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CHARACTERIZATION OF THE CORAL COMMUNITIES AT PALMYRA ATOLL IN THE REMOTE CENTRAL PACIFIC OCEAN

BY

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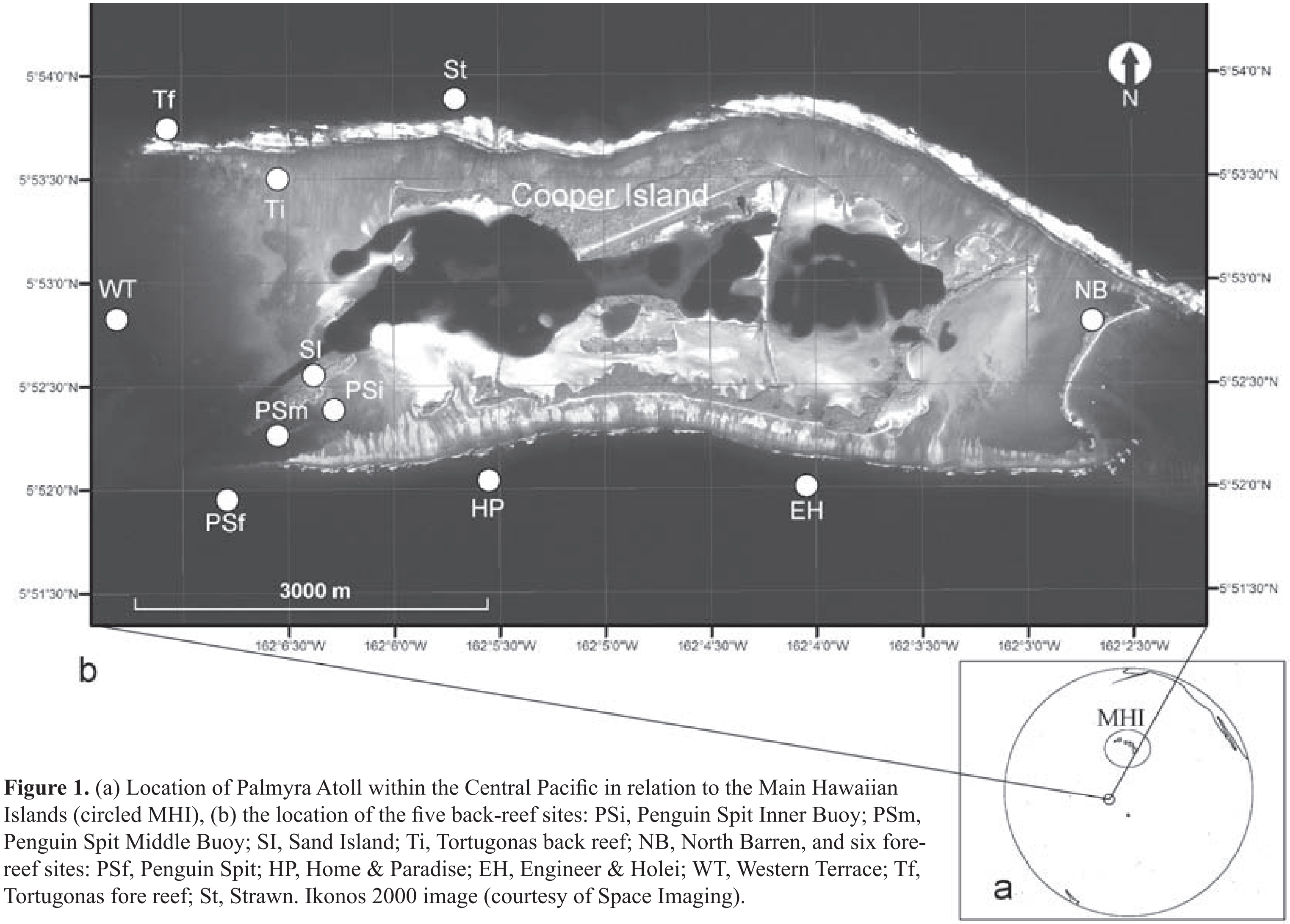

Figure 1. (a) Location of Palmyra Atoll within the Central Pacific in relation to the Main Hawaiian Islands (circled MHI), (b) the location of the five back-reef sites: PSi, Penguin Spit Inner Buoy; PSm, Penguin Spit Middle Buoy; SI, Sand Island; Ti, Tortugonas back reef; NB, North Barren, and six fore-reef sites: PSf, Penguin Spit; HP, Home & Paradise; EH, Engineer & Holei; WT, Western Terrace; Tf, Tortugonas fore reef; St, Strawn. Ikonos 2000 image (courtesy of Space Imaging).

CHARACTERIZATION OF THE CORAL COMMUNITIES AT PALMYRA ATOLL IN THE REMOTE CENTRAL PACIFIC OCEAN

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GARETH J. WILLIAMS,[1] JAMES E. MARAGOS,[2] AND SIMON K. DAVY[1*]

ABSTRACT

Detecting spatial differences between ecological communities is central for establishing baselines, future monitoring and ecosystem management. In remote locations field survey time is often limited but should be balanced with suitable survey effort. Adequate baselines of coral community structure are essential in order to monitor the effects of any environmental changes. Palmyra Atoll is a U.S. National Wildlife Refuge and an important ecosystem for conservation and compatible scientific investigation. WWII military construction impacted the atoll, and lagoon restoration has been proposed to facilitate reef recovery. A total of 84 coral species/morphological groups representing 31 genera were recorded during 2007 surveys at Palmyra. Significant differences in relative coral community structure were detected between reef types (back reef, fore reef) and among individual sites (5 back reef, 6 fore reef) around the atoll. Depth differences between the sites significantly explained 34.1% of the variation in coral community distribution.

The back reef was characterized by corals within the genera *Montipora*, *Astreopora* and *Acropora*, whereas the fore reef was characterised by *Pocillopora*, *Hydnophora*, *Leptoseris*, *Gardineroseris*, *Fungia*, *Favites* and *Favia*. A core of 36 species/morphological groups was found to be best discriminator between the 11 sites. The ability to detect among-site community differences was only compromised at the species presence/absence resolution for transect sizes of 10-30 m^2. Further monitoring and measuring of additional spatial and environmental variables at comparable levels would allow creation of an explanatory model for coral distribution at Palmyra and serve as a valuable management tool for predicting community changes in response to natural and proposed physical changes.

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INTRODUCTION

The world's coral reefs are in severe decline (Pandolfi et al., 2003; Bellwood et al., 2004; Mumby et al., 2007). The need for continued assessment and monitoring of coral communities has been acknowledged (Cleary et al., 2006), especially in light of more recently recognized threats to reef health such as coral bleaching (McWilliams et al., 2005) and disease (Weil et al., 2006). The ability to detect differences between species assemblages is central to the process of comprehensive monitoring, especially in documenting changes over time and supporting proposed efforts to restore reefs. Detailed documentations of coral distributions have been conducted in the past, but often presenting either a descriptive report or a univariate approach to any analysis (Goreau, 1959; Glynn, 1976; Dustan and Halas, 1987). More recently, a multivariate approach to community analysis has become common practice to look at many aspects relating to coral diversity and distribution (DeVantier et al., 1998; Karlson and Cornell, 1998; De'ath, 2002; Berumen and Pratchett, 2006; Cleary et al., 2006; DeVantier et al., 2006; Done et al., 2007; Smith et al., 2008). When assessing for change in coral communities, detailed information on community structure is required and simply measuring and tracking coral cover over time can mask more subtle changes in individual species abundances (Gardner et al., 2003) and size/age structure of coral populations. The detail of the information collected during surveys, for example taxonomic resolution, also can affect the ability to detect significant differences between assemblages (van Woesik and Done, 1997).

Efficient and successful monitoring therefore requires both a sound investigative and analytical methodology for quantifying relative species and population distributions, thus creating a baseline with which to compare and assess for change over time. A subsequent need is then the characterization of any differences found between any *a priori* defined factor(s) in the investigation. This can be achieved through the identification of indicator species, a process which gives ecological meaning to the results (Dufrêne and Legendre, 1997). Over time, changes in the abundance of indicator species and their contribution to driving differences among *a priori* defined factor(s) can also be monitored. Although the detection of differences between communities is a key component for successful monitoring, the point at which differences cannot be detected could possibly be more useful to management, as this can help to alter survey design to make optimal use of time and effort.

Palmyra Atoll is a U.S. National Wildlife Refuge (NWR) and represents an important marine ecosystem for both conservation and science. Throughout its history, Palmyra has lacked an indigenous population and there have rarely been more than 20 human residents at one time, with the exception of during the WWII era when the atoll was modified to serve as a U.S. military base. Modifications included land reclamation, the building of an airstrip and the dredging of an eight meter deep channel to allow ship access into the lagoon (Dawson, 1959). The need for monitoring and modelling of these reefs has been recently emphasised by a proposal to enhance lagoon circulation to promote coral and reef recovery (Maragos et al., 2008a, b). A thorough characterization of the reefs around the atoll is needed in order that changes to coral community compositions can be predicted accurately via models before modifications and detected and managed effectively after modifications via long-term monitoring. In addition to the restoration proposal, coral disease has been discovered in the area (Williams et al., 2008a), a threat that has the potential to severely alter coral community structures (Aronson and Precht, 2001). In a wider context, due to its location and lack of present-day direct anthropogenic impacts, Palmyra represents an important baseline for coral communities in the remote Central Pacific (Sandin et al., 2008). Quantitative descriptions of remote coral assemblages are important for providing information for large-scale meta-analyses that allow population decline trajectories (e.g. Gardner et al., 2003), or species susceptibilities to extinction (e.g. McClanahan et al., 2007), to be quantified over wide areas. This is the first study to conduct a detailed multivariate analysis of the coral communities of Palmyra Atoll, and indeed in the remote Central Pacific, and hence it offers valuable baseline data for the future management of these sites.

The main aims of the present mensurative investigation were to 1) quantitatively characterize the coral communities of Palmyra Atoll by identifying indicator species in order to create a baseline for the Refuge prior to management restoration 2) examine the effects of sampling effort and taxonomic resolution (recording to species, genus, or presence/absence of species) on the ability to detect spatial differences in community structure, in order to refine survey methods for future studies, and 3) outline a succession of analytical procedures for effectively characterizing species assemblages that can be implemented for the successful management and restoration of Palmyra Atoll NWR, as well as other reefs around the world.

METHODS

Study Site

Surveys took place at Palmyra Atoll (05°52'N, 162°06'W) in the remote Central Pacific over a six-week period during the summer months of June - July 2007 (Fig. 1). Previously substantial univariate data on coral species and distributions at Palmyra have been collected by JEM and others at Palmyra from 1987-2005 (Table 1) that helped in the qualitative characterization of habitats and abundance and distribution of corals at Palmyra. The atoll lies approximately 1,930 km south of the main Hawaiian Islands and is third from the north end of the Line Islands group. The atoll was designated a U.S. National Wildlife Refuge in 2001 and is now owned by U.S. Fish and Wildlife except for the main island (Cooper) which is owned by The Nature Conservancy. The coral reefs surrounding the atoll cover an area of approximately 6,000 ha.

Coral Community Surveys

Eleven sites (5 back reef and 6 fore reef) were surveyed around the atoll (Fig. 1). Sites were chosen on the basis of accessibility and the need for a representative spread around the atoll. A minimum of five belt transects (25 x 2 m) were randomly placed along depth contours at each site, creating a total of 58 transects covering 2900 m^2 around the atoll. Depth regimes surveyed were 1 - 4 m at the back-reef sites and 12 - 14 m at the fore-reef sites. Every coral colony whose center fell within 1 m either side of the belt transect line was counted and identified, where possible, to species level. Identification to species was not possible for massive *Porites* species or *Montipora* species. Massive *Porites* species were therefore grouped together, and the *Montipora* species were placed into the 12 morphological groups defined by Veron (2000). Within the back-reef sites, coral abundances (expressed as number of colonies per m^2) were recorded in five-meter intervals along each transect line in order to examine the effect of sampling effort on the ability to detect significant differences among assemblages. Sampling was conducted by a single observer (GJW) and randomized in time over the survey period.

Statistical Analyses

To assess sampling effectiveness, true species-accumulation was plotted against three nonparametric-permuted extrapolators: Chao 1 and Chao 2 (Chao 1984), and Bootstrap (Smith and van Belle, 1984). These extrapolators attempt to predict the true total number of species that would be observed as the number of samples (e.g. 50 m^2 sites) tends to infinity, assuming that a closed community is being successively sampled (Clarke and Gorley, 2006). Indices used to assess site diversity were total number of species (S), Hill numbers N1 and N2 (to assess the influence of rare and dominant species on community diversity respectively), and the modified Hill's ratio (N21′) (see Clarke and Gorley, 2006 for a summary of each index). The modified Hill's ratio was used as a measure of equitability (spread between taxa) as it has an advantage over traditional measures of evenness by its nondependency on the number of species (Rogers et al., 1999).

Multivariate analyses were carried out to examine for differences in coral community structure at two defined factor levels: reef area (back reef versus fore reef) and at the individual site level. Prior to multivariate analyses, coral count data were subjected to a dispersion-weighting pretreatment in which the abundances of the different species were weighted differentially on the basis of their observed variability between replicate samples (Clarke et al., 2006a). Tests were based on 1,000 random permutations. This was considered an appropriate transformation as some of the species displayed a degree of spatial clumping and local clustering of conspecifics can significantly reduce the similarity between sampled subregions (Plotkin and Muller-Landau, 2002). Similarity matrices were based on zero-adjusted Bray-Curtis coefficients to account for the denuded nature of some sites (Clarke et al. 2006b). Unconstrained nonmetric multidimensional scaling (nMDS), constrained canonical analysis of principal coordinates (CAP) (Anderson and Willis, 2003; Anderson, 2004), and analysis of similarities (ANOSIM) (Clarke, 1993) were used to graphically display and statistically test coral assemblage structure between reef areas and among sites. The use of both unconstrained and constrained ordination techniques in tandem is a useful approach when examining for differences among species assemblages (Anderson, 2004; Williams et al., 2008b). ANOSIM was used to determine where any significant differences lay at the site level.

ANOSIM and CAP analyses were carried out using 999 random permutations. The leave-one-out procedure of the CAP analysis allowed "allocation success" to be calculated (Anderson and Robinson, 2003).

Allocation success (expressed as a percentage) gives a measure of how distinct an assemblage is relative to another assemblage(s). Allocation success was considered indicative of a more distinct assemblage type than expected by chance alone when values exceeded 50% and 9.09% for testing between reef areas and among sites, respectively. These threshold percentages came from the possibility of each individual observation being allocated to two possible groups at the reef area level (i.e., 50% chance of being placed in the back reef or fore reef group), and 11 possible groups at the site level (i.e., 9.09% chance of being placed into one of the 11 individual sites). Individual species that might be responsible for any group differences in the CAP plot were investigated by calculating product-moment correlations of canonical ordination axes with the original species variables (Anderson et al., 2004; Terlizzi et al., 2007). Species with strong correlations (defined as ≥ 0.4 in this study) were then graphically displayed as a bi-plot.

To start building an explanatory model of coral distribution at Palmyra Atoll, the relationship between the multivariate species data and depth was analysed using nonparametric multivariate regression (McArdle and Anderson, 2001) with the programme DISTLM*forward* (Anderson, 2003). This allowed the proportion of variation in the biological matrix explained by variations in depth between sites to be quantified. The variable "depth" actually consisted of the mean, standard deviation and minimum and maximum values for each transect grouped as one single variable in the model (e.g., Williams et al., 2008b).

EARLIER INFORMATION ON CORAL SPECIES AND DISTRIBUTION

Approximately 186 coral and cnidaria species within seven definable habitats have been reported at 50 Palmyra Atoll sites since 1987 (Table 1). In terms of magnitude, the most abundant habitats for corals are the northern and southern fore reefs and the western and eastern reef terraces. Although there are extensive lagoon and back-reef areas at the atoll, WWII military construction destroyed lagoon coral communities that have failed to recover in the subsequent 70 years (Dawson, 1959; Maragos, 1993; Maragos et al., 2008a, b). Hence, only a few coral surveys to date have covered these habitats. The most accessible habitats have been northern and southern fore reefs, and to a lesser extent, the western terrace. WWII era construction included a dredged ship channel that served as new habitat for corals, and several channel sites were surveyed for corals. An eighth habitat, the eastern reef terrace has been virtually inaccessible because of prevailing heavy surf, onshore winds, and strong currents. Table 1 provides summaries of the number of species and genera reported through to 2006 at the seven accessible habitats.

In decending order, *Acropora, Montipora, Porites, Pocillopora, Fungia, Favia, Favites, Pavona, Leptastrea, Platygyra* and *Psammocora,* account for the most species, and these 11 genera (out of a total of 51) account for 130 species (out of a total of 186).

Because of greater sampling effort, most species have been reported off the southern fore reef (155 species at 19 sites), northern fore reef (121 species at 13 sites), and the western reef terrace (93 species at 7 sites). Despite surveys at only two eastern back-reef sites (the north-eastern and south-eastern "coral gardens"), 74 species and 20 genera have already been reported there. In contrast, only 25 species and 13 genera have been reported off two western back-reef sites, and these lower numbers have been attributed to a possible bleaching event in the late 1990s, the effects of which may have been exacerbated by the residual effects of earlier military construction (Maragos et al., 2008b). Except for a few western back-reef areas outside the lagoon, all other fore-reef and back-reef habitats appear to be healthy at the present time, although south eastern back reefs may now also be threatened by the residual effects of WWII military construction (Maragos et al., 2008b).

RESULTS OF 2007 SURVEYS

Coral Community Structure

A total of 84 coral species/morphological groups representing 31 genera were recorded during the survey (Table 2). The most diverse genus was *Acropora*, with 20 species recorded. Other diverse genera included *Pavona*, *Fungia*, *Favites*, and *Pocillopora*. Of the 12 morphological *Montipora* groups defined by Veron (2000), groups two-four and six-eight inclusive were recorded at the atoll (Table 3). Although *Porites* was a very abundant genus at Palmyra, it was difficult to distinguish to either species or ecomorph in the field and therefore this genus may also be diverse. The rate of novel species encounter, with increased replication across the atoll as a whole, did not reach a true asymptote (Fig. 2). However, the rate slowed considerably beyond approximately 20 replicate transects (50 m^2 each), and only eight and three novel species were encountered for the last 1000 m^2 and 350 m^2 surveyed, respectively. All three extrapolator coefficients estimated that a higher number of species could exist within the survey area as the number of samples tends to infinity, with Chao 2 predicting the highest total of 103 species (Fig. 2). Total number of species observed was generally higher within the fore reef compared to the back reef (Fig. 3).

Among the back-reef sites, Penguin Spit Middle Buoy (southwest) had the highest number of species present (S = 29), and Sand Island (southwest) the lowest (S = 7). Among the fore-reef sites, Tortugonas (northwest) had the highest number of species present (S = 34), and Western Terrace (west fore reef) the lowest (S = 24) (Fig. 3). Hill number diversity followed a similar pattern for both N1 and N2 among sites (Fig. 3). Within the back reef, both indices showed diversity to be highest at Tortugonas (north back reef) and Penguin Spit Middle Buoy, and lowest at Sand Island. Among fore-reef sites, Strawn (north shore) and Penguin Spit (southwest) had higher Hill number diversity than all other fore-reef sites (Fig. 3). Evenness was highest at Sand Island and lowest at Penguin Spit Inner Buoy (southwest) among the back-reef sites. Among fore-reef sites, evenness was highest at Strawn and lowest at Tortugonas.

Table 1. Number of coral and other cnidarian species per genus per habitat reported at Palmyra Atoll from 1987-2005. Taxa: Alcyonaria[1], Actiniaria[2], Corallimorpharia[3], Hydrozoa[4], Zoanthidea[5], and Scleractinia (the remainder). S fr, south fore reef; N fr, north fore reef; E br, east back reef and pools; W br, west back reef; W t, west terrace; D ch, dredged channel; L, lagoon.

Habitat	S fr	N fr	E br	W br	W t	D ch	L	Totals / genus
Number of sites	19	13	2	2	7	5	2	
Acropora	31	18	23	7	11	13	1	41
Alveopora	1	1		1				1
Astreopora	3	4	2	1	1			4
Cladiella[1]	1	1						1
Cladopsammia	1							1
Cryptodendrum[2]	1							1
Ctenactis	1							1
Cycloseris	2	1			1			2
Cyphastrea						1		1
Discosoma[3]		1				1		1
Distichopora[4]	1	1			1			1
Echinophyllia	2	1						2
Favia	7	7	3	2	3	2	1	8
Favites	8	6			5	2	1	8
Fungia	9	7	4	4	7	2		9
Gardineroseris	1	1			1			1
Goniastrea	2	1	1			1		3
Gymnangium[4]	1							1
Halomitra	1	1	1		1			1
Herpolitha	1	1	1		1			1
Heteractis[2]	1							1
Hydnophora	3	2	1		2	1		3
Leptastrea	7	5	2		1			7
Leptoseris	1	1	1		1			1
Lobophyllia	2	2		1	1	1		2
Lobophytum[1]	1	1	1		1			1
Millepora[4]		1						1
Merulina	1	1						1
Montastrea	2	3	1	1	2	1		3
Montipora	17	12	12	2	13	3	1	20
Pachyclavularia[1]		1				1		1
Pachyseris	1							1
Palythoa[5]	2	2			2			2
Pavona	7	6	4	2	5	3		7
Platygyra	5	3	1		3			5
Plesiastrea						1		1
Pocillopora	6	7	5	1	7	3	2	8
Porites	9	7	7	1	6	5	3	11
Psammocora	4	4	2		4			6
Rhodactis[3]	1	1			1			1
Sandalolitha	1	1	1		2			1
Sarcophyton[1]	1	1		1	3			1
Sinularia[1]	1	1		1		1		1
Stereonephthya[1]	1				1			1
Stichodactyla[2]	1							1
Stylaster[4]	1				1			1
Stylophora	1	1			1	1		1
Subergorgia[1]	1							1
Symphyllia		1			1			1
Tubastraea		1			1	1	1	1
Turbinaria	3	4	1		2	1		4
Total species / habitat	155	121	74	25	93	45	10	186
Total genus / habitat	44	39	20	13	32	20	7	51

Table 2. Scleractinian corals, soft corals, hydrozoan corals, and miscellaneous Anthozoa found during 58 belt transects (2 x 25 m) at five back-reef and six fore-reef sites at Palmyra Atoll, Central Pacific, *Montipora* groups as defined by Veron (2000).

SCLERACTINIAN CORALS
Acropora acuminata
Acropora cerealis
Acropora cf. *cerealis*
Acropora clathrata
Acropora cytherea
Acropora elseyi
Acropora formosa
Acropora gemmifera
Acropora glauca
Acropora globiceps
Acropora hyacinthus
Acropora latistella
Acropora nana
Acropora nasuta
Acropora nobilis
Acropora cf. *palmerae*
Acropora robusta
Acropora spicifera
Acropora subulata
Acropora valida
Astreopora gracilis
*Astreopora myriophthalm*a
Astreopora suggesta
Cycloseris cyclolites
Echinophyllia sp
Favia matthaii
Favia pallida
Favia stelligera
Favites abdita
Favites flexuosa
Favites halicora
Favites pentagona
Favites russelli
Fungia concinna
Fungia fungites
Fungia granulosa
Fungia paumotensis
Fungia repanda
Fungia scutaria
Gardineroseris planulata
Goniastrea pectinata
Halomitra pileus
Herpolitha limax
Hydnophora exesa
Hydnophora microconos
Hydnophora pilosa
Leptastrea pruinosa
Leptastrea cf. *pruinosa*
Leptastrea purpurea
Leptoseris mycetoseroides
Leptoseris scabra
Lobophyllia corymbosa
Merulina ampliata
Montastrea annuligera
Montastrea curta
Montipora group 2
Montipora group 3
Montipora group 4
Montipora group 6
Montipora group 7
Montipora group 8
Pavona chiriquiensis
Pavona clavus
Pavona cf. *duerdeni*
Pavona explanulata
Pavona maldivensis
Pavona varians
Platygyra sp
Pocillopora damicornis
Pocillopora eydouxi
Pocillopora meandrina
Pocillopora verrucosa
Porites spp (massive)
Porites superfusa
Psammocora haimeana
Psammocora nierstraszi
Stylophora pistillata
Turbinaria reniformis

SOFT CORALS
Lobophytum sp
Sarcophyton sp
Sinularia sp
Stereonephthya sp

HYDROZOAN CORALS
Millepora platyphylla
Stylaster elegans

Miscellaneous ANTHOZOA
Palythoa tuberculosa (Zoanthidea)
Rhodactis howesii (Corallimorpharia)

Relative coral community composition was significantly different between reef areas (ANOSIM, R = 0.829, P = <0.001) and among sites (ANOSIM, R = 0.887, P = <0.001, Fig. 4a, b). The CAP analysis confirmed this pattern between reef areas (CAP, $\delta^2 = 0.932$, P = <0.001) and among sites (CAP, $\delta^2 = 0.985$, P = <0.001, Fig. 4c, d), thus showing the significant effect of reef area and site on the maximum variability calculated by the unconstrained ordination. ANOSIM found relative coral community composition to differ between all sites ($P \leq 0.01$ for all pairwise comparisons), with the exception of the two fore-reef sites along the south coast of the atoll (ANOSIM, R = 0.184, P = 0.108). Allocation success confirmed the highly distinct nature of the coral assemblages at the reef-area and individual-site levels (Table 4). Mean allocation success equalled 100% for both reef areas, and 89.7% for the 11 individual sites. Each site displayed higher allocation success than expected by chance alone (Table 4). Nonparametric multivariate regression showed differences in depth between sites to explain 34.1% of the variation in coral community distribution (DISTLM*forward*, F = 14.22, P = 0.001).

Indicator Species

Several species were identified as driving separation between reef areas (Fig. 5), and individual sites within the back reef (Fig. 6a) and fore reef (Fig. 6b). The most dramatic abundance changes between reef areas were the high numbers of *Astreopora gracilis* (13 ± 3, mean ± SE per 50 m^2 transect), and *Montipora* groups four and six (14 ± 4 and 19 ± 4, respectively) within the back-reef sites, and the high numbers of *Fungia scutaria*, *Favia stelligera*, *Pocillopora meandrina*, and *Pavona chiriquiensis* within the fore-reef sites (49 ± 12, 15 ± 2, 37 ± 3 and 22 ± 3, respectively) (Fig. 7).

At the site level, the most dramatic changes in species abundances among the back-reef sites were high numbers of *A. gracilis* and the soft coral *Sarcophyton* sp. at Penguin Spit Inner Buoy (41 ± 5 and 9 ± 3, respectively), high numbers of *F. scutaria* at Penguin Spit Middle Buoy (9 ± 3), high numbers of *Leptastrea purpurea*, *Pocillopora damicornis* and *Pocillopora verrucosa* at Sand Island (65 ± 16, 62 ± 13 and 35 ± 8, respectively), and high numbers of *Montipora* groups four and six at North Barren (43 ± 6 and 51 ± 12, respectively) (Fig. 8). Among the southern and northern fore-reef sites, the most dramatic changes in species abundances were high numbers of *Fungia concinna*, *Hydnophora pilosa* and *Lobophyllia* sp. at Penguin Spit (13 ± 6, 6 ± 2 and 13 ± 1, respectively) high numbers of *Montipora* group six and *Pavona* cf. *duerdeni* at Western Terrace (10 ± 2 and 60 ± 11, respectively), and high numbers of *Hydnophora microconos*, *Montastrea curta* and *Sarcophyton* sp. at Strawn (19 ± 4, 29 ± 5 and 25 ± 7, respectively) (Fig. 9).

Table 3. Groups of *Montipora* species found at Palmyra Atoll, remote Central Pacific based on their growth-form and skeletal characters. Adapted from Veron (2000)

Group	Description
2	Laminar species without conspicuous coenosteum ridges
3	Encrusting or massive species with prominent coenosteum tuberculae
4	Encrusting or massive species with prominent thecal papillae
6	Encrusting species with very small corallites
7	Species with funnel-shaped (foveolate) corallites
8	Species with large coenosteum tuberculae forming verrucae

Table 4. (a) Results of CAP analyses examining effects of reef area and site for 84 species/groups of scleractinian corals, soft corals, hydrozoan corals, and miscellaneous Anthozoa at Palmyra Atoll, Central Pacific. (b) Allocation successes of the individual sites. PSi, Penguin Spit Inner Buoy; PSm Penguin Spit Middle Buoy; SI, Sand Island; Ti, Tortugonas back-reef; NB, North Barren; PSf, Penguin Spit; HP, Home & Paradise; EH, Engineer & Holei; WT, Western Terrace; Tf, Tortugonas fore reef; St, Strawn.

(a)

			Allocation Success				
Factor	*m*	%Var	Back-reef	Fore-reef	Total	δ^2	P-value
Reef area	5	96.56	100	100	100	0.932	0.001
Site	7	99.51	-	-	89.66	0.985	0.001

(b)

PSi	PSm	SI	Ti	NB	PSf	HP	EH	WT	Tf	St
100	100	100	100	100	100	40	50	100	100	100

Notes: Analyses based on 999 random permutations. m, the number of principal coordinate (PCO) axes used in the CAP procedure; %Var, percentage of the total variance explained by the first *m* PCO axes; allocation success, the percentage of points correctly allocated into each group; δ^2, squared canonical correlation.

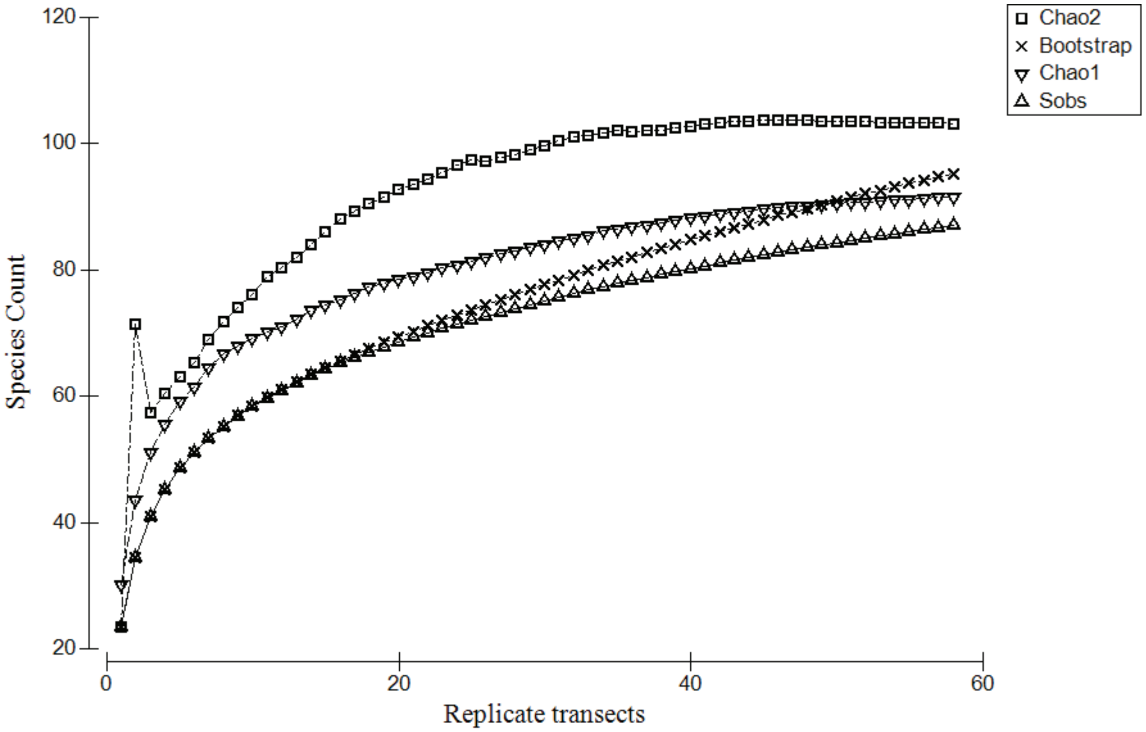

Figure 2. Species-accumulation curve for 58 transects (25 x 2 m) across 11 sites (five back reef and six fore reef) at Palmyra Atoll, Central Pacific and three nonparametric extrapolators: Chao 1, Chao 2 and Bootstrap. Sobs, actual number of species observed.

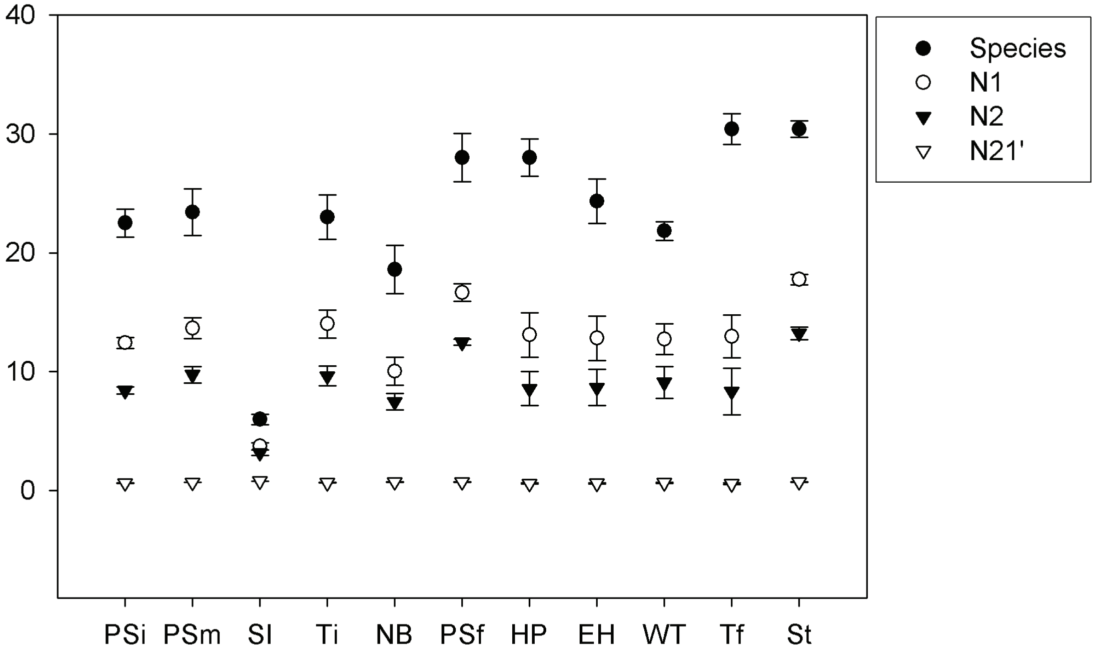

Figure 3. Diversity indices (mean ± SE) of coral species among back-reef and fore-reef sites at Palmyra Atoll, Central Pacific. PSi, Penguin Spit Inner Buoy; PSm, Penguin Spit Middle Buoy; SI, Sand Island; Ti, Tortugonas back-reef; NB, North Barren; PSf, Penguin Spit; HP, Home & Paradise; EH, Engineer & Holei; WT, Western Terrace; Tf, Tortugonas fore reef; St, Strawn.

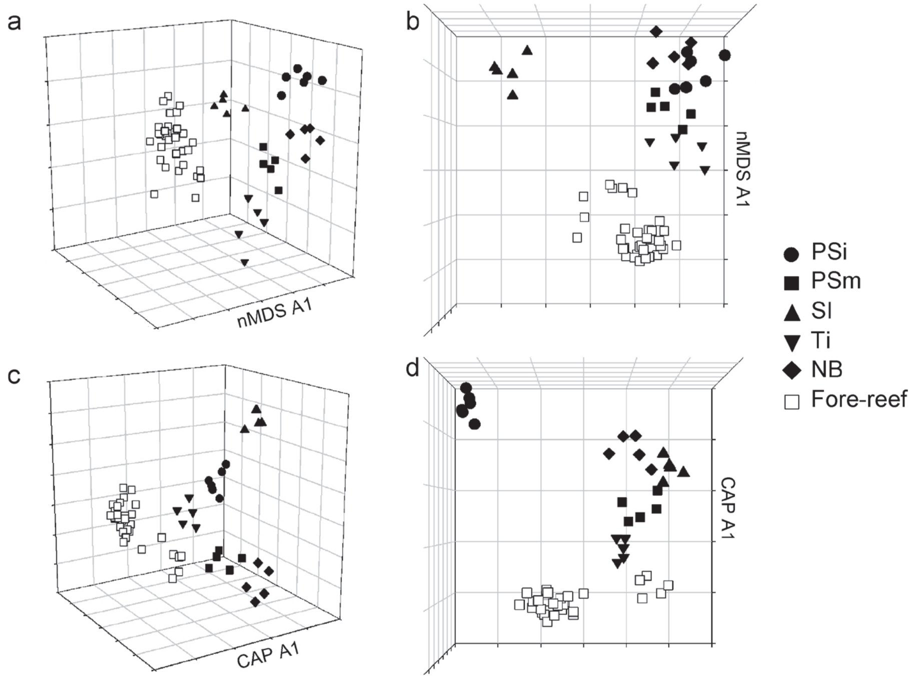

Figure 4. (a, b) Unconstrained nMDS ordination and (c, d) constrained CAP ordination of coral assemblages at Palmyra Atoll, Central Pacific among five back-reef and six fore-reef sites (n = 58). Ordinations based on a zero-adjusted Bray-Curtis coefficient with a dispersion-weighting pretreatment applied to the raw colony count data. The fore-reef sites have not been displayed separately to ease interpretation. Stress value for the nMDS ordination = 0.09. PSi, Penguin Spit Inner Buoy; PSm, Penguin Spit Middle Buoy; SI, Sand Island; Ti, Tortugonas back reef; NB, North Barren.

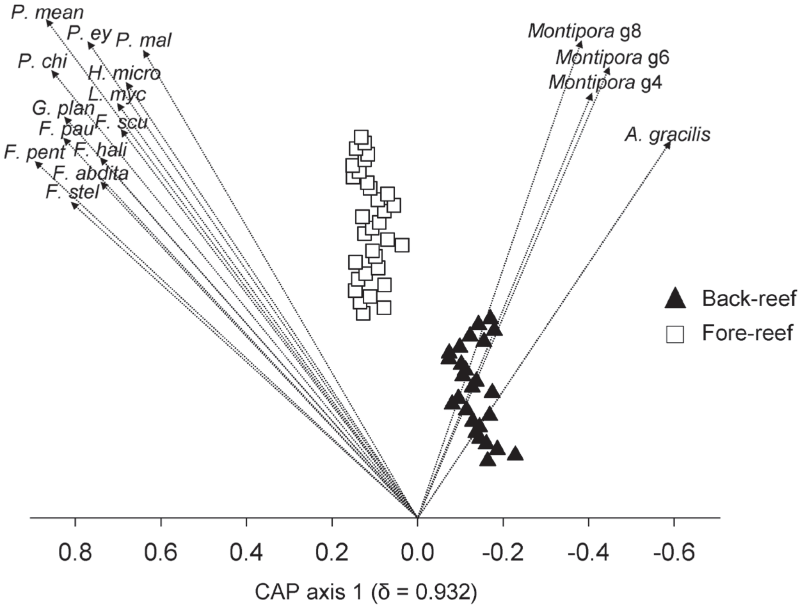

Figure 5. CAP bi-plot showing those coral species most responsible for driving separation between two reef areas (back reef and fore reef) at Palmyra Atoll, Central Pacific. Based on a zero-adjusted Bray-Curtis coefficient with a dispersion-weighting pretreatment applied to the colony raw count data. *F. pau*, *Fungia paumotensis*; *F. pent*, *Favites pentagona*; *F. scu*, *Fungia scutaria*; *F. stel*, *Favia stelligera*; *G. plan*; *Gardineroseris planulata*; *F. hali*, *Favites halicora*; *H. micro*, *Hydnophora microconos*; *L. myc*, *Leptoseris mycetoseroides*; *P. chi*, *Pavona chiriquiensis*; *P. ey*, *Pocillopora eydouxi*; *P. mal*, *Pavona maldivensis*; *P. mean*, *Pocillopora meandrina*.

Sampling Effort and Taxonomic Resolution

Generally, as sampling effort decreased multivariate dispersion increased between replicate transects within the five back-reef sites at all three taxonomic resolutions (Fig. 10). When recording to species or genus, ANOSIM found all sites to differ significantly from each other at all sampling efforts (Table 5). The ability to detect significant differences between sites using ANOSIM was only compromised when recording to a resolution of species presence/absence, and first occurred when sampling effort reached 30 m^2 per transect (Table 5). The inability to detect differences was most apparent at the lowest sampling effort (10 m^2 per transect), where three of the 10 ANOSIM pairwise comparisons were not significant (Table 5). Drops in individual site allocation success generally also occurred with decreasing sampling effort, although all values for all sites were higher than expected by chance alone even at the species presence/absence resolution (Table 5). However, a drop in allocation success with decreasing sampling effort was not universal as two sites, Sand Island and North Barren, retained an allocation success of 100% at all times (Table 6).

DISCUSSION

Coral Communities and Indicator Species

The unprecedented need for effective monitoring of coral-reef environments has become apparent due to their widely acknowledged global decline (Gardner et al., 2003; Hughes et al., 2003; Pandolfi et al., 2003; Bellwood et al., 2004; Mumby et al., 2007). These declines often are associated with a subsequent phase shift from coral-to algal-dominated communities (Bellwood et al., 2004). Palmyra Atoll is a U.S. National Wildlife Refuge and therefore represents an important resource both for species/ecosystem conservation and scientific investigation in the absence of major present-day anthropogenic impacts. This mensurative investigation is the first to carry out detailed multivariate characterization of coral communities at Palmyra Atoll, and additionally within any reef system in the remote Central Pacific.

Palmyra is one of six atolls among the 12 atolls and low reef islands comprising the Line Islands. Together with neighboring Kingman Reef National Wildlife Refuge 60 km to the northwest, Palmyra periodically lies within the path of the eastward moving North Pacific Equatorial Countercurrent (ECC). As such, the two atolls support more species of corals compared to others in the Line and Phoenix Islands, their closest neighbors (1200 km to the southwest). The ECC may be transporting the larvae of additional Western Pacific coral species to both atolls that might not otherwise reach the Central Pacific. In addition, the lack of permanent human occupation throughout their history, their larger habitat areas, greater habitat variety due to the presence of lagoons and their close proximity to neighboring reef islands and atolls in the Line Islands may also contribute to the high species richness of both atolls (Maragos et al., 2008b). Both Palmyra and Kingman also support unusually elongated reef terraces, especially off their

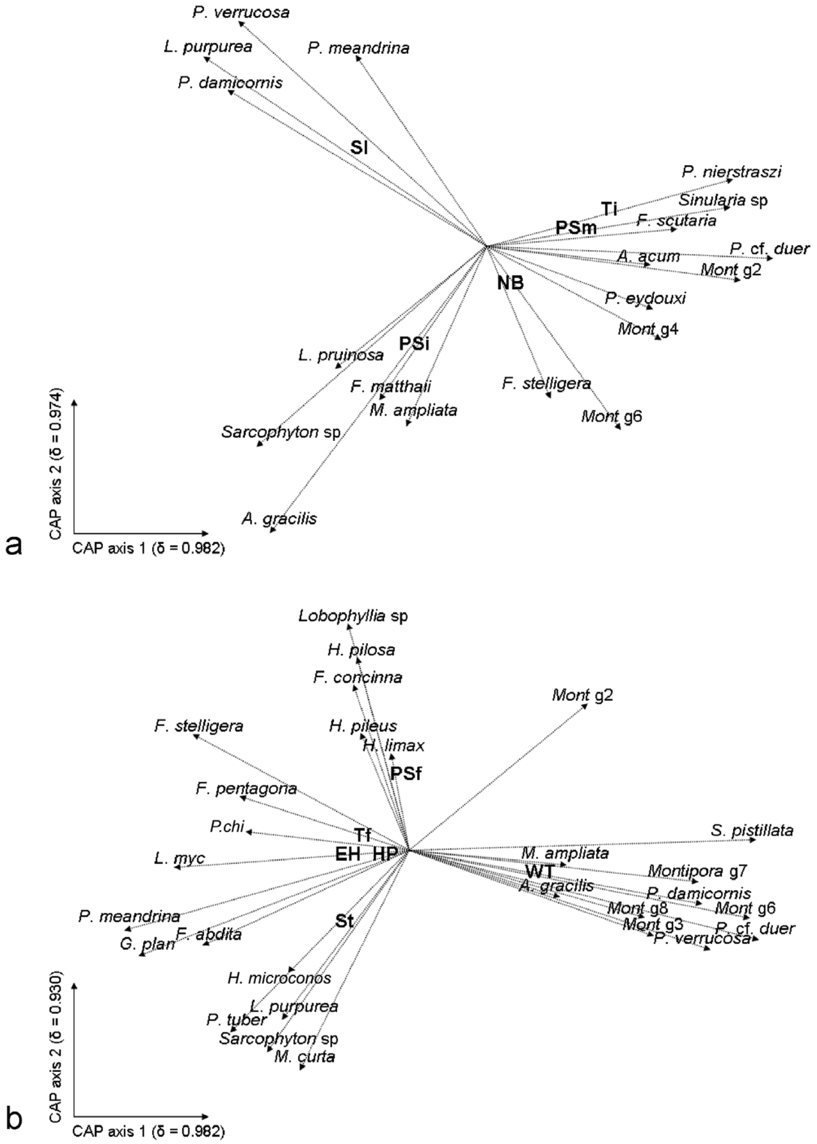

Figure 6. CAP bi-plots showing those species/groups most responsible for driving separation between (a) five back-reef sites and (b) six fore-reef sites at Palmyra Atoll, Central Pacific. Site group centroids are displayed in each case. PSi, Penguin Spit Inner Buoy; PSm, Penguin Spit Middle Buoy; SI, Sand Island; Ti, Tortugonas back-reef; NB, North Barren; PSf, Penguin Spit; HP, Home & Paradise; EH, Engineer & Holei; WT, Western Terrace; Tf, Tortugonas fore reef; St, Strawn. Based on a zero-adjusted Bray-Curtis coefficient with a dispersion-weighting pretreatment applied to the raw colony count data.

A. acum; *Acropora acuminata*; *A. gracilis*, *Astreopora gracilis*; *F. matthaii*, *Favia matthaii*; *F. stelligera*, *Favia stelligera*; *F. abdita*, *Favites abdita*; *F. pentagona*, *Favites pentagona*; *F. concinna*, *Fungia concinna*, *F. scutaria*, *Fungia scutaria*; *G. plan*, *Gardineroseris planulata*; *H. pileus*, *Halomitra pileus*; *H. limax*, *Herpolitha limax*; *H. microconos*, *Hydnophora microconos*; *H. pilosa*, *Hydnophora pilosa*; *L. pruinosa*, *Leptastrea pruinosa*; *L. purpurea*, *Leptastrea purpurea*; *L. myc*, *Leptoseris mycetoseroides*; *M. ampliata*, *Merulina ampliata*; *M. curta*, *Montastrea curta*; *Mont* g2, 3, 4, 6, 7, 8, *Montipora* groups two, three, four, six, seven, eight; *P. tuber*, *Palythoa tuberculosa*; *P. chi*, *Pavona chiriquiensis*; *P.* cf. *duer*, *Pavona* cf. *duerdeni*; *P. damicornis*, *Pocillopora damicornis*; *P. eydouxi*, *Pocillopora eydouxi*; *P. meandrina*, *Pocillopora meandrina*; *P. verrucosa*, *Pocillopora verrucosa*; *P. nierstraszi*, *Psammocora nierstraszi*. *Montipora* groups as defined by Veron (2000).

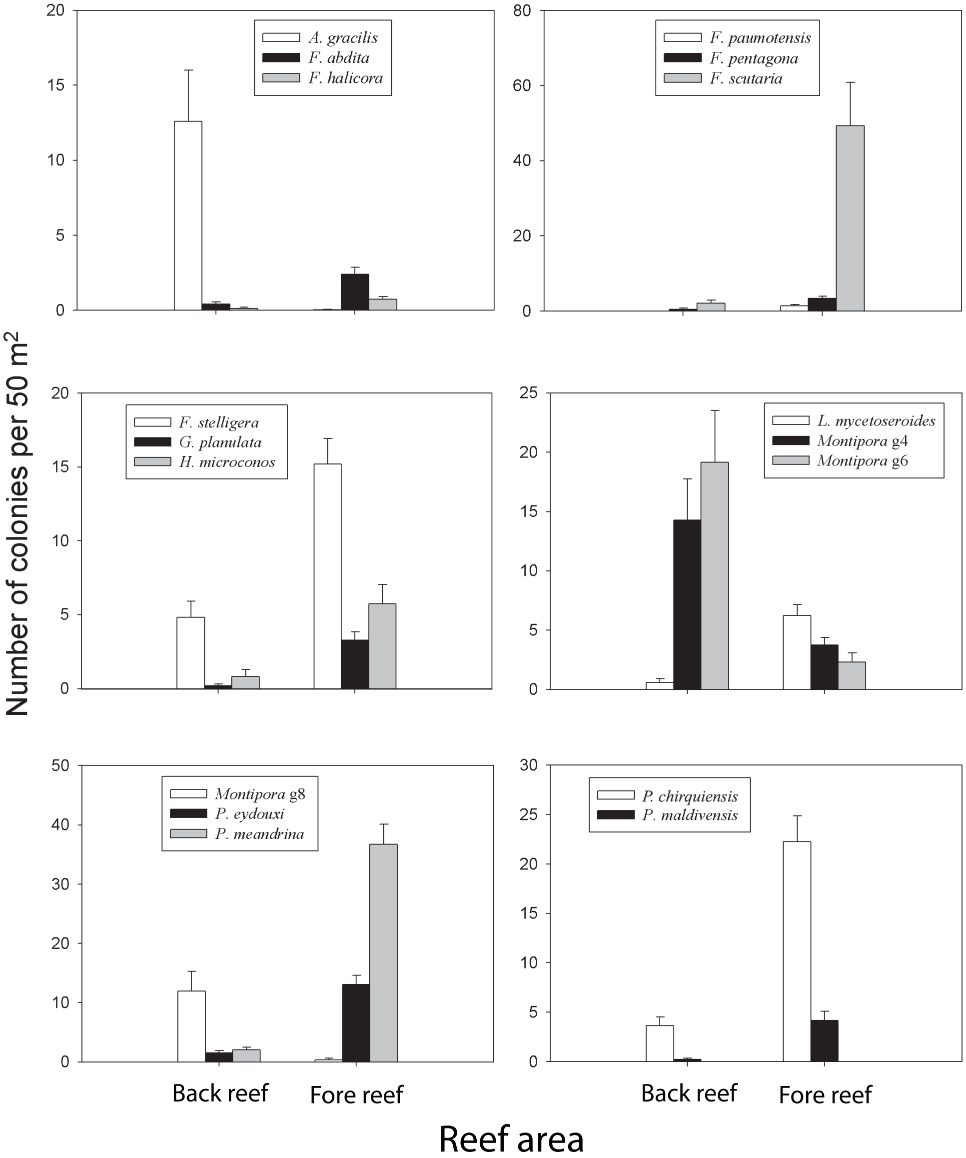

Figure 7. Relative abundances of species/groups responsible for separation between two reef areas (back reef and fore reef) at Palmyra Atoll, Central Pacific. Mean + SE.

A. gracilis, *Astreopora gracilis*; *F. abdita*, *Favites abdita*; *F. halicora*, *Favites halicora*; *F. paumotensis*, *Fungia paumotensis*; *F. pentagona*, *Favites pentagona*; *F. scutaria*, *Fungia scutaria*; *F. stelligera*, *Favia stelligera*; *G. planulata*, *Gardineroseris planulata*; *H. microconos*, *Hydnophora microconos*; *L. mycetoseroides*, *Leptoseris mycetoseroides*; *Montipora* g4, 6, 8, *Montipora* groups four, six, eight; *P. chiriquiensis*, *Pavona* chiriquiensis; *P. eydouxi*, *Pocillopora eydouxi*; *P. meandrina*, *Pocillopora meandrina*; *P. maldivensis*, *Pavona maldivensis*. *Montipora* groups as defined by Veron (2000).

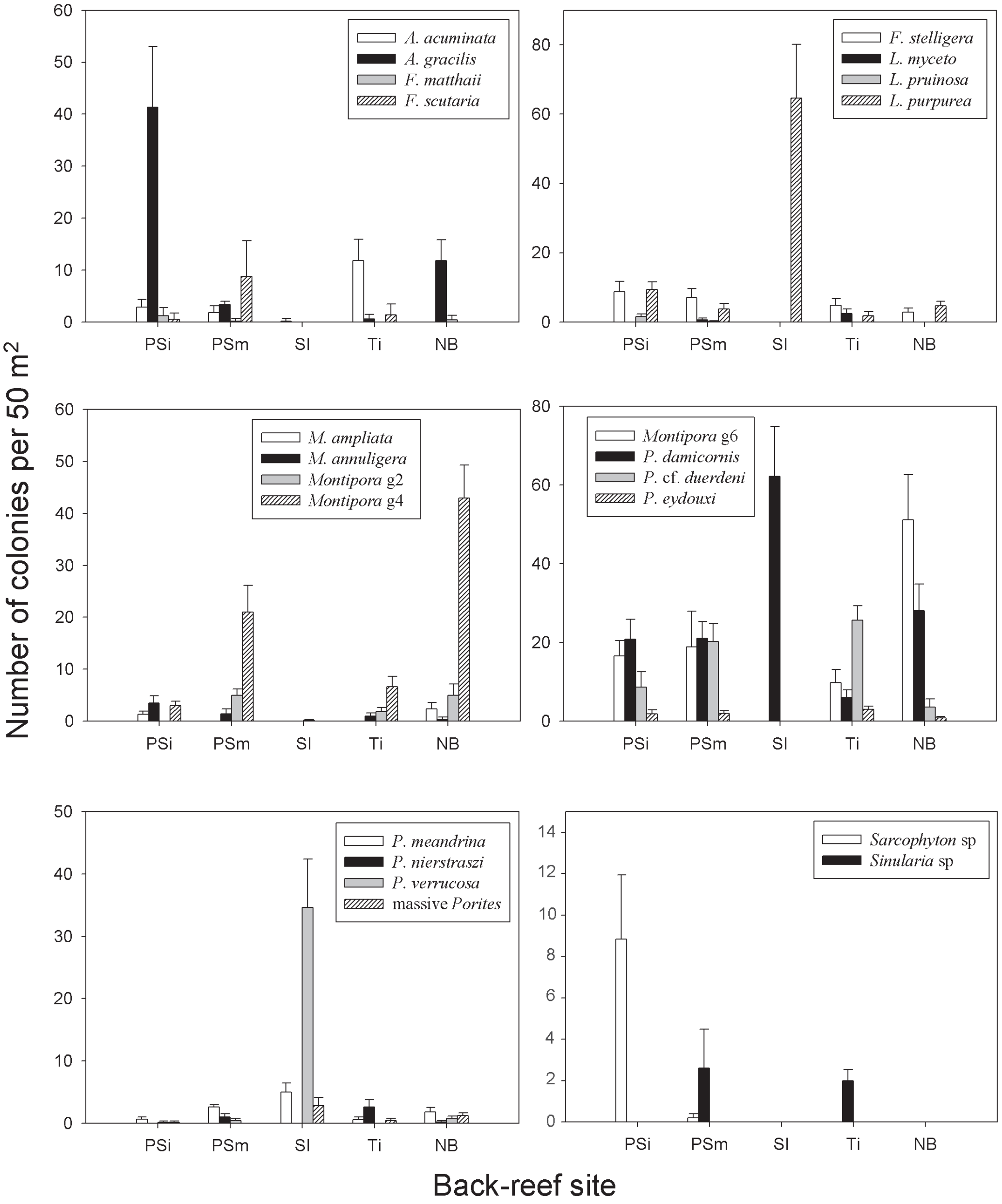

Figure 8. Relative abundances of species/groups responsible for separation between 5 back-reef sites at Palmyra Atoll, Central Pacific: PSi, Penguin Spit Inner Buoy; PSm Penguin Spit Middle Buoy; SI, Sand Island; Ti, Tortugonas back-reef; NB, North Barren. Mean + SE.

A. acuminata, *Acropora acuminata*; *A. gracilis*, *Astreopora gracilis*; *F. matthaii*, *Favia matthaii*; *F. scutaria*, *Fungia scutaria*; *F. stelligera*, *Favia stelligera*; *L. myceto*, *Leptoseris mycetoseroides*; *L. pruinosa*, *Leptastrea pruinosa*; *L. purpurea*, *Leptastrea purpurea*; *M. ampliata*, *Merulina ampliata*; *M. annuligera*, *Montastrea annuligera*; *Montipora* g2, 4, 6, *Montipora* groups two, four, six; *P. damicornis*, *Pocillopora damicornis*; *P.* cf. *duerdeni*, *Pavona* cf. *duerdeni*; *P. eydouxi*, *Pocillopora eydouxi*; *P. meandrina*, *Pocillopora meandrina*; *P. nierstraszi*, *Psammocora nierstraszi*; *P. verrucosa*, *Pocillopora verrucosa*. *Montipora* groups as defined by Veron (2000).

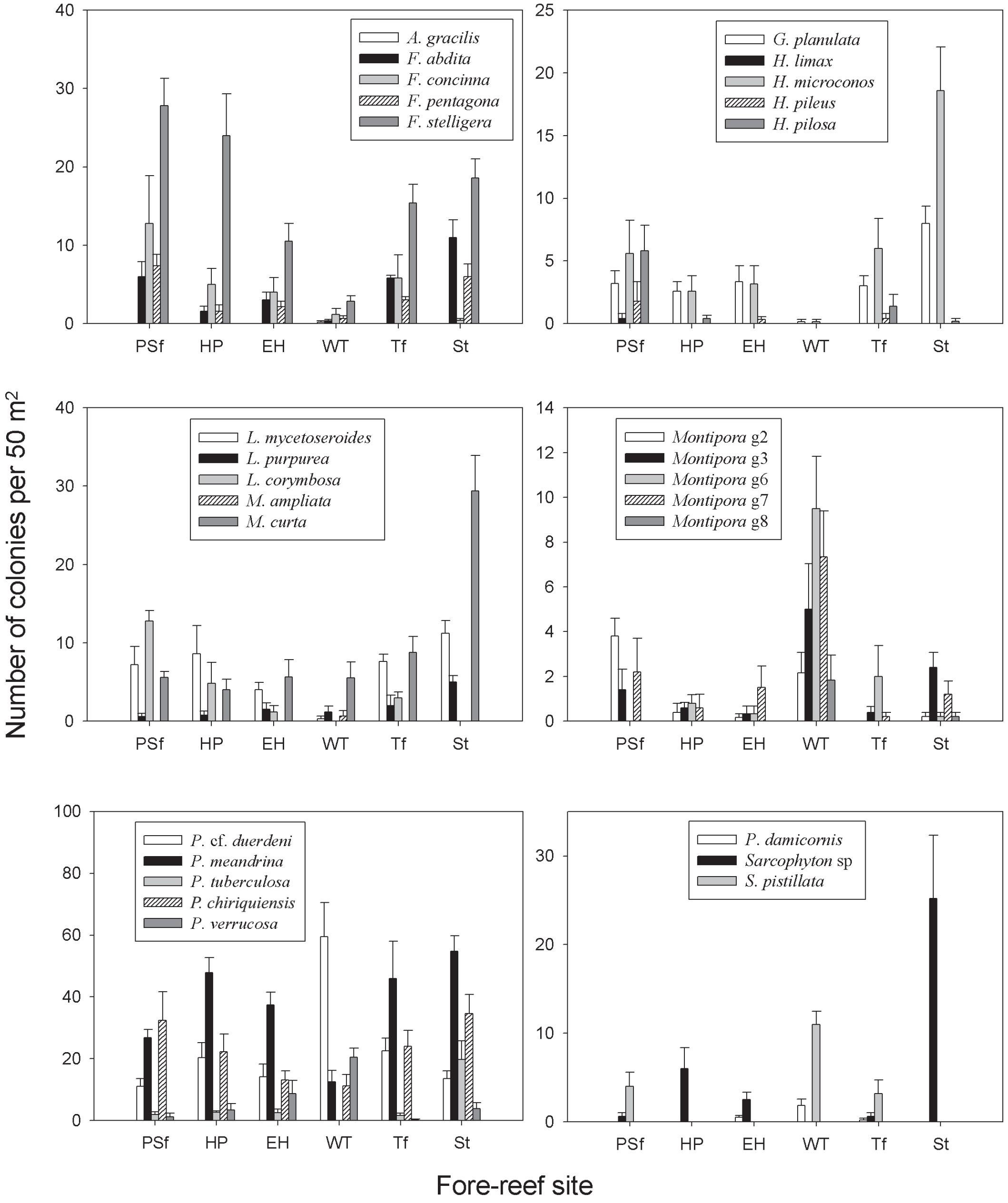

Figure 9. Relative abundances of species/groups responsible for separation between 6 fore-reef sites at Palmyra Atoll, Central Pacific. PSf, Penguin Spit; HP, Home & Paradise; EH, Engineer & Holei; WT, Western Terrace; Tf, Tortugonas; St, Strawn. Mean + SE.

A. gracilis, *Astreopora gracilis*; *F. abdita*, *Favites abdita*; *F. concinna*, *Fungia concinna*; *F. pentagona*, *Favites pentagona*; *F. stelligera*, *Favia stelligera*; *G. planulata*, *Gardineroseris planulata*; *H. limax*, *Herpolitha limax*; *H. microconos*, *Hydnophora microconos*; *H. pileus*, *Halomitra pileus*; *H. pilosa*, *Hydnophora pilosa*; *L. mycetoseroides*, *Leptoseris mycetoseroides*; *L. purpurea*, *Leptastrea purpurea*; *L. corymbosa*, *Lobophyllia corymbosa*; *M. ampliata*, *Merulina ampliata*; *M. curta*, *Montastrea curta*; *Montipora* g2, 3, 6, 7, 8, *Montipora* groups two, three, six, seven, eight; *P. chiriquiensis*, *Pavona chiriquiensis*; *P.* cf. *duerdeni*, *Pavona* cf. *duerdeni*; *P. meandrina*, *Pocillopora meandrina*; *P. tuberculosa*, *Palythoa tuberculosa*; *P. verrucosa*, *Pocillopora verrucosa*; *P. damicornis*, *Pocillopora damicornis*; *S. pistillata*, *Stylophora pistillata*. *Montipora* groups as defined by Veron (2000).

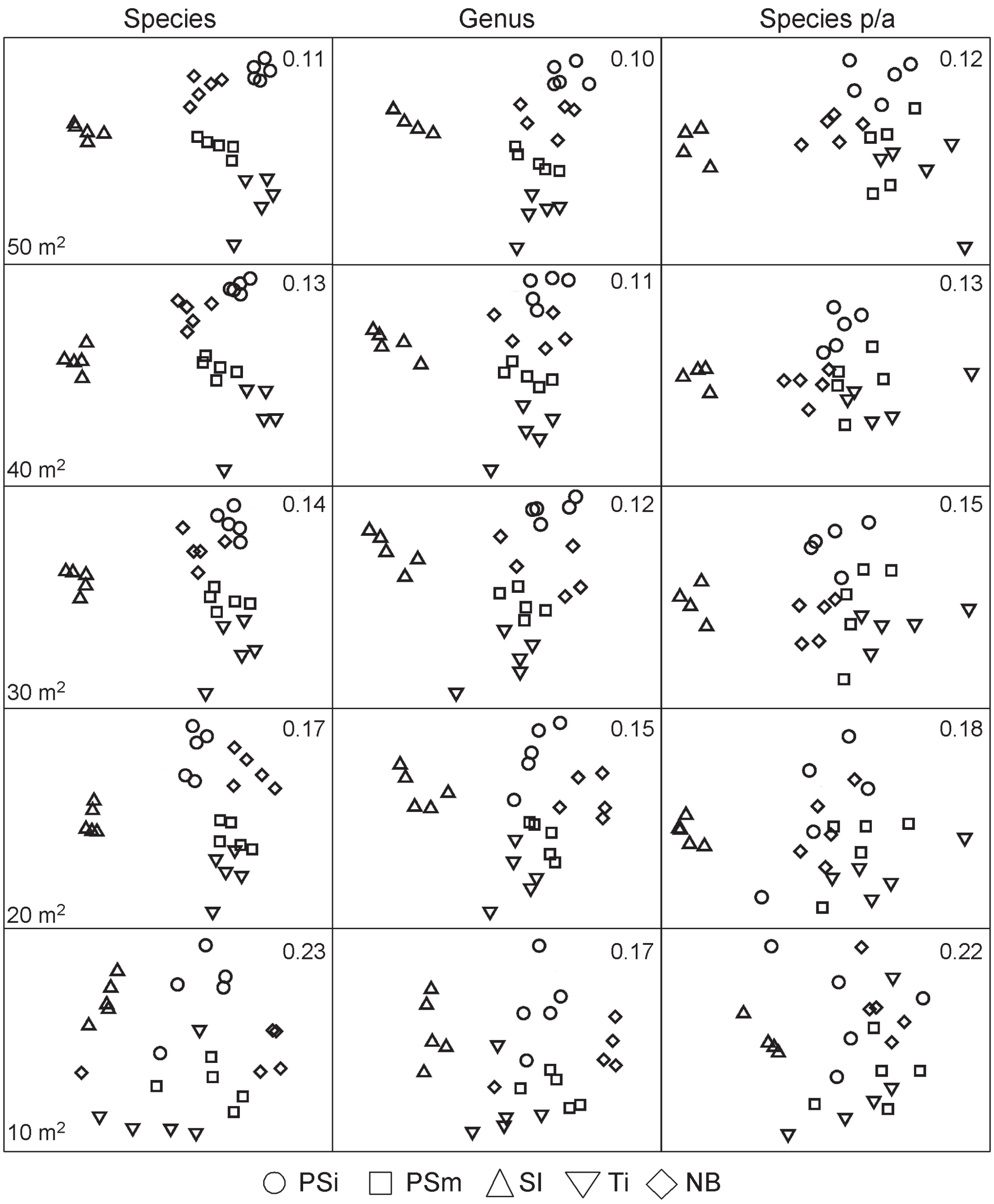

Figure 10. Unconstrained nMDS ordinations of coral assemblages at five back-reef sites at Palmyra Atoll, Central Pacific over three taxonomic resolutions and five different levels of sampling effort. Ordinations based on a zero-adjusted Bray-Curtis coefficient with a dispersion-weighting pretreatment applied to the raw colony count data. Stress values are reported in the top right corner of each ordination. PSi, Penguin Spit Inner Buoy; PSm, Penguin Spit Middle Buoy; SI, Sand Island; Ti, Tortugonas back-reef; NB, North Barren. (n = 5 for each site for the purposes of this analysis.)

Table 5. Summary of ANOSIM pairwise comparisons between back-reef sites at Palmyra Atoll, Central Pacific examined for significant differences in relative coral community composition with varying levels of sampling effort (expressed as transect area), and taxonomic resolutions. PSi, Penguin Spit Inner Buoy; PSm, Penguin Spit Middle Buoy; Ti, Tortugonas back-reef; NB, North Barren.

Resolution	Transect area (m^2)	Global R	Non-sig. Pairwise Comparisons
Species	50	0.963	†
	40	0.938	†
	30	0.945	†
	20	0.916	†
	10	0.713	†
Genus	50	0.983	†
	40	0.971	†
	30	0.953	†
	20	0.927	†
	10	0.786	†
P/A	50	0.801	†
	40	0.788	†
	30	0.758	PSm, Ti
	20	0.679	PSm, Ti
	10	0.510	PSi, Ti; PSm, Ti; Ti, NB

Notes: Analyses based on 999 random permutations and a zero-adjusted Bray-Curtis similarity matrix at all three taxonomic resolutions. A dispersion-weighted pretreatment was applied to the raw count data when recording to species or genus. †, all pairwise comparisons were significantly different; P/A, recording the presence/absence of species only; Non-sig., non significant.

western sides.

The total number of coral species observed at Palmyra increased outwards from shore, with a higher total found within the fore reef compared to the back reef. This is a widely acknowledged pattern within reef systems (Cornell and Karlson, 2000) as documented in earlier Palmyra surveys (Table 1). Coral communities at Palmyra were distinct and significantly different between both reef areas (back reef versus fore reef) and among individual sites representing each reef area, as tested by an array of multivariate techniques. It is acknowledged that statistical significance and ecological relevance are two separate things (Cole and McBride, 2004). The differences detected in this study were generally owing to large changes in species abundance; for example the high numbers of *Sarcophyton* sp. at Strawn fore reef on the north shore, or the low diversity of species present at Sand Island on the south back reef. These differences were therefore deemed to be ecologically, and not just statistically, meaningful.

Several species were identified as being responsible for driving separation between reef areas and among sites. The back reef was characterized by a high number of individuals within the genera *Montipora* and *Astreopora*, whereas the fore reef was

Table 6. Summary of allocation success, the percentage of points correctly allocated into each group, for five back-reef sites at Palmyra Atoll, Central Pacific with varying sampling effort (expressed as transect area), over three taxonomic resolutions. PSi, Penguin Spit Inner Buoy; PSm, Penguin Spit Middle Buoy; SI, Sand Island;Ti, Tortugonas back-reef; NB, North Barren.

Sampling effort (m^2)	Site	Species	Genus	P/A
50	PSi	100	100	83.3
	PSm	100	100	80.0
	SI	100	100	100
	Ti	100	100	100
	NB	100	100	100
	Overall	100	100	92.3
40	PSi	100	100	83.3
	PSm	100	100	100
	SI	100	100	100
	Ti	100	100	80.0
	NB	100	100	100
	Overall	100	100	92.3
30	PSi	100	100	100
	PSm	100	100	80.0
	SI	100	100	100
	Ti	100	100	60.0
	NB	100	100	100
	Overall	100	100	88.5
20	PSi	100	100	66.7
	PSm	100	100	80.0
	SI	100	100	100
	Ti	100	100	60.0
	NB	100	100	100
	Overall	100	100	80.8
10	PSi	83.3	83.3	66.7
	PSm	100	100	80.0
	SI	100	100	100
	Ti	80.0	80.0	60.0
	NB	80.0	80.0	100
	Overall	88.4	88.4	80.8

Notes: Analyses based on 999 random permutations and a zero-adjusted Bray-Curtis similarity matrix at all three resolutions. A dispersion-weighted pretreatment was applied to the raw count data when recording to species or genus. overall, overall allocation success of the five sites. P/A, recording the presence/absence of species only.

characterized by high numbers of *Pocillopora*, *Hydnophora*, *Leptoseris*, *Gardineroseris*, *Fungia*, *Favites*, and *Favia* individuals. Branching *Acropora* species were also generally more abundant within the back reef compared to the fore reef, although as colony counts were conducted, their high overall contribution to coral cover did not exert a high influence on reef area dissimilarity. At the site level, clusters of sites displaying similar community compositions were not necessarily associated with high proximity to each other both within the back reef and fore reef. For example, Penguin Spit Inner and Middle Buoys were separated by only a few hundred meters although they showed very distinct and different community compositions. In contrast, Tortugonas and Penguin Spit Middle Buoy were approximately 2500 m apart, although they harbored very similar coral communities. The distinct nature of the communities at Sand Island and Penguin Spit Inner Buoy were largely driven by high numbers of *Pocillopora* species, and high numbers of *Astreopora gracilis* and *Sarcophyton* sp. at the two sites respectively. Sand Island represents a harsh environment where temperature and salinity fluctuate greatly (23.48 – 31.12°C, 31.09 – 34.76 ppt, over the 6-week period of this survey) due to the shallow nature of the site, and where wave energy can become high during storm periods. *Pocillopora* species are known to be more resilient to high wave energy due to their dense skeletal structure (Dollar, 1982), and this may explain their high dominance at Sand Island.

High numbers of the soft coral *Sarcophyton* sp. at Penguin Spit Inner Buoy may be indicative of a more competitive and regularly disturbed environment (Maida et al., 1995; Wakeford et al., 2008), although the ability of soft coral species to replace scleractinian coral species postdisturbance has been argued against (Fabricius, 1997). This idea of disturbance frequency (Wakeford et al., 2008) could also offer some explanation for the differences in coral communities observed among the fore-reef sites around the atoll. For instance, the northern shore of Palmyra Atoll is subjected to large northwest swell originating from winter storms from the Bering Sea, Aleutian Islands, North Pacific and Kamchatka, creating a regularly disturbed environment. These swells, as an act of disturbance, may explain the high abundance of *Sarcophyton* sp. at Strawn compared to all other fore-reef sites. The paucity of branching *Acropora* species at Strawn (as well as at all the other fore reef compared to back-reef sites) again reflects exposure to increased wave energy and long-period swells (Kenyon et al., 2006). Moreover, with regard to disturbance events, there have been at least two episodes of large *Acanthaster planci* (crown-of-thorns starfish) aggregations at Palmyra off the south-western fore reef of the atoll. *A. planci* is a common predator of corals and outbreaks have been shown to reduce dramatically hard coral cover (Wakeford et al., 2008). This particular predator may be contributing to periodic disturbances and species shifts in coral communities at Palmyra.

Although changes in depth between sites were found to explain a significant proportion of the species variation between sites, a large amount of variation (65.9%) went unexplained, suggesting that other spatial and environmental variables are important in structuring the coral communities at Palmyra. The structure and composition of coral-reef communities are likely to be determined by the interaction of multiple forcing functions operating on a variety of scales (Murdoch and Aronson, 1999). Several spatial and environmental variables have been noted as determining coral species distribution, including light and sediment transport (Glynn, 1976), wave energy and storm frequency (Dollar, 1982), and water motion and irradiance (Done, 1982). More recently, influential variables have been found to include depth, distance to mainland and exposure (van Woesik and Done, 1997); depth, water clarity, reef slope and cross-shelf position (De'ath and Fabricius, 2000); temperature, sedimentation and salinity (Lirman et al., 2003); and shelf depth and island size (Cleary et al., 2006). Coral-recruit settlement patterns and post-settlement survival are also likely to explain a large amount of variation in the relative distribution of coral species (Done, 1982). Further monitoring and measuring of additional spatial and environmental variables would allow the creation of an explanatory model for relative coral distribution around Palmyra Atoll and identify the most influential proximate parameters. The model would serve as a valuable management tool for the refuge for predicting possible changes in coral abundance/distribution in response to changing environmental conditions.

Future Sampling and Analytical Methodology

Monitoring, by its very definition, relies on the ability to detect spatial and temporal change within the system in question and therefore requires both sound investigative and analytical methodology. Altering both sampling effort and taxonomic resolution for surveys within the back reef at Palmyra had an effect on both the site-distinctness of the coral communities (relative to other back-reef sites) and the ability to detect significant differences among sites. Even though within-site multivariate dispersion generally increased with reduced sampling effort for all back-reef sites at all taxonomic resolutions, the ability to detect significant differences among sites was only compromised at the resolution of species presence/absence for a sampling effort of 30 m^2 or less per transect when using ANOSIM as the analytical tool. The complementary procedure CAP, however, maintained the ability to detect significant site-distinctness at all sampling efforts over all taxonomic resolutions. CAP also was able to detect significant relative community differences among the two south fore-reef sites that ANOSIM was unable to detect. Although recording to genus would seem appropriate in some instances, especially in concert with size frequency distribution data, recording to species level where possible should be maintained until further investigation. When reducing taxonomic resolution (from species to genus to presence/absence) a reduction in the number of variables and thus the number of zeros in the data set generally results (Vanderklift et al., 1996), and the subsequent effects are complex (Anderson et al., 2005) and were not examined or quantified in the present study. We recommend that future monitoring of coral communities at Palmyra Atoll involve higher numbers of smaller transects (10 m^2) at more sites, and include colony size class information to maximize the possibility of detecting subtle changes to community structure. We also recommend CAP over ANOSIM as part of the analytical procedure for assessing and characterizing relative coral community distinctness at Palmyra Atoll.

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REFERENCES

Anderson, M.J.
2003. DISTLM*forward*: a FORTRAN computer program to calculate a distance-based multivariate analysis for a linear model using forward selection. Department of Statistics, University of Auckland, New Zealand.
Anderson, M.J.
2004. CAP: a FORTRAN computer program for canonical analysis of principal coordinates. Department of Statistics, University of Auckland, New Zealand.
Anderson, M.J., S.D. Connell, B.M. Gillanders, C.E. Diebel, W.M. Blom, J.E. Saunders, and T.J. Landers
2005. Relationships between taxonomic resolution and spatial scales of multivariate variation. *Journal of Animal Ecology* 74:636-646.
Anderson, M.J., R.B. Ford, D.A. Feary, and C. Honeywill
2004. Quantitative measures of sedimentation in an estuarine system and its relationship with intertidal soft-sediment infauna. *Marine Ecology Progress Series* 272:33-48.
Anderson, M.J. and J. Robinson
2003. Generalized discriminant analysis based on distances. *Australian and New Zealand Journal of Statistics* 45(3):301-318.
Anderson, M.J. and T.J. Willis
2003. Canonical analysis of principal coordinates: a useful method of constrained ordination for ecology. *Ecology* 84:511-524.
Aronson, R.B. and W.F. Precht
2001. White-band disease and the changing face of Caribbean coral reefs. *Hydrobiologia* 460:25-38.
Bellwood, D.R., T. P. Hughes, C. Folke, and M. Nyström
2004. Confronting the coral reef crisis. *Nature* 429:827-833.
Berumen, M.L. and M.S. Pratchett
2006. Recovery without resilience: persistent disturbance and long-term shifts in the structure of fish and coral communities at Tiahura Reef, Moorea. *Coral Reefs* 25:647-653.

Chao, A.

1984. Non-parametric estimation of the number of classes in a population. *Scandinavian Journal of Statistics* 11:265-270.

Clarke, K.R.

1993. Non-parametric multivariate analyses of changes in community structure. *Australian Journal of Ecology* 18:117-143.

Clarke, K.R., M.G. Chapman, P.J. Somerfield, and H.R. Needham

2006a. Dispersion-based weighting of species counts in assemblage analyses. *Marine Ecology Progress Series* 320:11-27.

Clarke, K.R. and R.N. Gorley

2006. Primer v6: User manual/tutorial. PRIMER-E Ltd: Plymouth, United Kingdom.

Clarke, K.R., P.J. Somerfield, and M.G. Chapman

2006b. On resemblance measures for ecological studies, including taxonomic dissimilarities and a zero-adjusted Bray-Curtis coefficient for denuded assemblages. *Journal of Experimental Marine Biology and Ecology* 330:55-80.

Cleary, D.F.R., Suharsono, and B.W. Hoeksema

2006. Coral diversity across a disturbance gradient in the Pulau Seribu reef complex off Jakarta, Indonesia. *Biodiversity and Conservation* 15:3653-3674.

Cole, R.G. and G. McBride

2004. Assessing impacts of dredge spoil disposal using equivalence tests: implications of a precautionary (proof of safety) approach. *Marine Ecology Progress Series* 279:63-72.

Cornell, H.V. and R.H. Karlson

2000. Coral species richness: ecological vs. biogeographical influences. *Coral Reefs* 19:37-49.

Dawson, E.Y.

1959. Changes in Palmyra Atoll and its vegetation through the activities of man 1913–1958. *Pacific Naturalist* 1:1–51.

De'ath, G.

2002. Multivariate regression trees: a new technique for modelling species-environment relationships. *Ecology* 83:1105-1117.

De'ath, G. and K.E. Fabricius

2000. Classification and Regression Trees: a powerful yet simple technique for ecological data analysis. *Ecology* 81:3178-3192.

DeVantier, L.M., G. De'ath, T.J. Done, and E. Turak

1998. Ecological assessment of a complex natural system: a case study from the Great Barrier Reef. *Ecological Applications* 8:480-496.

DeVantier, L.M., G. De'ath, E. Turak, T.J. Done, and K.E. Fabricius

2006. Species richness and community structure of reef-building corals on the nearshore Great Barrier Reef. *Coral Reefs* 25:329-340.

Dollar, S.J.

1982. Wave stress and coral community structure in Hawaii. *Coral Reefs* 1:71-81.

Done, T.J.
1982. Patterns in the distribution of coral communities across the Central Great Barrier Reef. *Coral Reefs* 1:95-107.
Done, T., E. Turak, M. Wakeford, L. DeVantier, A. McDonald, and D. Fisk
2007. Decadal changes in turbid-water coral communities at Pandora Reef: loss of resilience or too soon to tell? *Coral Reefs* 26:789-805.
Dufrêne, M. and P. Legendre
1997. Species assemblages and indicator species: the need for a flexible asymmetrical approach. *Ecological Monographs* 67:345-366.
Dustan, P. and J.C. Halas
1987. Changes in the reef-coral community of Carysfort Reef, Key Largo, Florida: 1974 to 1982. *Coral Reefs* 6:91-106.
Fabricius, K.E.
1997. Soft coral abundance on the central Great Barrier Reef: effects of *Acanthaster planci*, space availability, and aspects of the physical environment. *Coral Reefs* 16:159-167.
Gardner, T.A., I.M. Côte, J.A. Gill, A. Grant, and A.R. Watkinson
2003. Long-term region-wide declines in Caribbean Corals. *Science* 301:958-960.
Glynn, P.W.
1976. Some physical and biological determinants of coral community structure in the eastern Pacific. *Ecological Monographs* 46:431-456.
Goreau, T.F.
1959. The ecology of Jamaican coral reefs. I. Species composition and zonation. *Ecology* 40:67-90.
Hughes, T.P., A.H. Baird, D.R. Bellwood, M. Card, S.R. Connolly, C. Folke, R. Grosberg, O. Hoegh-Guldberg, J.B.C. Jackson, J. Kleypas, J.M. Lough, P. Marshall, M. Nyström, S.R. Palumbi, J.M. Pandolfi, B. Rosen, and J. Roughgarden
2003. Climate change, human impacts, and the resilience of coral reefs. *Science* 301:929-933.
Karlson, R.H. and H.V. Cornell
1998. Scale-dependent variation in local vs. regional effects on coral species richness. *Ecological Monographs* 68:259-274.
Kenyon, J.C., P.S. Vroom, K.N. Page, M.J. Dunlap, C.B. Wilkinson, and G.S. Aeby
2006. Community structure of hermatypic corals at French Frigate Shoals, Northwestern Hawaiian Islands: capacity for resistance and resilience to selective stressors. *Pacific Science* 60:153-175.
Lirman, D., B. Orlando, S. Maciá, D. Manzello, L. Kaufman, P. Biber, and T. Jones
2003. Coral communities of Biscayne Bay, Florida and adjacent offshore areas: diversity, abundance, distribution, and environmental correlates. *Aquatic Conservation: Marine and Freshwater Ecosystems* 13:121-135.
Maida, M., P.W. Sammarco, J.C. Coll
1995. Effects of soft corals on scleractinian coral recruitment. I: Directional allelopathy and inhibition of settlement. *Marine Ecology Progress Series* 121:191-202.

Maragos, J.E.
1993. Impact of coastal construction on Coral Reefs in the U.S. affiliated islands. *Coastal Management* 21:235-269.
Maragos, J., A. M. Friedlander, S. Godwin, C. Musburge, R. Tsuda, E. Flint, O. Pantos, P. Ayotte, E. Sala, S. Sandin, S. McTee, D. Siciliano, and D. Obura.
2008a. U.S. coral reefs in the Line and Phoenix Islands, Central Pacific Ocean: Status, Threats and Significance, Pages 643-654, In: Bernhard Riegl and Richard Dodge (ed) *Coral Reefs of the U.S.A.* Springer.
Maragos, J., J. Miller, J. Gove, E. Demartini, A. Friedlander, and S. Godwin
2008b. U.S. coral reefs in the Line and Phoenix Islands, Central Pacific Ocean: History, Geology, Oceanography, and Biology, In: Bernhard Riegl and Richard Dodge (ed) *Coral Reefs of the U.S.A.* Springer.
McArdle, B.H. and M.J. Anderson
2001. Fitting multivariate models to community data: a comment on distance-based redundancy analysis. *Ecology* 82:290–297.
McClanahan, T.R., M. Ateweberhan, N.A.J. Graham, S.K. Wilson, C. Ruiz Sebastián, M.M.M. Guillaume, and J.H. Bruggemann
2007. Western Indian Ocean coral communities: bleaching responses and susceptibility to extinction. *Marine Ecology Progress Series* 337:1-13.
McWilliams, J.P., I.M. Cote, J.A. Gill, W.J. Sutherland, and A.R. Watkinson
2005. Accelerating impacts of temperature-induced coral bleaching in the Caribbean. *Ecology* 86:2055-2060.
Mumby, P.J., A. Hastings, and H.J. Edwards
2007. Thresholds and the resilience of Caribbean coral reefs. *Nature* 450:98-101.
Murdoch, T.J.T. and R.B. Aronson
1999. Scale-dependent spatial variability of coral assemblages along the Florida Reef Tract. *Coral Reefs* 18:341-351.
Pandolfi, J.M., R.H. Bradbury, E. Sala, T.P. Hughes, K.A. Bjorndal, R.G. Cooke, D. McArdle, L. McClenachan, M.J.H. Newman, G. Paredes, R.R. Warner, and J.B.C. Jackson
2003. Global trajectories of the long-term decline of coral reef ecosystems. *Science* 301:955-958.
Plotkin, J.B. and H.C. Muller-Landau
2002. Sampling the species composition of a landscape. *Ecology* 83:3344-3356.
Rogers, S.I, K.R. Clarke, and J.D. Reynolds
1999. The taxonomic distinctness of coastal bottom-dwelling fish communities of the North-east Atlantic. *Journal of Animal Ecology* 68:769–782.
Sandin, S.A., J.E. Smith, E.E. DeMartini, E.A. Dinsdale, S.D. Donner, A.M. Friedlander, T. Konotchick, M. Malay, J.E. Maragos, D. Obura, O. Pantos, G. Paulay, M. Richie, F. Rowher, R.E. Schroeder, and S. Walsh
2008. Baselines and degradation of coral reefs in the northern Line Islands. *PLoS One* 3 (2):e1548
Smith, E.P. and G. van Belle
1984. Nonparametric estimation of species richness. *Biometrics* 40:119-129.

Smith, L.D., J.P. Gilmour, and A.J. Heyward
2008. Resilience of coral communities on an isolated system of reefs following catastrophic mass-bleaching. *Coral Reefs* 27:197-205.
Terlizzi, A., M.J. Anderson, S. Fraschetti, and L. Benedetti-Cecchi
2007. Scales of spatial variation in Mediterranean subtidal sessile assemblages at different depths. *Marine Ecology Progress Series* 332:25-39.
Vanderklift, M.A., T.J. Ward, and C.A. Jacoby
1996. Effect of reducing taxonomic resolution on ordinations to detect pollution-induced gradients in macrobenthic infaunal assemblages. *Marine Ecology Progress Series* 136:137-145.
van Woesik, R. and T.J. Done
1997. Coral communities and reef growth in the southern Great Barrier Reef. *Coral Reefs* 16:103-115.
Veron, J.E.N
2000. *Corals of the world*. (vol. 1-3). Australian Institute of marine Science and CPR Qld Pyt Ltd., Townsville, Australia
Wakeford, M., T.J. Done, and C.R. Johnson
2008. Decadal trends in a coral community and evidence of changed disturbance regime. *Coral Reefs* 27:1-13.
Weil, E., G. Smith, and D.L. Gil-Agudelo
2006. Status and progress in coral reef disease research. *Diseases of Aquatic Organisms* 69: 1-7.
Williams, G.J., G.S. Aeby, and S.K. Davy
2008a. Coral disease at Palmyra Atoll, a remote reef system in the Central Pacific. *Coral Reefs* 27:207.
Williams, G.J., M.J. Cameron, J.T. Turner, and R.B. Ford
2008b. Quantitative characterisation of reef fish diversity among nearshore habitats in a northeastern New Zealand marine reserve. *New Zealand Journal of Marine and Freshwater Research* 42:33-45.

Appendix A. Species list of cnidarians reported at Palmyra Atoll from 1987-2005 (after Maragos 1987-2005 unpubl. and D. Obura 2005). Explanation for superscripts: Scleractinia = none, [1]Alcyonaria, [2]Actiniaria, [3]Antipatharia, [4]Corallimorpharia, [5]Hydrozoa, and [6]Zoanthidea.

Acropora abrotanoides (Lamarck, 1816)
Acropora aculeus (Dana, 1846)
Acropora acuminata (Verrill, 1864)
Acropora aspera (Dana, 1846)
Acropora cerealis (Dana, 1846)
Acropora cf. *clathrata* (Brook, 1891)
Acropora cf. *robusta* (Dana, 1846)
Acropora cytherea (Dana, 1846)
Acropora digitifera (Dana, 1846)
Acropora divaricata (Dana, 1846)
Acropora elseyi (Brook, 1892)
Acropora florida (Dana, 1846)
Acropora muricata Linnaeus, 1758
Acropora gemmifera (Brook, 1892)
Acropora globiceps (Dana, 1846)
Acropora granulosa (Milne Edwards & Haime, 1860)
Acropora humilis (Dana, 1846)
Acropora hyacinthus (Dana, 1846)
Acropora latistella (Brook, 1891)
Acropora monticulosa (Brüggemann, 1879)
Acropora multiacuta Nemenzo, 1967
Acropora nana (Studer, 1878)
Acropora nasuta (Dana, 1846)
Acropora paniculata Verrill, 1902
Acropora polystoma (Brook, 1891)
Acropora robusta (Dana, 1846)
Acropora rosaria (Dana, 1846)
Acropora samoensis (Brook 1891)
Acropora selago (Studer, 1878)
Acropora sp. Oken, 1815
Acropora spicifera (Dana, 1846)
Acropora squarrosa (Ehrenberg, 1834)
Acropora subulata (Dana, 1846)
Astreopora suggesta Wells, 1954
Acropora longicyathus (Milne Edwards & Haime, 1860)
Acropora tenuis (Dana, 1846)
Acropora valida (Linnaeus 1758)
Acropora variabilis (Klunzinger, 1879)
Acropora vaughani Wells, 1954
Acropora verweyi Veron & Wallace, 1984
Alveopora verrilliana Dana, 1872
Astreopora expansa Brüggemann, 1877
Acropora gracilis Bernard, 1896
Astreopora listeri Bernard, 1896
Astreopora myriophthalma (Lamarck, 1816)
Astreopora sp. Blainville, 1830
Balanophyllia sp. [small cups] Searles, Wood, 1844
Cladiella sp.[1] (Macfadyen, 1936)
Cryptodendrum adhaesivum[2] Klunzinger, 1877
Ctenactis echinata (Pallas, 1766)
Cycloseris cyclolites (Lamarck, 1801)
Cycloseris patelliformis (Boschma, 1923)
Cycloseris sp. Milne Edwards & Haime, 1849
Cyphastrea serailia (Forskål, 1775)
Discosoma sp.[4] Ehrenberg, 1834
Distichopora violacea[5] (Pallas, 1776)
Echinophyllia aspera (Ellis & Solander, 1788)
Echinophyllia sp. Klunzinger, 1879
Favia favus (Forskål, 1775)
Favia matthaii Vaughan, 1918
Favia pallida (Dana, 1846)
Favia rotumana (Gardiner, 1899)
Favia rotundata (Veron & Pichon, 1977)
Favia speciosa Dana, 1846
Favia stelligera (Dana, 1846)
Favia sp. Oken, 1815
Favites abdita (Ellis & Solander 1786)
Favites chinensis (Verrill, 1866)
Favites flexuosa (Dana, 1846)
Favites halicora (Ehrenberg, 1834)
Favites pentagona (Esper, 1794)
Favites russelli (Wells, 1954)
Favites sp. Link, 1807
Fungia concinna Verrill, 1864
Fungia danai Milne Edwards & Haime, 1851
Fungia fungites (Linnaeus, 1758)

Fungia granulosa Klunzinger, 1879
Fungia moluccensis Horst, 1919
Fungia paumotensis Stutchbury, 1833
Fungia repanda Dana, 1846
Fungia scutaria Lamarck, 1801
Fungia horrida Dana, 1846
Gardineroseris planulata (Dana, 1846)
Goniastrea edwardsi Chevalier, 1971
Goniastrea pectinata (Ehrenberg, 1834)
Goniastrea retiformis (Lamarck, 1816)
Gymnangium sp.[5] (Jäderholm, 1903)
Halomitra pileus (Linnaeus 1758)
Herpolitha limax Esper, 1797
Heteractis malu[2] (Haddon & Shackleton, 1893)
Heteractis crispa[2] (Ehrenberg, 1834)
Hydnophora exesa (Pallas, 1766)
Hydnophora microconos (Lamarck, 1816)
Hydnophora pilosa (Veron, 1985)
Hydnophora rigida (Dana, 1846)
Isopora brueggemanni (Brook, 1893)
Isopora cuneata (Dana, 1846)
Isopora palifera (Lamarck, 1816)
Leptastrea agassizi Vaughan 1907
Leptastrea bewickensis Veron & Pichon, 1977
Leptastrea pruinosa Crossland, 1952
Leptastrea purpurea (Dana, 1846)
Leptastrea transversa Klunzinger, 1879
Leptastrea sp. C [small round calices] Milne Edwards & Haime 1848
Leptastrea sp. A [large angular calices] Milne Edwards & Haime 1848
Leptastrea sp. B Milne Edwards & Haime 1848
Leptoria phrygia (Ellis & Solander, 1786)
Leptoseris mycetoseroides Wells, 1954
Lobophyllia corymbosa (Forskå1, 1775)
Lobophyllia hemprichii (Ehrenberg, 1834)
Lobophytum sp.[1] Gosliner, Behrens & Williams, 1996
Millepora platyphylla[5] Hemprich & Ehrenberg, 1834
Merulina ampliata (Ellis & Solander, 1786)
Montastrea annuligera (Milne-Edwards & Haime, 1849)
Montastrea curta (Dana, 1846)
Montastrea sp. Blainville, 1830

Montipora aequituberculata Bernard, 1897
Montipora caliculata (Dana, 1846)
Montipora capitata (Dana, 1846)
Montipora danae (Milne Edwards & Haime, 1851)
Montipora efflorescens Bernard, 1897
Montipora dilatata Studer, 1901
Montipora flabellata Studer, 1901
Montipora foliosa (Pallas, 1766)
Montipora foveolata (Dana, 1846)
Montipora hoffmeisteri Wells, 1954
Montipora cf. *incrassata* (Dana, 1846)
Montipora informis Bernard, 1897
Montipora monasteriata (Forskå1, 1775)
Montipora millepora Crossland, 1952
Montipora patula Verrill, 1864
Montipora peltiformis Bernard, 1897
Montipora spongodes Bernard, 1897
Montipora sp. Blainville, 1830
Montipora tuberculosa (Lamarck, 1816)
Montipora venosa (Ehrenberg, 1834)
Montipora verrilli Vaughan 1907
Pachyclavularia violacea[1] (Quoy & Gaimard 1833)
Pachyseris sp. Milne Edwards & Haime 1849
Palythoa sp.[6] Dana, 1848
Palythoa tuberculosa[6] (Esper, 1791)
Pavona cactus
Pavona chiriquiensis Glynn, Mate & Stemann, 2001
Pavona clavus (Dana, 1846)
Pavona duerdeni Vaughan, 1907
Pavona explanulata (Lamarck, 1816)
Pavona frondifera (Lamarck, 1816)
Pavona maldivensis (Gardiner, 1905)
Pavona minuta Wells, 1954
Pavona varians Verrill, 1864
Platygyra daedalea (Ellis & Solander, 1786)
Platygyra lamellina (Ehrenberg, 1834)
Platygyra pini Chevalier, 1973
Platygyra ryukyuensis Yabe & Sugiyama, 1936
Platygyra sp. Ehrenberg, 1834
Platygyra sinensis (M. Edwards & Haime, 1849)

Plesiastrea versipora (Lamarck, 1816)
Pocillopora brevicornis Lamarck, 1816
Pocillopora damicornis (Linnaeus, 1758)
Pocillopora capitata Verrill, 1864
Pocillopora eydouxi Milne Edwards & Haime 1860
Pocillopora meandrina Dana 1846
Pocillopora sp. Lamarck, 1816
Pocillopora verrucosa (Ellis & Solander, 1786)
Pocillopora zelli Veron 2000
Porites annae Crossland, 1952
Porites australiensis Vaughan, 1918
Porites evermanni Vaughan, 1907
Porites lichen Dana, 1846
Porites lobata Dana, 1846
Porites lutea Milne Edwards & Haime, 1851
Porites murrayensis Vaughan, 1918
Porites rus (Forskå1, 1775)
Porites solida (Forskå1, 1775)
Porites sp. [nodular] Link, 1807
Porites sp. Link, 1807
Porites superfusa Gardiner, 1898
Porites vaughani Crossland, 1952
Psammocora contigua (Esper, 1797)
Psammocora haimeana Milne Edwards & Haime, 1851
Psammocora nierstraszi Horst, 1921
Psammocora profundacella Gardiner, 1898
Psammocora stellata Verrill, 1864
Psammocora verrilli Vaughan, 1907
Rhodactis howesii[4] (Ehrenberg, 1834)
Sandalolitha robusta Quelch, 1886
Sarcophyton sp.[1] Gosliner, Behrens & Williams, 1996
Sinularia sp.[1] Gosliner, Behrens & Williams, 1996
Stereonephthya sp.[1] Gosliner, Behrens & Williams, 1996
Stichodactyla mertensii[2] Brandt, 1835
Stylaster elegans.[5] Verrill, 1864
Stylophora pistillata Esper, 1797
Symphyllia recta (Dana, 1846)
Tubastraea coccinea Lesson, 1831
Turbinaria reniformis Bernard 1896
Turbinaria frondens (Dana, 1846)
Turbinaria sp. Oken, 1815