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A comparison of coral reef and coral community fish assemblages in Pacific Panama and environmental factors governing their structure

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We compared the reef fish assemblages of two habitats, coral reefs and coral communities (rocky substratum with coral colonies), in the Las Perlas Archipelago in Pacific Panama and attempted to determine associations with habitat variables. We used a modified Atlantic and Gulf Rapid Reef Assessment (AGRRA) survey to record fish species and quadrat transects to determine benthic composition. Multivariate non-parametric multi-dimensional scaling (MDS) ordinations were performed in PRIMER and univariate correlations were used to determine relationships. The reef fish of coral communities were significantly more diverse and species rich than those of coral reefs. The two habitats had significantly different species and size composition, but trophic and family groups overlapped between habitats. Topography, exposure, and the percentage cover of branching and massive corals correlated significantly with differences in fish parameters. The reef fish assemblages of this region appear to be determined more by the larger scale structural features that characterize the two habitats than by features that vary over small scales within the habitats.

Keywords: fish, coral, reef, composition, habitat, diversity

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INTRODUCTION

Fish species interact closely with their habitat for the majority of their lives (Jones & Syms, 1998) and therefore, there is reason to hypothesize that the distribution and structure of reef fish communities should correlate with variables of the habitats present (McGehee, 1994; Öhman, 1998). Factors previously found to influence reef fish community structure include benthic diversity, habitat complexity, live coral cover, macroalgal cover, depth and exposure. Topographically complex reef habitats or those with high numbers of growth forms or high benthic diversity should provide more microhabitats, refuge sites, and food resources for a higher number of individuals and species. Research in the literature supports this in general, with positive relationships being found with fish diversity, species richness and abundance (Luckhurst & Luckhurst, 1978; Carpenter *et al.*, 1981; Ault & Johnson, 1998; Lara & Gonzalez, 1998; Öhman & Rajasuriya, 1998; Lirman, 1999; Nagelkerken *et al.*, 2000; García-Charton & Pérez-Ruzafa, 2001; McClanahan & Arthur, 2001; Friedlander *et al.*, 2003; Dominici-Arosemena & Wolff, 2005, 2006; Espinoza & Salas, 2005; Gratwicke & Speight, 2005a; Brokovich *et al.*, 2006; Kuffner *et al.*, 2007).

Live bottoms offer food sources and often higher structural variability and shelter (Huntsman & Waters, 1987) and positive relationships have been found between live coral cover and reef fish diversity, richness and abundance (Bell & Galzin, 1984; Bouchon-Navaro & Bouchon, 1989; Chabanet *et al.*, 1997; Connell & Kingsford, 1998; Jones *et al.*, 2004; Bozec *et al.*, 2005) with declines in fish communities found after coral cover loss (Wilson *et al.*, 2006, 2008), although this was not found in other studies (Roberts & Ormond, 1987; Chapman & Kramer, 1999; Lecchini *et al.*, 2003). Williams & Polunin (2001) reported positive relationships between algae cover and biomass of reef fish, but other researchers found no such relationship (Chabanet *et al.*, 1997; Friedlander & Parrish, 1998; Eagle *et al.*, 2001). Depth and exposure has also been found to positively correlate with species richness, diversity and abundance on coral and rocky reefs (Roberts & Ormond, 1987; Adjeroud *et al.*, 1998; Friedlander & Parrish, 1998; Öhman & Rajasuriya, 1998; Ferreira *et al.*, 2001; Arreola-Robles & Elorduy-Garay, 2002; Lecchini *et al.*, 2003; Dominici-Arosemena & Wolff, 2005, 2006; Brokovich *et al.*, 2006).

Studying fish–habitat associations can provide insight into the effects of habitat structure that can be accounted for when other variables are examined; it enables a fuller understanding of how disturbances affect fish communities; and an improved understanding of the spatial distribution of reef fish has implications for reef management. Despite an increasing number of

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studies on reef fish–habitat associations, a broader range of species, habitats, and biogeographical regions must be studied to better understand how reef fish communities are structured (Jones & Syms, 1998; Öhman, 1998). In addition, studies on reefs of non-biotic origin in tropical areas also require study (Öhman, 1998; Ferriera *et al.*, 2001).

The reef-associated fish communities of the Las Perlas Archipelago (LPA), Panama have received little attention. Previous coral reef studies were concentrated around the northern islands (Glynn & Stewart, 1973; Wellington, 1982). Two dominant reef types are present in the archipelago: coral reefs (CRs) and coral communities (CCs). Although the CRs of the LPA are not as diverse or extensive as those found in the western Pacific or the Caribbean, their simplicity make them ideal for investigating reef fish–habitat relationships (Glynn & Maté, 1996). CCs are the term given in this study to rocky reefs composed of sandstone and basaltic rock provides a substratum that supports scleractinian corals and gorgonians. They differ from CRs because they lack live coral frameworks. CCs fringe much of the coastline of the islands and provide an extensive reef habitat for fish.

This study is the first investigation of reef fish assemblages throughout the whole of the LPA. The aim was to describe and compare the fish communities found on CRs and CCs around the LPA in relation to their habitat. Specifically, we addressed the following questions: (1) do reef fish assemblages of CRs and CCs differ in their composition, diversity, abundance, and fish length?; and (2) do the differences observed between and within these two habitats correlate to measured habitat variables?

MATERIALS AND METHODS

Study site

The LPA lies between 08°40′19″N 79°03′49″W and 08°11′46″N 78°46′31″W within the Gulf of Panama (Figure 1). It is composed of 250 mostly uninhabited basaltic rock islands and islets that lie within the 50 m isobath and fall within the Tropical Eastern Pacific (TEP) biogeographical zone. The LPA experiences an upwelling period during the dry season (January–April) that results in plankton blooms and high marine productivity. The mean tidal range for the archipelago is 3.8 m (Glynn & Maté, 1996).

Historically, no CRs were thought to exist within the TEP because of the cool currents and upwelling. However, studies conducted over the last 30 years have found extensive reefs in the Gulf of Chiriquí and in the Gulf of Panama (Glynn & Stewart, 1973; Glynn, 1976; Guzman *et al.*, 2004). The CRs of this region are characterized by their small size (a few hectares), discontinuous distribution, and low species diversity (Cortés, 1997). The largest aggregation of CRs in the Gulf of Panama occurs in the LPA (Glynn & Maté, 1996). The main reef-building corals are branching species of *Pocillopora*, but massive *Pavona* coral species also occur in deeper areas (Glynn & Stewart, 1973; Glynn, 1976). CCs also contain *Pocillopora*, and *Pavona* species, as well as gorgonians (Guzman *et al.*, 2008). Currently, the CRs and associated marine habitats of the LPA are affected by El Niño Southern Oscillation events, sedimentation, pollution, overfishing, and coastal tourism development. Detailed information was not available on the degree to which these factors affected our study sites, but they are believed to be minimally fished in an artisanal nature (personal observation).

Survey method

We selected 45 survey locations (31 CRs and 14 CCs) based on where reefs existed (Figure 1), as identified by manta tow surveys of the coastline and by satellite image classification (Benfield *et al.*, 2007; Guzman *et al.*, 2008). Surveys occurred in August 2003, May 2004 and August 2004. The depth range surveyed was narrow, with a maximum survey depth of 12 m, but most sites had a maximum depth of less than 6 m due to the shallow distribution of CRs.

We adapted our survey methods from the Atlantic and Gulf Rapid Reef Assessment methodology (AGRRA, Kramer *et al.*, 2005). At each site, we surveyed four 2 m × 30 m transects, which was a revision to the AGRRA methodology that recommends ten. Ten surveys were not possible on most reefs as their small and narrow size would have led to overlapping transects. We used stratified random sampling to place transects, which ran parallel to the shore. When a slope was present, we placed two transects near the top and two closer to the bottom, although the depth variation between the two sections was never more than 5 m. Replicate transects were placed randomly within the stratified zones, separated by a minimum of 5 m (estimated by fin kicks) to prevent overlap between the fish counted.

In this study we examined all diurnally active post-recruitment individuals from 1 cm long upwards, excluding gobies and blennies because these small, cryptic species were too difficult to identify rapidly in the field. This approach was a revision to the AGRRA protocol, which was developed for a different geographical location and recommends counting only selected families. Individuals were identified to species level, with identifications based on Allen & Robertson (1994); counted; and placed in a size category (0–5, 6–10, 11–20, 21–30, 31–40 and >40 cm) according to their total length. For fish over 40 cm, estimated lengths to the nearest centimetre were recorded. We estimated lengths using a graduated PVC t-piece with an arm width of 1 m (*sensu* Kramer *et al.*, 2005). When individuals were present in a large school, a small group was counted and that number was multiplied up to the size of the school. The lengths of large groups were classified into one or more size-categories as necessary. Test dives took place before surveying commenced for divers to familiarize themselves with species and equipment and to assess the divers' surveying accuracy (*sensu* Kramer *et al.*, 2005).

The bottom composition of each site was assessed simultaneously by another team of two divers who surveyed 90 1-m^2 quadrats that were placed end to end along transects that ran parallel to the shore in the same areas where the fish surveys were conducted (*sensu* Guzman *et al.*, 2004). Percentage cover of scleractinian and soft coral species were recorded to species level, and the cover of sponges, crustose coralline algae (CCA), macroalgae, turf algae and dead coral also were recorded. Wave exposure, tide state, sea state, topography and slope were graded (Table 1), and depth below chart datum was calculated.

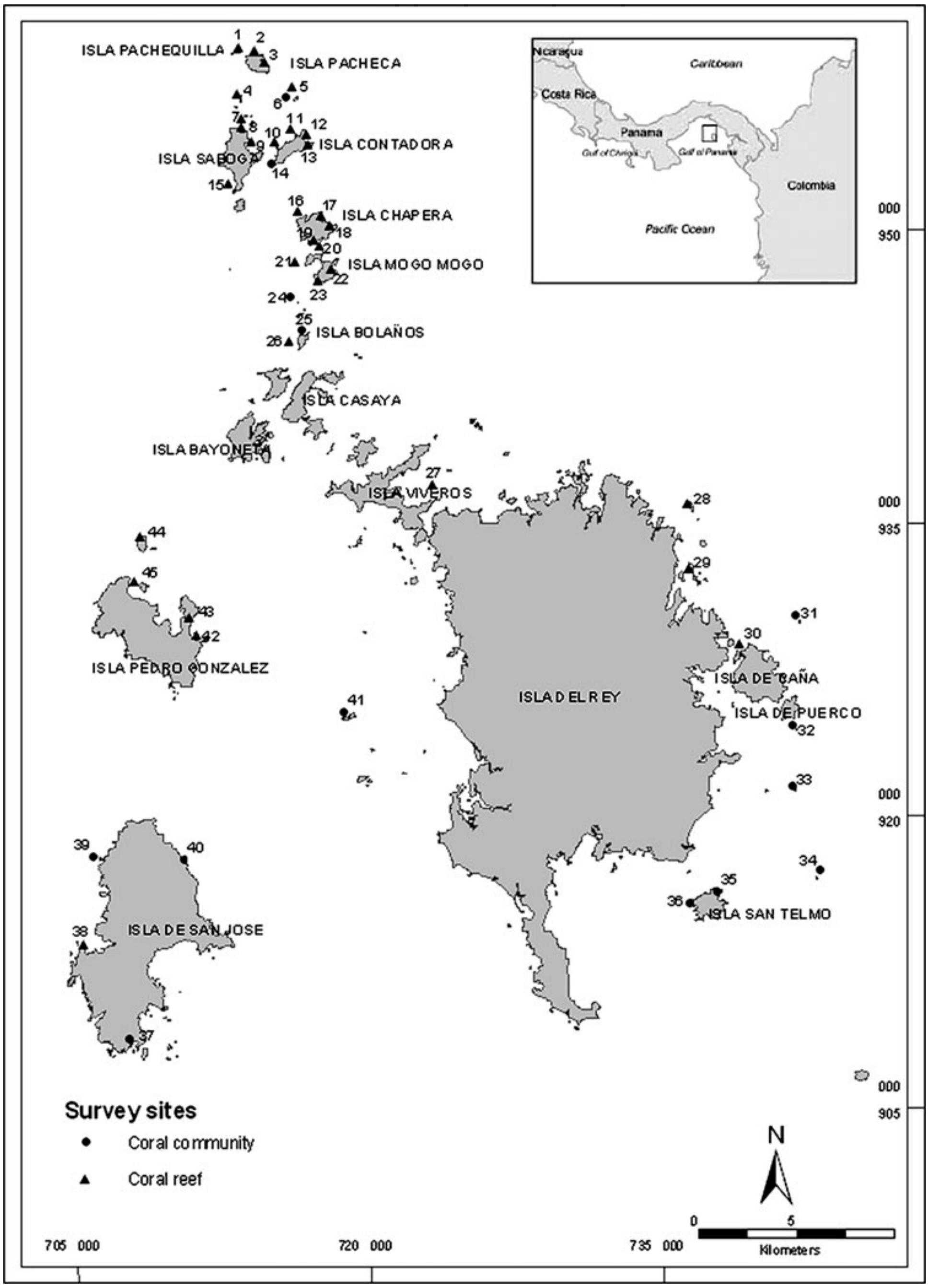

Fig. 1. Coral reef and coral community sites surveyed in Las Perlas Archipelago.

Data analysis

For each site we calculated species richness, Shannon diversity ($\log_{10}$), and mean abundance of each fish species. We calculated the mean length for each species per site by multiplying the number of fish in each size-category by the midpoint of the size-category (2, 7, 15, 25 and 35 cm), summing these values, and then dividing it by the total number of the species counted. We also calculated the mean length of all fish per site. Additionally, fish species were allocated into families and broad trophic groups based upon Allen & Robertson (1994) and FishBase (Froese & Pauly, 2005).

We examined the relationships between habitat type, benthic composition, and fish community parameters using univariate and multivariate methods. Shannon diversity, species richness, mean abundance, and mean length met the requirements for ANOVA (i.e. homogeneity of variance and normality), although mean abundance and mean length per site had to be square-root transformed to allow the use of parametric statistics. ANOVAs were performed to confirm that no significant difference existed in Shannon diversity, species richness, mean abundance, and mean length among the survey seasons ($P > 0.05$ in all cases), which allowed data from habitat sites sampled at different times to be combined in the same analyses. ANOVAs on sea state and *t*-tests for tide state confirmed that these variables had no significant effect on the aforementioned parameters ($P > 0.05$). Thus,

Table 1. Environmental variables recorded for each survey site.

Environmental variable	Scale
Wave exposure	1. Sheltered (e.g. within a bay)
	2. Moderately exposed (e.g. at the edge of a bay)
	3. Exposed (e.g. headland)
Tide state	1. Rising
	2. Falling
Sea state	1. Calm
	2. Calm to moderate
	3. Moderate
	4. Moderate to swell
Slope	1. None to slight
	2. Moderate slope up to 45°
	3. Steep slope greater than 45°
Topography	1. Very low vertical structure
	2. Low vertical structure with slight undulations of 0–0.5 m
	3. Moderate vertical structure with 0.5–1.5 m outcrops. Some boulders, overhangs, and crevices.
	4. High vertical structure with >1.5 m outcrops. Many overhangs, boulders, and crevices.

the data from all survey seasons, tide states, and sea states were pooled for use in the analyses. We used a two-sample *t*-test to test for significant differences in diversity, species richness, mean abundance, and mean length between the two habitats. Relationships between habitat variables (benthic diversity (Shannon diversity, $\log_{10}$) and the percentage cover of branching coral, massive coral, macroalgae, CCA, soft coral and sponge) and fish parameters (fish diversity, species richness, mean abundance, mean length, mean abundance of families and mean abundance of trophic groups) were investigated using Spearman's rank correlation within each habitat.

We implemented non-parametric multi-dimensional scaling (MDS) using the multivariate statistical software PRIMER v5 to further test for differences in fish community composition between and within coral reef and coral community sites and to examine the relationships with habitat variables (Clarke & Ainsworth, 1993; Clarke & Gorley, 2001; Clarke & Warwick, 2001). The abundance data for species, families, and trophic groups and the length data for species were square-root transformed prior to the implementation of the Bray–Curtis similarity measure to create a similarity matrix. This technique was used because it down-weighted the importance of very abundant variables, which we believed was a valuable step as the samples often were dominated by a few species. The similarity matrices then were converted to MDS ordinations and an analysis of similarity (ANOSIM) test was used to test for significant differences in species, family, or trophic composition between the two habitats. We also produced similarity matrices using normalized Euclidean distance (as recommended for environmental data by Clarke & Warwick (2001)) for the habitat data for both reef types combined. The habitat variables examined were wave exposure, depth, topography, slope, benthic diversity, and the percentage cover of branching coral, massive coral, soft coral, macroalgae, CCA, and sponge. The percentage cover data were square-root transformed prior to analysis because they differed by an order of magnitude, and data were normalized because they were not in the same units. We used the BIO-ENV module in PRIMER to determine the combination of environmental variables whose similarity matrix had the highest Spearman rank-correlation with the fish similarity matrix. The significance of the correlation between the habitat and fish matrices was tested using the RELATE command in PRIMER and a weighted Spearman rank correlation, ρ (Clarke & Ainsworth, 1993; Clark & Gorley, 2001; Clarke & Warwick, 2001). This procedure was repeated within coral reef and coral community sites to examine the influence of habitat variables on any of the observed differences in species, family, or trophic composition. We used the SIMPER command of PRIMER to identify those species, families, and trophic groups that contributed to 90% of the fish composition of each habitat and those that played a part in any observed differences between CRs and CCs.

RESULTS

Descriptive results

During the surveys we counted 34,336 fish (26 families, 79 species), with an average of 715.3 ± 304.5 SD per site (Table 2). The three most abundant fish were *Thalassoma lucasanum*, *Chromis atrilobata* and *Stegastes acapulcoensis*, which constituted up to 66.5% of the total number of fish found. *Thalassoma lucasanum* was the only species found at all 45 sites. A few rare species were found only at one site in low numbers (less than 30 individuals): *Apogon pacifici*, *Caranx caballus*, *Scarus compressus*, *Lutjanus aratus*, *Caranx sexfasciatus*, *Gnathanodon speciosus*, *Lutjanus inermis*, *Mycteroperca xenarcha* and *Anisotremus taeniatus*. Over 90% of the fish surveyed were members of the Labridae, Pomacentridae, or Haemulidae families. The family with the greatest abundance was the Labridae (45%), followed by Pomacentridae (36.3%). Species from Labridae, Serranidae, and Pomacentridae families were recorded at all sites, and members of Tetraodontidae were recorded at all but one site. Members of Haemulidae were found at only 28 of the 45 sites, but often occurred in large aggregations. The most dominant trophic groups found across all sites combined were plantivores (53.5%), invertivores (20.1%) and herbivores (18.3%), with the rest of the fish surveyed being omnivores.

The reef fish surveyed were dominated by small species and individuals, with 72% being ≤10 cm in length and the majority being 6–10 cm long. We found very few fish >40 cm long, and these were generally fish such as *Fistularia commersonii* and members of the Scaridae.

The greatest mean abundance of fish occurred at site 14 (CC), and the top three sites with the highest abundance were CCs. Site 19 had the highest mean fish length per site; although this site was a CR, three out of the five sites with the highest mean fish length were CCs. The majority of sites with low mean length were CRs in the northern part of the archipelago. The mean species richness per site was 20 ± 4.9 SD and the most species rich sites were generally CCs. Site 40 was the most species rich site, and site 21 had the least species. The five sites with the lowest richness, each with <15 species, lie close together around Isla Mogo Mogo, Isla Chapera and Isla Bolaños in the northern area of the archipelago, and all were CRs. Isla Elefante and Isla Casaya had the highest fish diversity with the lowest being found at CR sites 22 and 26.

Table 2. Species found during surveys of CRs and CCs in Las Perlas Archipelago, Pacific Panama.

Abudefduf concolor
Abudefduf troschelii
Acanthurus xanthopterus
Aetobatus narinari
Alphestes immaculatus
Aluterus scriptus
Anisotremus caesius
Anisotremus taeniatus
Apogon dovii
Apogon pacifici
Arothron hispidus
Arothron meleagris
Balistes polylepis
Bodianus diplotaenia
Canthigaster punctatissima
Canthingaster jathinopterous
Caranx caballus
Caranx lugubris
Caranx sexfasciatus
Chaetodon humeralis
Chromis atrilobata
Cirrhitichthys oxycephalus
Cirrhitus rivulatus
Diodon holocanthus
Diodon hystrix
Echida nocturna
Echnida nebulosa
Elagatis bipinnulata
Epinephelus analogus
Epinephelus panamensis
Fistularia commersonii
Gerres cinereus
Gnathanodon speciosus
Gymnomuraena zebra
Gymnothorax castaneus
Haemulon flaviguttatum
Haemulon maculicauda
Haemulon scudderi
Haemulon sexfasciatum
Haemulon steindachneri
Halichoeres chierchiae
Halichoeres dispilus
Halichoeres melanotis
Halichoeres nicholsi
Halichoeres notospilus
Hippocampus ingens
Holacanthus passer
Johnrandallia nigrirostris
Kyphosus elegans
Lutjanus aratus
Lutjanus argentiventris
Lutjanus guttatus
Lutjanus inermis
Microlepidotus brevipinnis
Microspathodon bairdii
Microspathodon dorsalis
Muraena clepsydra
Muraena lentiginosa
Mycteroperca xenarcha
Myripristis berndti
Paranthias colonus
Pareques viola
Pomacanthus zonipectus
Prionurus laticlavius
Pseudobalistes naufragium
Rypticus bicolor
Sargocentron suborbitalis
Scarus compressus
Scarus ghobban
Scarus perrico
Scarus rubroviolaceus
Seriola rivoliana
Serranus psittacinus
Stegastes acapulcoensis
Stegastes flavilatus
Sufflamen verres
Synodus lacertinus
Thalassoma lucasanum
Trachinotus stilbe

COMPARISON OF REEF FISH PARAMETERS IN CORAL REEF AND CORAL COMMUNITY HABITATS AND RELATIONSHIPS WITH HABITAT VARIABLES

A two-sample *t*-test revealed a significant difference ($P < 0.05$) in diversity (mean H = 0.819 for CCs, 0.669 for CRs, T = 3.64, $P < 0.001$, df = 28) and species richness (mean species richness = 22.5 for CCs, 18.2 for CRs, T = 2.16, $P = 0.045$, df = 15) between CRs and CCs. However, we found no significant difference between the habitats for mean abundance (T = −0.31, $P = 0.759$, df = 15) and mean length (T = 1.63, $P = 0.120$, df = 18).

The clustering of sites found using non-parametric MDS ordination based on the abundance of fish species surveyed was related significantly to the habitat type (ANOSIM, R = 0.296, $P < 0.001$; Figure 2). Exposure, topography and coverage of massive corals were generally greater in CCs than CRs, whereas branching coral cover was higher in the coral reef sites. BIO-ENV confirmed that the similarity matrix produced from exposure, depth, topography, percentage branching and massive coral cover was significantly correlated with the fish abundance matrix (Table 3; Figure 2). There was also a significant difference in family composition (R = 0.174, $P = 0.026$) between the habitats although this was not great as the difference found using species abundance. Similar habitat variables were found to correlate with this, with the addition of benthic diversity (Table 3). A significant difference in composition between CRs and CCs was also found based on trophic group abundance (R = 0.16, $P = 0.026$). The low R value indicates the two groups were not well separated but similar habitat variables were found to be influential in explaining this pattern, with the addition of sponge cover which was greater in CCs (Table 3). The length composition of fish species on CRs and CCs also differed significantly (R = 0.295, $P < 0.001$) and this was correlated with slope, topography, and the percentage cover of branching coral and CCA (Table 3; Figure 3).

The SIMPER analyses revealed that the average dissimilarity between the two habitats was 51.4%, 36.0%, and 43.8% for species, family, and trophic group abundance, respectively. Differences between the two habitats were due to variation in abundance of *T. lucasanum*, *C. atrilobata*, *Halichoerus dispilus* and *S. acapulcoensis. Thalassoma lucasanum* contributed most to the dissimilarity and was more abundant in CRs, whereas the other three species were more abundant in CCs.

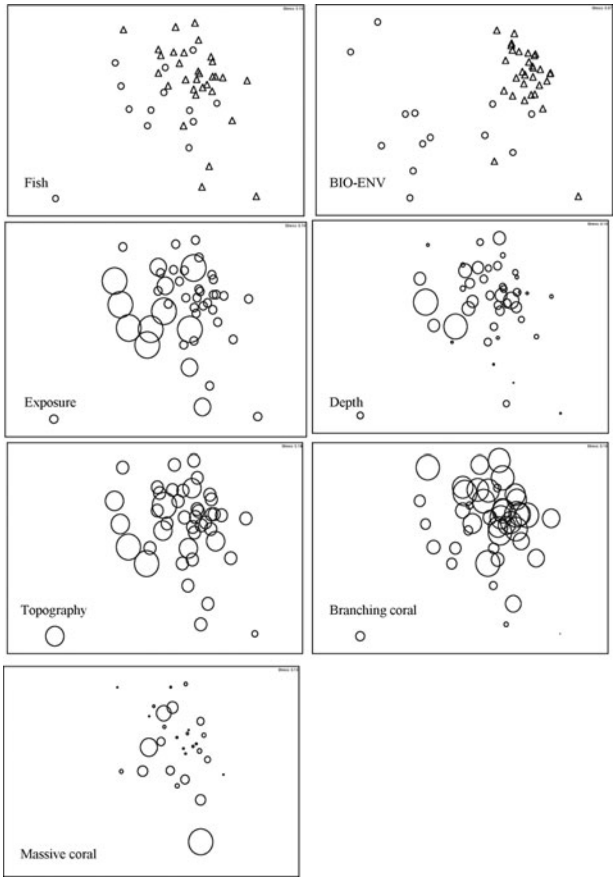

Fig. 2. MDS ordinations of species abundance and habitat variables selected through BIO-ENV. Triangles, coral reef; circles, coral community. Ordinations for habitat variables that showed the highest correlation with the clustering of the species abundance ordination also are shown. Bubble size is proportional to the habitat value at each site.

Table 3. BIO-ENV and RELATE results of the similarity between the multivariate pattern of the fish community and habitat variables. Significance level of $P < 0.05$ is denoted by * and $P < 0.001$ **. ρ, Spearman rank-correlation; H, Shannon diversity of benthic composition; CCA, crustose coralline algae. Stress of the fish and habitat MDS relate to the 2-D MDS configuration.

	Exposure	Depth (m)	Slope	Topography	H	% Soft coral	% Branching coral	% Massive coral	% Laminar coral	% Macro algae	% CCA	% Sponge	Significance level (*P*)	p	Stress Fish MDS	Stress Habitat MDS
Coral reef and coral community sites combined																
Species abundance	✓	✓		✓			✓	✓					0.399	<0.001**	0.19	0.07
Family abundance	✓	✓		✓	✓		✓	✓					0.305	<0.001**	0.18	0.14
Trophic group abundance				✓			✓	✓				✓	0.311	<0.001**	0.12	0.1
Species length			✓	✓			✓				✓		0.408	<0.001**	0.21	0.07
Coral reef sites only																
Species abundance		✓			✓		✓			✓			0.396	0.001**	0.16	0.01
Family abundance		✓		✓	✓		✓	✓		✓			0.323	0.002*	0.15	0.07
Trophic group abundance				✓			✓			✓			0.354	0.001**	0.11	0.01
Species length			✓	✓			✓	✓	✓		✓		0.243	0.026*	0.1	0.07
Coral community sites only																
Species abundance	✓				✓			✓					0.327	0.061	0.01	0.07
Family abundance	✓		✓		✓		✓						0.285	0,069	0.12	0,08
Trophic group abundance								✓				✓	0.367	0.038*	0.07	0.01
Species length	✓							✓				✓	0.434	0.001**	0.1	0.07

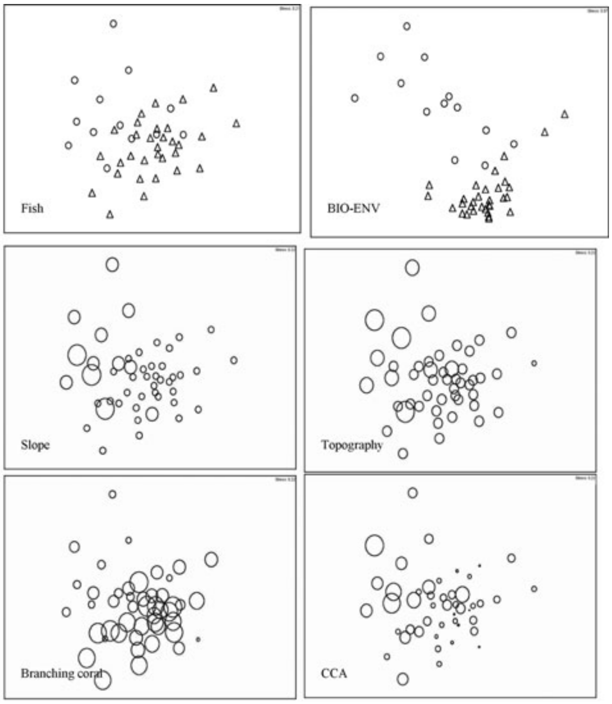

Fig. 3. MDS ordinations of species length and habitat variables selected through BIO-ENV. Triangles, coral reef; circles, coral community. The ordinations for the habitat variables that showed the highest correlation with the pattern of clustering of the MDS ordination of species length also are given. Bubble size is proportional to the habitat value at each site.

Members of the Labridae contributed the most to the dissimilarity in family abundance between the habitats and was the most common family in CRs, whereas members of the Pomacentridae were more abundant in CCs. The abundance of planktivores was important in accounting for the dissimilarity in trophic group composition; they were the most commonly found trophic group in CRs, whereas herbivores were the most abundant in CCs. Plantivores were the dominant trophic group in both habitats although this was higher in CRs (55.4%) compared to CCs (48.2%). Herbivores were the second most dominant group in CCs (22.7%), unlike CRs where invertivores were (20.1%). Herbivores composed 18.3% of the fish in CRs and invertivores 21.1% in CCs.

RELATIONSHIPS BETWEEN REEF FISH PARAMETERS AND HABITAT VARIABLES IN CRS

A positive, significant correlation was found between species richness and the percentage cover of massive corals and Labridae abundance and benthic diversity as well as other non-significant but notable correlations (Table 4). A significant positive correlation existed between Pomacentridae abundance and percentage of CCA. We hypothesized that CCA cover might be positively correlated with topography because the area available for CCA colonization would increase, but an ANOVA revealed no significant difference in mean CCA cover in response to topography category ($F = 0.08$, $P = 0.782$, $df = 1$). Several significant correlations for trophic groups were also found (Table 4). MDS ordinations were run using all variables except topography, slope, and exposure, as these did not

Table 4. Spearman rank-correlation results for coral reef fish parameters and habitat variables. H, Shannon diversity; CCA, crustose coralline algae; *, significant at $P < 0.05$; values in roman type, correlation value; values in italic type, significance value.

	Benthic H	% Branching	% Massive	% Macroalgae	% CCA	% Sponge
H	0.052	−0.048	0.330	0.005	0.061	−0.110
	0.783	*0.798*	*0.070*	*0.979*	*0.743*	*0.557*
Species richness	0.316	−0.155	0.384	0.080	0.042	−0.299
	0.083	*0.404*	*0.033**	0.669	0.823	0.103
Mean abundance	0.274	−0.042	0.030	−0.024	0.174	−0.139
	0.135	*0.824*	*0.871*	*0.899*	*0.350*	*0.456*
Mean length (cm)	−0.108	0.280	0.001	−0.289	0.020	0.029
	0.563	*0.126*	*0.998*	*0.155*	*0.917*	*0.878*
Labridae	0.400	−0.075	−0.143	0.041	0.131	−0.002
	0.026*	*0.687*	*0.444*	*0.828*	*0.483*	*0.992*
Pomacentridae	0.123	0.251	0.090	−0.318	0.369	0.172
	0.509	*0.173*	*0.630*	*0.081*	*0.041**	*0.355*
Seranidae	−0.014	−0.192	0.260	0.212	−0.264	−0.194
	0.940	*0.300*	*0.158*	*0.253*	*0.151*	*0.295*
Tetraodontidae	−0.169	0.128	0.385	−0.156	0.063	−0.110
	0.363	*0.491*	*0.032**	*0.401*	*0.733*	*0.555*
Haemulidae	−0.017	−0.114	0.273	0.097	−0.262	−0.255
	0.930	*0.542*	*0.137*	*0.603*	*0.154*	*0.167*
Chaetodontidae	0.017	−0.270	−0.227	0.237	0.018	0.004
	0.926	*0.141*	*0.220*	*0.199*	*0.924*	*0.983*
Scaridae	0.082	−0.082	0.249	0.143	−0.144	−0.028
	0.659	*0.660*	*0.176*	*0.443*	*0.439*	*0.881*
Pomacanthidae	−0.057	0.299	−0.017	−0.316	0.306	0.088
	0.761	*0.102*	*0.927*	*0.083*	*0.094*	*0.636*
Piscivore	0.029	−0.188	−0.336	0.173	−0.217	−0.141
	0.876	*0.310*	*0.065*	*0.351*	*0.242*	*0.450*
Planktivore	0.364	0.150	−0.032	−0.210	0.325	0.025
	0.044*	*0.420*	*0.864*	*0.256*	*0.074*	*0.895*
Invertivore	0.029	−0.424	0.177	0.380	−0.153	−0.368
	0.876	*0.017**	*0.340*	*0.035**	*0.410*	*0.042**
Invertebrates and fish	−0.084	−0.087	0.283	0.076	−0.142	−0.158
	0.654	*0.641*	*0.123*	*0.685*	*0.445*	*0.395*
Omnivore	−0.159	0.138	−0.156	0.074	−0.085	−0.293
	0.394	*0.140*	*0.403*	*0.691*	*0.648*	*0.109*
Herbivore	0.060	0.251	0.205	−0.301	0.408	0.268
	0.747	*0.173*	*0.268*	*0.100*	*0.023**	*0.145*

change among coral reef sites. Combinations of depth, benthic diversity and the branching coral and macroalgae cover provided the highest significant correlation with the species, family and trophic group abundance similarity matrices (Table 3). Massive and laminar coral cover was found to significantly influence species length composition.

SIMPER analysis revealed that average similarity among coral reef sites was 56.1%, 67.6%, and 61.3% for species, family, and trophic group abundance, respectively. *Thalassoma lucasanum*, *S. acapulcoensis* and *C. Atrilobata* contributed to over 50% of the similarity in species composition among CR sites, with *T. lucasanum* being the most dominant. Labridae and Pomacentridae contributed to over 70% of the similarity in family composition and planktivores contributed most out of the trophic groups to the similarity among sites.

RELATIONSHIPS BETWEEN REEF FISH PARAMETERS AND HABITAT VARIABLES IN CCS

Species richness, mean length and abundance of Pomacentridae, Scaridae and piscivores were positively correlated with CCA cover (Table 5). Unlike CRs an ANOVA test identified a significant difference in the mean CCA cover in response to topography category ($F = 4.75$, $P = 0.035$, $df = 2$), with CCA cover being greater in more topographically complex sites. Seranidae and Chaetodontidae abundance were positively correlated with the coverage of coral cover (Table 5). Herbivore abundance showed a positive significant correlation with the cover of branching coral and a negative correlation with macroalgae cover (Table 5).

The association between habitat variables and fish community composition was not as significant for CCs as it was for coral reef sites. Although combinations of exposure, slope, benthic diversity, and branching and massive coral cover provided the best correlation with the MDS ordinations of species and family abundance in coral community sites, the correlations were not significant (Table 3). However, exposure and the cover of massive coral and sponge were significant in explaining the observed pattern in the ordination produced from trophic group abundance and species length (Table 3).

SIMPER analysis revealed that average similarity among coral community sites was 49.6%, 64.2%, and 57.4% for species, family, and trophic group abundance, respectively. The top three species characterizing CCs were the same as for CRs, except that *S. acapulcoensis* was the main

Table 5. Spearman rank-correlation results for coral community fish parameters and habitat variables. H, Shannon diversity; CCA, crustose coralline algae; *, significant at $P < 0.05$; values in roman type, correlation value; values in italic type, significance value.

	Benthic H	% Branching	% Massive	% Macroalgae	% CCA	% Sponge	% Soft
H	0.166	0.192	−0.234	−0.192	−0.055	−0.239	0.384
	_0.588_	_0.529_	_0.441_	_0.529_	_0.859_	_0.431_	_0.195_
Species richness	0.125	−0.296	−0.356	−0.257	0.550	−0.029	0.487
	_0.684_	_0.326_	_0.232_	_0.396_	_0.050_*	_0.926_	_0.092_
Mean abundance	0.028	−0.269	0.020	−0.137	0.082	−0.219	0.164
	_0.929_	_0.374_	_0.948_	_0.655_	_0.789_	_0.472_	_0.593_
Mean length (cm)	0.453	0.088	−0.613	−0.255	0.665	0.151	0.300
	_0.120_	_0.775_	_0.026_*	_0.459_	_0.013_*	_0.623_	_0.320_
Labridae	0.215	0.022	0.202	−0.313	0.027	0.125	−0.435
	_0.480_	_0.943_	_0.507_	_0.297_	_0.929_	_0.683_	_0.137_
Pomacentridae	0.425	0.077	−0.621	-0.355	0.610	0.256	0.271
	_0.147_	_0.803_	_0.023_*	_0.263_	_0.027_*	_0.398_	_0.370_
Seranidae	0.379	0.547	−0.299	−0.481	−0.135	0.083	−0.051
	_0.262_	_0.053_	_0.320_	_0.096_	_0.611_	_0.788_	_0.869_
Tetraodontidae	0.195	0.429	−0.026	−0.211	−0.008	0.451	−0.516
	_0.523_	_0.143_	_0.932_	_0.490_	_0.979_	_0.122_	_0.071_
Haemulidae	−0.367	−0.511	0.232	0.343	−0.020	−0.208	0.006
	_0.217_	_0.075_	_0.446_	_0.251_	_0.950_	_0.495_	_0.985_
Chaetodontidae	−0.096	−0.067	−0.238	0.092	0.346	−0.135	0.675
	_0.756_	_0.828_	_0.434_	_0.765_	_0.246_	_0.661_	_0.011_*
Scaridae	0.280	−0.344	−0.431	−0.287	0.787	0.096	0.228
	_0.355_	_0.250_	_0.141_	_0.341_	_0.001_*	_0.755_	_0.454_
Pomacanthidae	0.345	0.048	−0.338	−0.507	0.521	0.072	0.303
	_0.249_	_0.876_	_0.258_	_0.077_	_0.068_	_0.815_	_0.314_
Piscivore	0.209	−0.141	−0.282	−0.208	0.557	0.403	−0.331
	_0.493_	_0.646_	_0.350_	_0.495_	_0.048_*	_0.172_	0.269
Planktivore	−0.050	−0.407	0.150	−0.055	0.187	−0.316	0.232
	_0.872_	_0.168_	_0.624_	_0.859_	_0.541_	_0.293_	_0.446_
Invertivore	−0.110	−0.132	0.251	0.060	−0.341	−0.305	−0.102
	_0.719_	_0.668_	_0.407_	_0.845_	_0.255_	_0.312_	_0.741_
Invertebrates and fish	0.144	0.275	−0.207	−0.352	−0.135	−0.088	0.130
	_0.639_	_0.363_	_0.498_	_0.238_	0.661	_0.774_	_0.672_
Omnivore	−0.116	−0.022	0.136	0.181	0.000	−0.279	0.057
	_0.706_	_0.943_	_0.658_	_0.553_	_1.000_	_0.356_	_0.854_
Herbivore	0.564	0.571	−0.523	−0.654	0.137	0.658	−0.170
	_0.045_*	_0.041_*	_0.067_	_0.015_*	_0.655_	_0.015_*	_0.580_

contributing species. CCs also had a greater number of typical species compared to CRs, and in particular *Halichoerus* species were important. The main families were similar to those from CRs, except that the Pomacentridae was the top contributory family. Additionally, the Chaetodontidae was as a typical family for CCs but not for CRs.

DISCUSSION

Composition

Generally, the CRs and communities of the LPA surveyed in this study were dominated by relatively few species, by three main families (Labridae, Pomacentridae and Haemulidae) similar to Dominici-Arosemena & Wolff (2006), and by small individuals and species. For the sites surveyed, coral community sites had higher mean abundance, length, species richness, and diversity compared to CRs. We found a significant difference in composition between the two habitats for species, family, and trophic group abundance and for species length, with the largest difference between the habitats being found for species abundance and length composition. Although the ANOSIM analyses detected a significant difference in species composition, the fairly low R value indicates that an overlap between the habitats exists. The habitats were dominated by similar species, although the abundances varied and CCs had more typifying species than CRs, meaning that the similarity of species composition among coral community sites was lower than that of CRs. The composition of family and trophic group composition was similar both between habitats and within habitats.

Reef fish–habitat relationships

The results of this research suggest that reef fish communities in the LPA are influenced to some degree by the structure of their habitat. A combination of topography, exposure, depth, and the percentage of branching and massive corals consistently correlated with the pattern of clustering observed in the fish ordinations for both habitats. The relative importance of these environmental variables could not be easily separable without experimental manipulation, but we concluded that they act together and can account for some of the observed differences in community structure. However, the literature (Luckhurst & Luckhurst, 1978; Chabanet *et al.*, 1997; Connell & Kingsford, 1998; Friendlander & Parrish, 1998; Lara & Gonzalez, 1998; Öhman & Rajasuriya, 1998; Nagelkerken *et al.*, 2000; Dominici-Arosemena & Wolff, 2005, 6; Gratwicke & Speight, 2005a; Brokovich *et al.*, 2006; Garpe *et al.*, 2006; Kuffner *et al.*, 2007) provides reason to believe that topographical complexity is one of the most influential environmental factors on fish community composition and where it is reduced by disturbance it has negative effects (Wilson *et al.*, 2006).

At the outset of this research we noted the striking physical difference between the CRs and CCs of the LPA. The CCs have greater vertical height and topography with outcrops, crevices, and boulders, around which fish were seen to aggregate (*sensu* Grigg 1994; Parrish & Boland 2004; Gratwicke & Speight, 2005b), in contrast to the structurally simple CRs. More rugose sites offer a larger surface area for colonization by algae, gorgonians and sponges. Thus, these sites can have higher productivity and provide more microhabitats and resources to support fish populations, thereby resulting in higher diversity, greater species richness, larger fish, and higher abundances (Connell & Kingsford, 1998; Dominici-Arosemena & Wolff, 2005; Espinoza & Salas, 2005; Gratwicke & Speight, 2005a, b). The higher complexity of coral community sites is an explanation for the differences observed (Öhman & Rajasuriya, 1998) and the lower complexity of CRs may account for the greater similarity in species composition amongst coral reef sites.

Branching coral cover and exposure were correlated with habitat type. CRs were found in more sheltered sites compared to CCs due to their inability to develop in locations exposed to upwelling (Glynn & Stewart, 1973). Exposure also contributed to differences in species length composition between CC sites. In studies of coral and rocky reefs, researchers found that exposure influenced species composition and fish length (Ferreira *et al.*, 2001; Arreola-Robles & Elorduy-Garay, 2002; Dominici-Arosemena & Wolff, 2005), which concurs with our findings. CRs had a much higher coverage of branching coral than CCs, which we expected because these corals form the basic structure of CRs in the LPA. Branching coral cover helps explain the pattern of clustering we observed in the CR fish ordinations and supports previous work showing its importance (Bouchon-Navaro & Bouchon, 1989; Chabanet *et al.*, 1997; Connell & Kingsford, 1998; Jones *et al.*, 2004; Bozec *et al.*, 2005; Wilson *et al.*, 2006, 2008). This parameter also correlated negatively with invertivores within coral reef sites, which contradicts findings by Connell & Kingsford (1998). We did find a positive relationship between live branching coral cover and the Serranidae, in agreement with Connell & Kingsford (1998). In the current research, members of the Serranidae associated closely with branching corals in both habitats and used these structures as refuge sites (e.g. *Epinephelus analogus* and *Serranus psittacinus*). Herbivores also were positively correlated with live branching coral cover within coral community sites, and a similar pattern was observed by Öhman & Rajasuriya (1998). Filamentous algae grow on and between the colonies and branches of the coral provide a food source (Öhman & Rajasuriya, 1998) and many of the herbivorous members of the Pomacentridae, which were common in this habitat, utilize branching coral for shelter (Wellington, 1982; Öhman & Rajasuriya, 1998).

The percentage cover of live massive coral was important in explaining the difference in community structure between CRs and CCs and explained some of the observed differences in species length composition in CR sites and trophic group composition within CCs. Massive corals generally were more abundant in CCs as their colonization and growth are not as restricted compared to CRs where they are limited to deeper areas because of the dominance of branching corals (Glynn & Maté, 1996; Maté, 2003). During the surveys we found different species (e.g. *Microspathodon dorsalis*, *Holacanthus passer*, *Abudefduf troschelii* and members of Balistidae) aggregating around the massive coral species compared to those generally found around the *Pocillopora* coral framework. This is supportive of the work of Dominici-Arosemena & Wolff (2005) who found the presence of massive corals was related to higher levels of species richness and diversity. Thus, massive corals, especially when large (>1 m diameter) increase the variety of growth forms and provide areas of topographical complexity in a landscape of low variability, which attract fish. Massive corals provide microhabitats that offer refuge and food (e.g. crabs, tunicates, bivalves and brittlestars; Glynn & Maté, 1996) that boost fish species richness and alter the abundance of certain groups, e.g. Balistidae, invertivores and omnivores. The positive relationship between Tetradontidae and the abundance of massive corals can be explained by the preference of this family for this food resource (Guzman & Robertson, 1989). In our study, the species found associated with the massive corals were generally larger which would account for the correlation between massive corals and the species length ordination for coral community sites.

We also found that benthic diversity, macroalgal cover, and CCA cover showed correlations in the MDS ordinations and univariate methods. Previous studies have also reported positive correlations between benthic diversity and fish diversity, species richness, and abundance on coral and rocky reefs (Roberts & Ormond, 1987; Chabanet *et al.*, 1997; Öhman & Rajasuriya, 1998; García-Charton & Pérez-Ruzafa, 2001). Sites with higher benthic diversity offer a wider variety of habitats and resources to meet the needs of more species. The negative relationship between algae cover and herbivore abundance in CCs found in this study is similar to that reported by Williams & Polunin (2001), but it contradicts other results (Chabanet *et al.*, 1997; Friedlander & Parrish, 1998).

Crustose corralline algae was found to correlate positively with several fish parameters and families in CCs with Pomacentridae and herbivore abundance on CRs. CCA is a food resource for herbivores, such as the Scaridae, which scrape it from substrate surfaces (Williams & Polunin, 2001). Correlations with the Pomacentridae on CRs can be attributed to space: members of the Pomacentridae family guard algal territories, where there is potential for macroalgae and CCA to take hold where coral is unable to colonize. In the CCs, CCA cover was significantly higher in more topographically complex sites and therefore, some of the correlations detected for CCs may relate to topography.

CONCLUSION

Our results suggest that the structure reef fish communities in the LPA are determined more by the large scale structural features that characterize the two habitats (e.g. topographical complexity, exposure and branching coral cover) than by those that vary over small scales (i.e. the size of a transect). However, we found small-scale differences, e.g. in massive coral cover, had a localized impact on fish communities. Based on these findings and the dominance of CCs in the LPA (Benfield *et al.*, 2007; Guzman *et al.*, 2008), we conclude that the contribution of tropical rocky reefs to fish diversity should not be overlooked, especially in biogeographical regions where CRs are impoverished.

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REFERENCES

Adjeroud M., Letourner Y., Procher M. and Salvat B. (1998) Factors influencing spatial distribution of fish communities on a fringing reef at Mauritius, SW Indian Ocean. *Environmental Biology of Fishes* 53, 169–182.

Allen G.R. and Robertson D.R. (1994) *Fishes of the tropical Eastern Pacific*. Honolulu: University of Hawaii Press.

Arreola-Robles J.L. and Elorduy-Garay J.F. (2002) Reef fish diversity in the region of La Paz, Baja California Sur, Mexico. *Bulletin of Marine Science* 70, 1–18.

Ault T.R. and Johnson C.R. (1998) Spatially and temporally predictable fish communities on CRs. *Ecological Monographs* 68, 25–50.

Bell J.D. and Galzin R. (1984) Influence of live coral cover on coral-reef fish communities. *Marine Ecology Progress Series* 15, 265–274.

Benfield S.L., Guzman H.M., Mair J.M. and Young J.A.T. (2007) Mapping the distribution of coral reefs and associated sublittoral habitats in Pacific Panama: a comparison of optical satellite sensors and classification methodologies. *International Journal of Remote Sensing* 28, 5047–5070.

Bouchon-Navaro Y. and Bouchon C. (1989) Correlation between Chaetodontid fishes and coral communities of the Gulf of Aqaba Red Sea. *Environmental Biology of Fishes* 25, 47–60.

Bozec Y.M., Dolédec S. and Kulbick M. (2005) An analysis of fish–habitat associations on disturbed coral reefs: chaetodontid fishes in New Caledonia. *Journal of Fish Biology* 66, 966–982.

Brokovich E., Baranes A. and Goren M. (2006) Habitat structure determines coral reef fish assemblages at the northern tip of the Red Sea. *Ecological Indicators* 6, 494–507.

Carpenter K.E., Miclat R.I., Albaladejo V.D. and Corpuz V.T. (1981) The influence of substrate structure on the local abundance and diversity of Philippine reef fishes. In *Proceedings of the 4th International Coral Reef Symposium, Manila*, Volume 2. Manila: International Society for Reef Studies; pp. 497–502.

Chabanet P., Ralambindrainy H., Amanieu M., Faure G. and Galzin R. (1997) Relationships between coral reef substrata and fish. *Coral Reefs* 16, 93–102.

Chapman M.R. and Kramer D.L. (1999) Gradients in coral reef fish density and size across the Barbados Marine Reserve boundary: effects of reserve protection and habitat characteristics. *Marine Ecology Progress Series* 181, 81–96.

Clarke K.R. and Ainsworth M. (1993) A method of linking multivariate community structure to environmental variables. *Marine Ecology Progress Series* 92, 205–219.

Clarke K.R. and Gorley R.N. (2001) *PRIMER v5: User manual/tutorial.* Plymouth: PRIMER-E

Clarke K.R. and Warwick R.M. (2001) *Change in marine communities: an approach to statistical analysis and interpretation*, 2nd edition. Plymouth: PRIMER-E

Connell S.D. and Kingsford M.J. (1998) Spatial, temporal and habitat-related variation in the abundance of large predatory fish at One Tree Reef, Australia. *Coral Reefs* 17, 49–57.

Cortés J. 1997. Biology and geology of Eastern Pacific coral reefs. *Coral Reefs* 16, S39–S46.

Dominici-Arosemena A. and Wolff M. (2005) Reef fish community structure in Bocas del Toro (Caribbean Panama): gradients in habitat complexity and exposure. *Caribbean Journal of Science* 41, 613–637.

Dominici-Arosemena A. and Wolff M. (2006) Reef fish community structure in the Tropical Eastern Pacific (Panamá): living on a relatively stable rocky reef environment. *Helgoland Marine Research* 60, 287–305.

Eagle J.V., Jones G.P. and McCormick M.I. (2001) A multi-scale study of the relationships between habitat use and the distribution and abundance patterns of three coral reef angelfishes (Pomacanthidae). *Marine Ecology Progress Series* 214, 253–265.

Espinoza M. and Salas E. (2005) Structure of reef fish communities in Catalinas Islands and Ocotal beach, North Pacific of Costa Rica. *Revista de Biología Tropical* 53, 523–536.

Ferreira C.E.L., José E.A., Gonçalves J.E.A. and Coutinho R. (2001) Community structure of fishes and habitat complexity on a tropical rocky shore. *Environmental Biology of Fishes* 61, 353–369.

Friedlander A.M., Brown E.K., Jokiel P.L., Smith W.R. and Rodgers K.S. (2003) Effects of habitat, wave exposure, and marine protected area status on coral reef fish assemblages in the Hawaiian archipelago. *Coral Reefs* 22, 291–305.

Friedlander A.M. and Parrish J.D. (1998) Habitat characteristics affecting fish assemblages on a Hawaiian coral reef. *Journal of Experimental Marine Biology and Ecology* 224, 1–30.

Froese R. and Pauly D. (2005) *FishBase.* Website address: http://www.fishbase.org

García-Charton J.A. and Pérez-Ruzafa Á. (2001) Spatial pattern and the habitat structure of a Mediterranean rocky fish local assemblage. *Marine Biology* 138, 917–934.

Garpe K.C., Yahya S.A.S., Lindahl U. and Öhman M.C. (2006) Effects of the 1998 coral bleaching event on reef fish assemblages. *Marine Ecology Progress Series* 315, 237–247.

Glynn P.W. (1976) Some physical and biological determinants of coral community structure in the eastern Pacific. *Ecological Monographs* 46, 431–456.

Glynn P.W. and Maté J.L. (1996) Field guide to the Pacific coral reefs of Panama. In *Proceedings of the 8th International Coral Reef Symposium Panama City, Panama*, Volume 1. Balhom, Panama: pp. 145–166.

Glynn P.W. and Stewart R.H. (1973) Distribution of coral reefs in the Pearl Islands (Gulf of Panama) in relation to thermal conditions. *Limnology and Oceanography* 18, 367–379.

Gratwicke B. and Speight M.R. (2005a) The relationship between fish species richness, abundance and habitat complexity in a range of shallow tropical marine habitats. *Journal of Fish Biology* 66, 650–667.

Gratwicke B. and Speight M.R. (2005b) Effects of habitat complexity on Caribbean marine fish assemblages. *Marine Ecology Progress Series* 292, 301–310.

Grigg R.W. (1994) Effects of sewage discharge, fishing pressure and habitat complexity on coral ecosystems and reef fishes in Hawaii. *Marine Ecology Progress Series* 103, 25–34.

Guzman H.M., Benfield S., Breedy O. and Mair J.M. (2008) Broadening reef protection across the Marine Conservation Corridor of the Eastern Tropical Pacific: distribution and diversity of reefs in Las Perlas Archipelago, Panama. *Environmental Conservation* 35, 46–54.

Guzman H.M., Guevara C.A. and Breedy O. (2004) Distribution, diversity, and conservation of coral reefs and coral communities in the largest marine protected area of Pacific Panama (Coiba Island). *Environmental Conservation* 31, 111–121.

Guzman H.M. and Robertson D.R. (1989) Population and feeding responses of the corallivorous pufferfish *Arothron meleagris* to coral mortality in the eastern Pacific. *Marine Ecology Progress Series* 55, 121–131.

Huntsman G.R. and Waters J.R. (1987) Development of management plans for reef fishes—Gulf of Mexico and US South Atlantic. In Polovina J.J. and Ralston S. (eds) *Tropical snappers and groupers: biology and fisheries management*. Boulder, Colorado: Westview Press, pp.533–560.

Jones G.P. and Syms C. (1998) Disturbance, habitat structure and the ecology of fishes on coral reefs. *Australian Journal of Ecology* 23, 287–297.

Jones G.P., McCormick M.I., Srinivasan M. and Eagle J.V. (2004) Coral decline threatens fish biodiversity in marine reserves. *Proceedings of the National Academy of Sciences* 101, 8251–8253.

Kramer P., Lang J., Marks K., Garza-Pérez R. and Ginsburg R.N. (2005) *Atlantic and Gulf Rapid Reef Assessment Methodology.* Website: http://www.agrra.org/method/methodhome.htm

Kuffner I.B., Brock J.C., Grober-Dunsmore R., Bonito V.E., Hickey T.D. and Wright C.W. (2007) Relationships between reef fish communities and remotely sensed rugosity measurements in Biscayne National Park, Florida, USA. *Environmental Biology of Fishes* 78, 71–82.

Lara E.N. and Gonzalez E.A. (1998) The relationship between reef fish community structure and environmental variables in the southern Mexican Caribbean. *Journal of Fish Biology* 53, 209–221.

Lecchini D., Adjeroud M., Pratchett M.S., Cadoret L. and Galzin R. (2003) Spatial structure of coral reef fish communities in the Ryukyu Islands, southern Japan. *Oceanologica Acta* 26, 537–547.

Lirman D. (1999) Reef fish communities associated with *Acropora palmata*: relationships to benthic attributes. *Bulletin of Marine Science* 65, 235–252.

Luckhurst B.E. and Luckhurst K. (1978) Analysis of the influence of substrate variables on coral reef fish communities. *Marine Biology* 49, 317–323.

Maté J.L. (2003) Corals and coral reefs of the Pacific coast of Panama. In Cortés J. (ed.) *American Coral Reefs*. Amsterdam: Elsevier Science BV, pp. 387–417.

McClanahan T.R. and Arthur R. (2001) The effect of marine reserves and habitat on populations of east African coral reef fishes. *Ecological Applications* 11, 559–569.

McGehee M.A. (1994) Correspondence between assemblages of coral reef fishes and gradients of water motion, depth, and substrate size off Puerto Rico. *Marine Ecology Progress Series* 105, 243–255.

Nagelkerken I., Dorenbosch M., Verberk W.C.E.P., Cocheret de la Morinière E. and van der Velde G. (2000) Importance of shallow-water biotopes of a Caribbean bay for juvenile coral reef fishes: patterns in biotope association, community structure and spatial resolution. *Marine Ecology Progress Series* 202, 173–192.

Öhman M.C. (1998) *Aspects of habitat and disturbance effects on tropical reef fish communities*. Sweden: Stockholm University.

Öhman M.C. and Rajasuriya A. (1998) Relationships between habitat structure and fish communities on coral and sandstone reefs. *Environmental Biology of Fishes* 53, 19–31.

Parrish F.A. and Boland R.C. (2004) Habitat and reef-fish assemblages of banks in the northwestern Hawaiian Islands. *Marine Biology* 144, 1065–1073.

Roberts C.M. and Ormond R.F.G. (1987) Habitat complexity and coral reef fish diversity and abundance on Red Sea fringing reefs. *Marine Ecology Progress Series* 41, 1–8.

Wellington G.M. (1982) Depth zonation of corals in the Gulf of Panama: control and facilitation by resident reef fishes. *Ecological Monographs* 52, 223–241.

Williams I.D. and Polunin N.V.C. (2001) Large-scale associations between macroalgal cover and grazer biomass on mid-depth reef in the Caribbean. *Coral Reefs* 19, 358–366.

Wilson S.K., Graham N.A.J., Pratchett M.S., Jones G.P. and Polunin N.V.C. (2006) Multiple disturbances and the global degradation of coral reefs: are reef fishes at risk or resilient? *Global Change Biology* 12, 2220–2234

and

Wilson S.K., Burgess S.C., Cheal A.J., Emslie M., Fisher R., Miller I., Polunin N.V.C. and Sweatman H.P.A. (2008) Habitat utilization by coral reef fish: implications for specialists vs. generalists in a changing environment. *Journal of Animal Ecology* 77, 220–228.

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