L)	*Chaetodon lunula*	TC (Fl)
Acropora humilis	Fr	*Chaetodon lunulatus*	TC, Fr (Fl)
Acropora intermedia	L (Fl, TC)	*Chaetodon ornatissimus*	TC, Fr (Fl)
Acropora nasuta	Fr	*Chaetodon punctatofasciatus*	Fr (L)
Acropora spicifera	Fr (Fl)	*Chaetodon ulietensis*	TC (Fl)
Echinopora lamellosa	Fr (Fl, TC)	*Cheilinus undulatus*	TC (Fl, L)
Favia matthaii	Fr (Fl)	*Chromis margaritifer*	TC (Fl)
Favia pallida	Fr (TC)	*Chromis weberi*	TC (Fl)
Favia stelligera	Fr (Fl)	*Chromis xanthura*	Fr (L)
Favites abdita	Fr (Fl)	*Ctenochaetus striatus*	Fr , L (Fl)
Galaxea fascicularis	Fr, L (Fl)	*Dascyllus aruanus*	L (Fl, TC, Fr)
Goniastrea pectinata	Fr (Fl)	*Forcipiger flavissimus*	TC, Fr (Fl, L)
Goniastrea retiformis	Fr	*Forcipiger longirostris*	TC (Fl, L)
Isopora palifera	Fr (Fl, L)	*Gomphosus varius*	TC (Fl)
Lobophyllia hemprichii	L (Fl)	*Halichoeres hortulanus*	TC, Fr (Fl)
Montastrea curta	Fr (Fl)	*Labroides dimidiatus*	TC, Fr, L (Fl)
Montastrea magnistellata	L (Fl)	*Lethrinus olivaceus*	TC (Fl)
Pavona varians	Fr (Fl)	*Lutjanus bohar*	TC (Fl)
Pocillopora eydouxi	TC (Fl, L)	*Lutjanus decussatus*	Fr (Fl)
Pocillopora verrucosa	Fr (Fl)	*Lutjanus gibbus*	Fr
Porites vaughani	Fr (L)	*Macropharyngodon meleagris*	TC (Fl)
Psammocora profundacella	Fr	*Monotaxis grandoculis*	TC, Fr, L (Fl)
Crustaceans		*Naso caesius*	Fr (L)
Calcinus gaimardii	TC (Fr, L)	*Naso lituratus*	TC, Fr, L (Fl)
Calcinus minutus	Fr	*Nemateleotris magnifica*	TC (L)
Molluscs		*Parupeneus barberinus*	TC (Fl)
Arca avellana/ventricosa	L (TC)	*Parupeneus crassilabris*	Fr (TC, L)
Cerithium echinatum	Fr (L)	*Parupeneus multifasciatus*	Fr (Fl)
Conus miles	Fr	*Pomacanthus imperator*	TC (Fl, Fr, L)
Conus miliaris	Fl (L)	*Pomacentrus moluccensis*	L (Fl, TC, Fr)
Coralliophila neritoidea	Fr	*Pomacentrus philippinus*	TC, Fr (Fl)
Cypraea moneta	Fl (TC, Fr, L)	*Pomacentrus vaiuli*	TC (Fl)
Drupella cornus	Fr (Fl)	*Pseudocheilinus hexataenia*	Fr (Fl, TC)
Lambis chiragra	Fl (Fr, L)	*Pygoplites diacanthus*	Fr (Fl)
Tridacna crocea	Fl, Fr, L	*Sargocentron spiniferum*	TC (Fl)
Tridacna maxima	Fr, L	*Scolopsis bilineata*	TC (Fl)
Turbo argyrostomus/chrysostomus	Fr (L)	*Stethojulis bandanensis*	TC (Fr, L)
Vasum turbinellum	Fr	*Sufflamen bursa*	TC (Fl, L)
Echinoderms		*Thalassoma amblycephalum*	TC, Fr (Fl)
Echinometra mathaei	TC	*Thalassoma hardwicke*	L (Fl)
		Thalassoma quinquevittatum	Fr (L)
		Zanclus cornutus	TC, Fr (Fl)

Table A2

Typifying (T) and discriminating (D) species for each atoll in the reef front habitat.
The atoll that a species typifies is listed first and then the atolls that it discriminates from are listed in brackets. Atolls: ME – Mermaid Reef, SS – South Scott Reef, NS – North Scott Reef, and SE – Seringapatam Reef.

Species	T (D)
Marine Plants	
Cladophora herpestica	ME (SE)
Dichotomaria marginata	NS (ME)
Haloplegma duperreyi	SE (ME, SS, NS)
Neomeris bilimbata	SS, NS (ME)
Pterocladiella caerulescens	SE (ME, SS, NS)
Tricleocarpa cylindrica	NS, SE (ME)
Sponges	
Cliona orientalis	SE (ME)
Gelliodes fibulata	NS, SE (ME)
Halichondria sp. NW2	NS (ME, SE)
Hyrtios erecta	NS (ME, SE)
Monanchora unguiculata	SS, SE (ME)
Myrmekioderma granulata	SE (ME, SS)
Niphates sp. NW1	NS, SE (ME)
Niphates sp. NW4	NS (ME, SS, SE)
Plakortis nigra	SS, NS, SE (ME)
Neopetrosia exigua	NS (ME, SS)
Corals	
Acanthastrea brevis	NS (ME, SS, SE)
Acropora polystoma	ME (SS, NS)
Acropora samoensis	NS (ME, SE)
Acropora subulata	NS, SE (ME)
Astreopora myriophthalma	NS (ME)
Ctenactis echinata	NS (ME, SS, SE)
Favites stylifera	SS, NS, SE (ME)
Fungia fungites	NS (ME, SS)
Heliopora coerulea	SS, SE (ME)
Isopora brueggemanni	ME, NS (SS)
Leptastrea aequalis	NS, SE (ME, SS)
Leptoseris scabra	NS (ME, SE)
Lithophyllon undulatum	SS, NS (ME)
Merulina scabricula	ME (SE)
Platygyra daedalea	SS (ME, NS)
Pocillopora damicornis	SS, NS, SE (ME)
Pocillopora eydouxi	SS, SE (ME)
Pocillopora meandrina	SE (SS)
Psammocora digitata	SE (SS)
Psammocora haimeana	ME (SS, NS)
Psammocora superficialis	SE (ME, SS)
Turbinaria reniformis	SS (ME), NS (ME)
Turbinaria stellulata	SE (ME)
Crustaceans	
Calcinus lineapropodus	NS (ME)
Chlorodiella ? laevissima	SS, SE (ME)
Hapalocarcinus marsupialis	SE (ME, SS)
Pilodius sp. 1	SS, SE (ME)
Tetralia fulva	SE (ME)
Tetralia sp. 1	SS, NS, SE (ME)
Trapezia guttata	NS, SE (ME, SS)
Trapezia septata	NS (SE)
Trapezia tigrina	ME (SS, SE)
Molluscs	
Barbatia aff. *coma*	NS (ME, SS, SE)
Barbatia foliata	NS (ME, SE)
Beguina semiorbiculata	NS (ME)
Chicoreus brunneus	NS (ME, SS, SE)
Chromodoris elisabethina	ME (NS, SE)
Molluscs cont.	
Drupa ricinus	ME, SS (SE)
Drupina grossularia	SE (ME)
Latirus turritus	ME, SS (SE)
Lioconcha castrensis	NS (ME, SS, SE)
Morula biconica	NS, SE (ME)
Morula uva	ME (SS, NS, SE)
Phyllidia coelestis	SS (ME, SE)
Pinna bicolor	NS (ME, SS, SE)
Rhinoclavis aspera	NS (ME, SS)
Septifer bilocularis	NS (ME)
Streptopinna saccata	NS, SE (ME)
Tectus pyramis	SS, NS, SE (ME)
Fishes	
Acanthurus blochii	SE (ME)
Acanthurus nigricauda	SE (ME)
Acanthurus nigrofuscus	SE (ME)
Acanthurus pyroferus	NS (ME)
Canthigaster solandri	SE (ME, SS)
Caranx melampygus	ME, SE (SS)
Centropyge bicolor	SE (ME)
Centropyge vrolikii	SS, SE (ME)
Chaetodon adiergastos	ME (SS, NS, SE)
Chaetodon oxycephalus	SE (ME)
Chaetodon trifascialis	ME (NS)
Chaetodon unimaculatus	ME (SS, NS, SE)
Chaetodon vagabundus	NS, SE (ME)
Cheilinus fasciatus	ME, SE (SS)
Cheilinus trilobatus	SS, NS, SE (ME)
Cheilodipterus quinquelineatus	NS (ME, SS, SE)
Chrysiptera rex	SS, NS, SE (ME)
Cirrhilabrus exquisitus	SS, SE (ME)
Coris gaimard	NS, SE (ME)
Forcipiger longirostris	NS (SE)
Halichoeres melanurus	ME, NS (SS, SE)
Halichoeres nebulosus	SE (ME, SS, NS)
Halichoeres prosopeion	NS (ME)
Hemigymnus fasciatus	ME (SS)
Hemigymnus melapterus	ME (NS, SE)
Labroides pectoralis	ME (SS, NS)
Lethrinus erythropterus	NS (ME)
Lutjanus rivulatus	ME (SS, NS, SE)
Macolor macularis	NS, SE (SS)
Meiacanthus atrodorsalis	NS (ME, SS)
Melichthys vidua	ME (NS, SE)
Nemateleotris magnifica	SS, NS, SE (ME)
Odonus niger	NS (ME)
Parapercis millepunctata	SE (ME)
Parupeneus barberinus	NS (ME)
Plectroglyphidodon dickii	ME (NS)
Plectroglyphidodon lacrymatus	SE (ME, NS)
Plectropomus oligacanthus	NS (ME)
Pomacentrus amboinensis	NS (ME, SS, SE)
Pomacentrus lepidogenys	SS, NS, SE (ME)
Pseudocheilinus octotaenia	NS (ME)
Siganus puellus	SE (SS)
Stethojulis bandanensis	SE (ME, SS, NS)
Stethojulis strigiventer	ME (SS, SE)

Table A3

Typifying (T) and discriminating (D) species for each atoll in the lagoon habitat.
Notation as in Table A2. NB. Seringapatam Reef – only one station was sampled in this habitat so typifying species could not be calculated, these are inferred from the species that distinguished this atoll from the others.

Species	T (D)
Marine Plants	
Actinotrichia fragilis	SE (SS, NS)
Amphiroa fragilissima	SE (ME, SS, NS)
Avrainvillea amadelpha	NS (ME, SS, SE)
Dictyota friabilis	NS, SE (ME)
Ganonema farinosum	SS (ME, NS, SE)
Hydrolithon gardineri	SE (ME, SS)
Lobophora variegata	SS, NS (SE)
Rhipilia crassa	SE (ME, SS, NS)
Rhipilia nigrescens	SE (ME, SS, NS)
Symploca hydnoides	SE (ME, SS)
Titanophora pikeana	SE (ME, SS, NS)
Udotea glaucescens	ME (SS, NS)
Valonia ventricosa	SS, NS (ME)
Sponges	
Callyspongia aerizusa	SE (ME, SS, NS)
Chondropsis sp. NW3	SE (ME, SS, NS)
Cliona sp. NW1	SE (ME, SS, NS)
Craniella sp. NW1	SE (ME, SS, NS)
Echinochalina sp. NW1	SE (ME, SS, NS)
Haliclona sp. NW5	SE (ME, NS)
Hyrtios erecta	SS (ME)
Iotrochota cf. *coccinea*	SE (ME, SS, NS)
Xestospongia bergquistia	SE (ME, SS, NS)
Neopetrosia exigua	ME, NS (SE)
Xestospongia testudinaria	SE (ME, SS, NS)
Corals	
Acropora abrolhosensis	ME, SS, NS (SE)
Acropora caroliniana	SS (ME), SE (SS, NS)
Acropora cerealis	NS (SE)
Acropora granulosa	SS (ME), SE (NS)
Acropora humilis	ME, SS (SE)
Acropora hyacinthus	SS (NS, SE)
Acropora microphthalma	ME, SS, NS (SE)
Acropora muricata	SS (SE)
Acropora nasuta	ME, SS (SE)
Acropora spicifera	SS (NS, SE)
Acropora tenuis	ME, SS (NS, SE)
Astreopora cucullata	NS (ME, SE)
Astreopora gracilis	SS, SE (ME)
Astreopora listeri	SE (ME, SS, NS)
Australomussa rowleyensis	SE (ME, SS)
Echinophyllia aspera	SE (ME, SS)
Echinophyllia echinata	SE (ME, SS, NS)
Echinopora horrida	SS (ME, NS, SE)
Echinopora lamellosa	ME, SS, NS (SE)
Echinopora mammiformis	SE (ME, NS)
Corals continued	
Favia helianthoides	NS (SS, SE)
Fungia fungites	NS (SE)
Fungia horrida	ME, NS (SE)
Goniastrea retiformis	ME, SS (SE)
Heliofungia actiniformis	SE (ME, SS, NS)
Isopora brueggemanni	ME (SE)
Lithophyllon mokai	SE (ME, SS)
Lithophyllon undulatum	SS, NS, SE (ME)
Merulina scabricula	NS (SE)
Montastrea curta	SS (ME, NS, SE)
Montipora incrassata	SE (ME, NS)
Montipora informis	SE (ME)
Montipora tuberculosa	SS (SE)
Montipora turgescens	SE (ME, NS)
Mycedium elephantotus	SS (ME, SE)
Oulophyllia bennettae	SE (SS, NS)
Pachyseris rugosa	SE (ME)
Pachyseris speciosa	SS (SE), NS (ME, SE)
Pavona varians	ME, SS (SE)
Physogyra lichtensteini	ME, NS, SE (SS)
Platygyra lamellina	SE (ME, SS, NS)
Pocillopora verrucosa	SS (ME, NS, SE)
Podabacia crustacea	NS, SE (ME, SS)
Porites lobata	SS, NS (SE)
Porites monticulosa	SE (ME, SS)
Sandalolitha robusta	SS, NS, SE (ME)
Seriatopora hystrix	ME, SS, NS (SE)
Stylophora pistillata	ME, SS (NS, SE)
Symphyllia recta	SE (ME, SS, NS)
Turbinaria frondens	SE (ME, SS)
Crustaceans	
Calcinus lineapropodus	NS (SE)
Calcinus minutus	SS (ME, SE)
Chlorodiella ? cytherea	ME (NS, SE)
Chlorodiella ? laevissima	SE (ME, SS)
Gaillardiellus sp. 1	SE (ME, SS)
Hapalocarcinus marsupialis	NS, SE (ME)
Pilodius pilumnoides	SE (ME, SS, NS)
Pilodius sp. 1	SS (ME, NS, SE)
Pilumnid sp. 3	SE (ME, SS, NS)
Tetralia fulva	SS (ME, SE)
Tetralia sp. 1	SS (SE), NS (ME, SE)
Tiarinia ? cornigera	SS (NS, SE)
Trapezia guttata	NS, SE (ME)
Trapezia septata	SS (ME, NS, SE)

Table A3 continued over

Table A3 (cont.)

Species	T (D)	Species	T (D)
Molluscs		Fishes continued	
Arca avellana/ventricosa	ME, SS, NS (SE)	*Chaetodon trifascialis*	ME (SE)
Barbatia aff. *coma*	NS (ME, SS, SE)	*Cheilodipterus artus*	SE (ME, SS)
Beguina semiorbiculata	SS, NS, SE (ME)	*Cheilodipterus macrodon*	SE (ME, NS)
Conus capitaneus	SE (ME, SS)	*Chromis xanthura*	SS (ME, NS, SE)
Conus miles	SS (ME, SE)	*Chrysiptera rex*	SS, NS, SE (ME)
Conus musicus	SS (ME, SE)	*Coris batuensis*	SE (ME)
Cypraea erosa	NS (ME, SS, SE)	*Cryptocentrus caeruleomaculatus*	SE (ME, SS, NS)
Drupella cornus	ME, SS, NS (SE)	*Cryptocentrus fasciatus*	SE (ME, SS, NS)
Isognomon isognomum	SE (ME, SS, NS)	*Ctenogobiops feroculus*	SE (ME, SS, NS)
Morula spinosa	SE (ME)	*Dascyllus reticulatus*	SS (ME, SE)
Octopus cyaneus	SE (SS, NS)	*Dascyllus trimaculatus*	SS (ME, NS, SE)
Phyllidiella pustulosa	SE (ME, SS)	*Dischistodus perspicillatus*	ME (SS, SE)
Pyrene deshayesii	SE (ME, SS, NS)	*Ecsenius schroederi*	SE (ME, SS, NS)
Septifer bilocularis	NS, SE (ME)	*Epinephelus maculatus*	SE (ME, SS, NS)
Streptopinna saccata	SS (ME)	*Epinephelus ongus*	SE (ME, SS)
Tridacna derasa	ME (SS, NS)	*Epinephelus polyphekadion*	ME (SS, SE)
Vasum turbinellum	NS (ME, SS, SE)	*Eviota prasites*	SE (ME, SS, NS)
Echinoderms		*Gnatholepis anjerensis*	SE (ME, SS, NS)
Bohadschia argus	ME (SS, SE)	*Gomphosus varius*	ME, NS (SS, SE)
Echinaster luzonicus	SE (NS)	*Halichoeres melanurus*	SS, NS, SE (ME)
Eucidaris metularia	SE (ME)	*Halichoeres prosopeion*	SE (ME, SS, NS)
Holothuria (Halodeima) atra	ME (SE)	*Halichoeres trimaculatus*	ME, SE (SS)
Holothuria (Halodeima) edulis	ME, SS (SE)	*Heniochus chrysostomus*	SS (ME, SE)
Nardoa tuberculata	SE (ME, SS, NS)	*Labrichthys unilineatus*	ME, SS (NS, SE)
Ophiactis savignyi	SE (ME, SS)	*Lethrinus erythropterus*	SS, NS, SE (ME)
Pearsonothuria graeffei	ME (SE)	*Lutjanus decussatus*	SS, NS (ME)
Fishes		*Lutjanus gibbus*	NS, SE (ME)
Acanthurus nigricans	SS (ME, NS, SE)	*Monotaxis grandoculis*	ME, SS, NS (SE)
Acanthurus nigricauda	SS (ME), SE (SS, NS)	*Plectroglyphidodon lacrymatus*	SS, NS (ME, SE)
Aethaloperca rogaa	SS, NS, SE (ME)	*Plectropomus areolatus*	NS, SE (SS)
Amblygobius decussatus	SE (ME, SS, NS)	*Pomacentrus adelus*	ME, SS (SE)
Amblygobius nocturnus	SE (ME, SS)	*Pomacentrus amboinensis*	NS, SE (ME, SS)
Amblygobius phalaena	ME (SS, NS, SE)	*Pomacentrus lepidogenys*	SS, NS (ME, SE)
Amblygobius rainfordi	NS (ME)	*Pomacentrus vaiuli*	ME, SS, NS (SE)
Aprion virescens	SE (ME, SS, NS)	*Pseudocheilinus evanidus*	NS, SE (ME)
Archamia fucata	SE (ME, SS, NS)	*Pseudocheilinus hexataenia*	ME, SS (SE)
Atrosalarias fuscus	SE (ME, SS, NS)	*Pseudocheilinus octotaenia*	NS (ME, SS, SE)
Balistapus undulatus	ME, SS (SE)	*Pterocaesio pisang*	SE (ME, SS, NS)
Caesio teres	SS, SE (ME, NS)	*Pygoplites diacanthus*	NS, SE (ME)
Caranx melampygus	SE (ME, SS, NS)	*Sargocentron spiniferum*	ME, NS (SE)
Centropyge bicolor	SS, NS (ME, SE)	*Scolopsis affinis*	SE (ME, SS, NS)
Centropyge eibli	ME (SS, NS, SE)	*Siganus punctatissimus*	SE (ME, SS)
Centropyge tibicen	SE (ME, SS, NS)	*Stegastes nigricans*	ME, NS (SS, SE)
Centropyge vrolikii	SS, SE (ME)	*Synodus binotatus*	SE (ME, SS)
Cephalopholis miniata	SS (ME, SE)		