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Differences between protected and unprotected reefs of the western Caribbean in attributes preferred by dive tourists

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Summary

Tropical marine protected areas (MPAs) may promote conditions that are attractive to dive tourists, but a systematic basis for assessing their effectiveness in this regard is currently lacking. We therefore interviewed 195 dive tourists in Jamaica to determine which reef attributes they most preferred to see on dives. Attributes relating to fishes and other large animals ('big fishes', 'other large animals', 'variety of fishes', 'abundance of fishes', and 'unusual fishes') were more appreciated than those relating to reef structure and benthos ('reef structure e.g., drop-offs', 'variety of corals', 'large corals', 'coral cover', 'unusual corals', 'sponges', 'unusual algae', 'lobsters, crabs etc.'). We then surveyed reef condition with regard to those aspects (abundance and variety of fishes, number of 'unusual', and number of 'large' fish) at four Caribbean MPAs and reference areas. In two cases, Hol Chan Marine Reserve in Belize and Parque Nacional Punta Frances in Cuba, these fish attributes were more pronounced in the MPAs than in the reference areas. Differences between the Montego Bay Marine Park in Jamaica (MBMP) and adjacent reference areas were mainly restricted to shallow sites (<6m), while at Grand Cayman no differences between fully protected and partially protected areas were detected. Management had not been fully effective in the MBMP in the preceding months, while fishing pressure in the partially protected areas on Grand Cayman was very light. We conclude that, if fishing restrictions are well enforced, western Caribbean MPAs can be expected to be effective in ways appreciated by dive tourists.

Keywords: conservation, fishes, management, reefs, divers, tourism, marine parks

Introduction

Globally, purposes of marine protected areas (MPAs) are varied (Jones 1994), but in the Caribbean the most widespread benefit appears to be derived from tourism (Dixon *et al*. 1995). Tourism contributes very substantially to the economies of many of the island countries concerned (Blommenstein 1985) and diving may locally be an important contributor to that income (Dixon *et al*. 1995). In spite of this, there appears to have been little consideration to date, for the Caribbean or further afield, of whether MPAs really are beneficial in ways relevant to the dive-tourism industry. It seems likely that the build up of fish populations within effectively managed MPAs (Polunin & Roberts 1993; McClanahan 1994; Jennings *et al*. 1996; McClanahan & Kaunda-Arara 1996; Rakitin & Kramer 1996; Russ & Alcala 1996; Wantiez *et al*. 1997) would make such areas more attractive to dive tourists, but few previous studies have investigated which aspects of reef condition are most preferred by dive tourists. Therefore, there is, as yet, no systematic basis for assessing how effective MPAs are in this regard.

The aims of this study were to determine which attributes of coral reefs are most important to dive tourists, and then to assess whether reef condition within four Caribbean MPAs (at Montego Bay, Jamaica; Ambergris Caye, Belize; Isle of Youth, Cuba; and Grand Cayman) differed from unprotected or less-protected references areas with respect to those attributes.

Methods

Diver preference survey

The preferences of divers for reef attributes were surveyed using questionnaires distributed to tourist divers in Negril and Montego Bay, Jamaica. Divers were selected haphazardly from those disembarking from boats after dive trips and asked to complete the questionnaire. In total, ten dive operators were visited between March and April 1997, and 195 completed questionnaires were returned to us. The principal question was 'what are the features of the marine environment which you most prefer to see on a dive?'. Respondents were asked to rank each of 14 attributes: 'reef structure, e.g. drop-offs'; 'big fishes'; 'other large animals'; 'variety of fishes'; 'abundance of fishes'; 'variety of corals'; 'large corals'; 'coral cover'; 'unusual fishes'; 'unusual corals'; 'sponges'; 'unusual algae'; 'lobsters crabs, etc.'; 'other') on a scale from 0 (not at all important) to 5 (most preferred). We also asked dive tourists to rate the diving locality for each of the reef attributes on the same point scale (0 lowest, 5 highest).

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Table 1 Summary of survey locations. Survey areas within MPAs are labelled with a 'P' and unprotected, or less-protected, reference areas with a 'U'.

Location	*Survey period*	*Reef*	*Shallow areas*	*Deep areas*	*Position*
Montego Bay, Jamaica	4/97	Montego Bay MR	P	P	77° 56.0' W, 18° 29.6'N
		Airport Reef	U	U	77° 55.4' W, 18° 30.3'N
Ambergris Caye, Belize	9/97	Hol Chan MR	P	P	87° 58.6' W, 17° 52.1'N
		San Pedro Cut	U1	U1	87° 56.5' W, 17° 56.1'N
		Mata Cut	U2		87° 54.9' W, 17° 58.6'N
		Mexico Rocks Cut		U2	87° 54.1' W, 17° 59.7'N
		Caye Caulker Cut		U3	87° 59.3' W, 17° 48.4'N
Grand Cayman, Cayman Islands	10/97	'Protected' zones		P1	81° 23.4' W, 19° 20.3'N
				P2	81° 24.1' W, 19° 21.8'N
		'Replenishment' zones		U1	81° 23.7' W, 19° 21.5'N
				U2	81° 23.5' W, 19° 18.7'N
Isle of Youth, Cuba	4/98	Punta Frances MR		P1	83° 10.4' W, 21° 36.4'N
				P2	83° 09.7' W, 21° 35.3'N
		Punta del Este		U1	82° 31.5' W, 21° 32.8'N
				U2	82° 35.8' W, 21° 31.2'N

Study areas

Between April 1997 and April 1998, after completion and analysis of the diver preference survey, we surveyed coral reef condition in MPAs and reference areas at four locations in the Caribbean: Montego Bay, Jamaica (Montego Bay Marine Park); Ambergris Caye, Belize (Hol Chan Marine Reserve); Grand Cayman, Cayman Islands (protected areas on the west coast); and the Isle of Youth, Cuba (Parque Nacional Punta Frances) (Table 1, Fig. 1). Depending on the number and size of protected areas, and the presence of suitable areas for comparison, between two and four reef areas were surveyed at each location, each 'reef area' consisting of a stretch of approximately 2 km of reef front. As far as was possible, reference areas were chosen that were close to the MPA, and ideally from the same continuous stretch of reef. Each area was sampled by dividing the reef into equal length sections of 125–150 m and randomly selecting five or six sections as survey sites. Gently sloping or flat sections of reef were selected in all cases. Surveys were conducted on 'deep' forereef sites (depth 12–15 m) at all locations, and also on 'shallow' reefs at Montego Bay (fringing reefs, depth <6 m) and at Ambergris Caye (behind reef crest, depth <2 m), the only locations with suitable reef habitat in shallow water.

Figure 1 Study locations, circles indicate the study areas. MPAs are represented by open circles (**o**), and fished areas by closed circles (●). North is indicated in each map by a bold arrow.

The Hol Chan Marine Reserve lies at the southern tip of Ambergris Caye, Belize, and includes approximately 1.8 km of reef-front which has been closed to fishing since 1987. The Reserve is centred on a deep channel through the reef known as the Hol Chan Cut; the three unprotected areas were therefore also centred around cuts in the same reef (Polunin & Roberts 1993), namely the northern Caye Caulker Cut (the closest cut south of Hol Chan, 6 km from Hol Chan Cut), and the two closest cuts north of Hol Chan, one in front of San Pedro Town (4 km north of Hol Chan) and the other, Mexico Rocks/Mata Cut, another 8km further north. Violations of the no-fishing rule within the MPA were believed to be rare (Miguel Alamilla, Hol Chan Marine Reserve manager, personal communication September 1997), partly because a ranger was always present in the Reserve between 0900 and 1700 hr to collect park-use fees, but also because of strong local support for the Reserve.

The entire western end of Grand Cayman, consisting of more than 15 km of continuous coastline and associated reefs, falls within the Cayman Islands marine park system. It is divided into three 'marine park' zones, which are closed to all fishing, and two 'replenishment' zones, in which recreational line fishing is allowed. Reef development is patchy in the southern-most 'marine park' zone in front of Georgetown harbour, and reefs on the northern and southern coasts of Grand Cayman are very different in terms of general appearance and structure from those in the protected areas. We therefore surveyed only those reefs in the two 'replenishment' and the two northerly 'marine park' zones. The comparison was therefore between fully protected and less protected areas in a region where fishing is not intense.

The first marine park in Montego Bay Jamaica was established in 1966, but, in its current form, the Montego Bay Marine Park (MBMP) was opened in 1992. In the core area of the MBMP, consisting of approximately 2 km of reef front, spearfishing is banned but trap fishing allowed, so that the comparison in this study was between partially protected and unprotected areas. In this case, the single protected area in the MBMP was compared with an adjacent reef area immediately east of the marine park.

Licences have not been given for fishing in the Parque Nacional Punta Frances in Cuba (PNPF) for 20 years and the area is considered to have been protected effectively for that time (Jorge Angulo, University of Havana, personnel communication April 1998). The PNPF contains about 20 km of nearly continuous reef front, comprising virtually all the reef areas at the south-western edge of the Isle of Youth, and therefore we were unable to find comparable fished reef areas immediately adjacent to the protected areas. Consequently, both fringing and barrier reef areas within the PNPF were compared with reef areas around Punta del Este, off the south-eastern end of the same island. The fringing reef areas compared were approximately 63 km apart and the barrier reefs 70 km apart, for want of closer reference area with similar aspect and general habitat conditions to the Cuban MPA.

Quantification of fish populations

Fish counts were made by a single diver throughout, using a variation of the stationary underwater visual census method (Bohnsack & Bannerot 1986), in which target fishes were counted within an imaginary cylinder of fixed diameter extending from the reef up to the water surface. Fishes in six families, namely snappers (Lutjanidae), groupers (Serranidae), surgeonfishes (Acanthuridae), parrotfishes (Scaridae), triggerfishes (Balistidae), and grunts (Haemulidae), were counted. Relatively mobile fishes (Balistidae and pelagic Lutjanidae, i.e. *Ocyurus chrysurus*) were counted before entering the cylinder. A diameter line was then laid out and the remaining target families counted in three slow 360° turns with, where possible, the observer remaining in the centre of the cylinder. The aim was to make an instantaneous count in each sweep. In the first sweep, acanthurids were counted, in the next, haemulids and demersal lutjanids were counted, and in the last, scarids were counted. Because of the tendency for serranids to retreat into crevices but otherwise to be relatively stationary, the position of serranids was noted on all sweeps unless it was obvious that they had just moved into the cylinder.

Fish were identified to species and an estimated length (cm) was recorded for each individual. Only fishes estimated to be longer then 12cm were recorded, because we considered that smaller fishes would not be vulnerable to fishing. For each fish censused, biomass was estimated using previous published length–weight relationships for Caribbean fishes (Bohnsack & Harper 1988). Accuracy of length estimates was established by initially practising with pre-cut lengths of electrical cable of known length and then maintained by regularly checking estimates of length of benthic objects with a scale on the side of the recording slate. Mean fish density per site was estimated from the average of four replicate cylinders of diameter 15 m (Montego Bay) or five 10 m diameter cylinders (Ambergris Caye, Grand Cayman, Isle of Youth). Fish counts were conducted on areas of hard-bottom, haphazardly separated by approximately 25 m.

Modification to survey methodology for Belize shallow sites

Shallow reef areas in front of Ambergris Caye are very patchy, with small areas of coral separated by large areas of seagrass and sand. The most consistent habitat among study areas was deemed to be the 1–2 m deep rubble zone approximately 50–100 m behind the reef crest, and therefore sites were selected from that zone. As the habitat is comparatively flat, and absolute fish density was low, the sample size of fish counts at each site was increased to six replicates and, rather than do instantaneous counts, all fishes within or passing through the 10 m diameter cylinder were counted in a 10-minute period.

Quantification of habitat characteristics

With a view to controlling for any broad habitat differences among sites censused, visual estimates were also made of dominant components of the benthos within each census area (i.e. % coral, % sand, % rubble, and where relevant % seagrass). The structural complexity (rugosity) of the substratum was also estimated on a 6 point scale: 0 = no vertical relief; 1 = low and sparse relief; 2 = low, but widespread relief; 3 = moderately complex; 4 = very complex with numerous caves and fissures; and 5 = exceptionally complex with high coral cover and numerous caves and overhangs. All habitat estimates were performed by the same observer.

Data analysis

Diver preference data

The main criterion for assessing diver preferences was the average rating given to each of the reef attributes. Mann-Whitney tests were used to identify significant differences in median rating between each pair of attributes (1-tailed,

$p < 0.05$). So that we could investigate what aspects of reef condition divers were most disappointed by at locations where both fish and coral communities are considered to be substantially degraded (Goreau 1992; Hughes 1994), we calculated a 'disappointment' rating for each attribute by subtracting the rating of reef condition from the rating of importance. We assumed that improvements in the attributes with highest disappointment ratings would be among those most appreciated by dive tourists.

Fish census data

To better explore the nature of any possible differences between protected and unprotected fish assemblages, fish data were analysed by trophic groups derived from the diet-composition data of Randall (1967). Three trophic groups were defined: (1) invertebrate-feeder/generalized carnivore (fish comprising <50% diet); (2) herbivore; and (3) piscivore (fish > 50% diet) (Table 2). Two other categories were also used: 'big' fish and 'unusual' fish. At most sites there were sufficient data for statistical analysis of 'big' fish only if all fish longer than 20 cm were considered 'big', but where there were sufficient data, a more restrictive category, abundance of all fishes longer than 30 cm, was also tested. 'Unusual' fish was a *posthoc* category: fish were considered 'unusual' if they were present in 25% or less of all samples.

Within study locations, differences among areas in terms of fish species richness, abundance and biomass were tested using ANOVA, and, where suitable, Tukey's studentized range test was used to distinguish significant pairwise differences. The Belize and Jamaica data sets both consisted of data from one protected area and one or more unprotected areas and so areas were compared using one-way ANOVAs, but data from Grand Cayman and Cuba, where two protected areas were compared with two unprotected areas, were analysed using two-way designs. For the Cuban data, a crossed design was used with reef-type (fringing or barrier) and protection level ('protected' or 'unprotected') as the two factors. For the Caymanian data, a two-way nested ANOVA was used with area nested under protection level. Prior to analysis, abundance, biomass and species richness data were tested for homoscedasticity (Levene's test) and where necessary ln (x + 1), or in one case $\sqrt{\ }\sqrt{\ }$ transformations, were applied.

Power of statistical tests

A common tendency for there to be large variability associated with fish census data means that statistical tests to detect reserve/fishing effects often have low power to detect other than very large effects, as sufficient replication to detect smaller differences is impractical (DeMartini *et al.* 1996; Jennings & Kaiser 1998). We therefore calculated the power of each ANOVA to detect two-fold differences in density among survey areas using the method of Sokal and Rohlf (1981). In a small number of cases, differences in mean density among different reef areas were considerable but the power of tests was low (<30%). In these cases, in recognition of the possibility of type II statistical error (accepting the null hypothesis of no difference among areas, when it should be rejected), we indicate where the results of ANOVA were 'marginally significant', i.e. test had low power and $p < 0.1$.

Table 2 Fishes recorded in the census, unusual status (R = present in <25% of surveys) and trophic groups, derived from Randall (1967): IV, invertebrate-feeder/generalized carnivore (fish < 50% diet); HB, herbivore; PK, planktivore ; PV, piscivore (fish > 50% diet).

	Trophic group	*Unusual*
Acanthuridae		
Acanthurus bahianus	HB	
A. chirurgus	HB	
A. coeruleus	HB	
Balistidae		
Balistes vetula	IV	R
Melichthys niger	PK	
Haemulidae		
Anisotremus surinamensis	IV	R
A. virginicus	IV	R
H. album	IV	R
H. aurolineatum	IV	R
H. carbonarium	IV	R
H. chrysargyreum	IV	R
H. flavolineatum	IV	
H. parrai	IV	R
H. plumieri	IV	
H. sciurus	IV	
Lutjanidae		
Lutjanus analis	IV	R
L. apodus	PV	
L. cyanopterus	PV	R
L. griseus	IV	R
L. jocu	PV	R
L. mahogoni	PV	R
L. synagris	IV	R
Ocyurus chrysurus	PK	
Scaridae		
Scarus croicensis	HB	
S. taeniopterus	HB	
S. vetula	HB	R
Sparisoma aurofrenatum	HB	
S. chrysopterum	HB	
S. radians	HB	R
S. rubripinne	HB	R
S. viride	HB	
Serranidae		
Epinephelus adscensionis	IV	R
E. cruentatus	PV	
E. fulvus	IV	
E. guttatus	IV	
E. striatus	PV	R
Mycteroperca bonaci	PV	R
M. interstitialis	PV	R
M. tigris	PV	R
M. venenosa	PV	R

Analysis of habitat characteristics

Two methods were used to test for differences in habitat characteristics among or between study areas at each location, namely multivariate analysis of similarities (ANOSIM) of all habitat attributes (Clarke & Warwick 1994; Carr 1997), and ANOVA of individual habitat characteristics. Where ANOVA or ANOSIM of the habitat data showed significant differences among the study areas there was the possibility that any differences among areas at different levels of protection would have been confounded by those habitat differences. Therefore in order to reduce the possibility of such confounding we tried to resolve those differences by excluding the data from one site in each area that contributed most to the habitat differences among or between areas. If there were no significant differences in habitat characteristics among areas using those remaining sites, we would then use that sub-set of sites for all future analyses. When it was not possible to resolve differences in that way, we tried to estimate the potential importance of the difference in habitat for the fish abundance we found in each area by calculating the Spearman's Rank Correlation Coefficient between fish abundance and the habitat variable concerned.

Results

Diver survey

Ratings for each attribute by individual divers tended to be clustered around the extremes of the ranking scale; in general, they were either indifferent to an attribute (gave it a rating of 0) or rated it as quite important (rating of 3–5). Other than for a few very low ranking attributes, the absolute differences in mean rating were relatively small, for example, the nine highest-rated attributes had mean ratings between 3.5 and 4.3 (Table 3). However, multiple pair-wise comparisons indicated that the five attributes 'variety of fish', 'abundance of fish', 'variety of corals', 'other large animals', and 'unusual fish' were significantly more highly rated than the other attributes. None of those attributes had a greater median rating than any other ($p > 0.05$), but all were rated more highly than all the other attributes ($p < 0.05$) except in the case of one paired comparison between 'unusual fish' and 'reef structure' ($p < 0.1$). Five divers identified other attributes not listed by us, three mentioned 'good visibility', and two specified 'wrecks' as being important to them.

The largest disappointment ratings (the difference between rating of importance and rating of actual condition at Jamaican dive sites) were for 'other large animals' and several fish attributes: 'big fish'; 'unusual fishes'; 'variety of fish'; and 'abundance of fish' (Table 3), indicating that increases in these aspects at the Jamaican dive sites might have been particularly appreciated by the divers interviewed. Surveyed divers were not so apparently disappointed by reef-benthos attributes including variety of corals that they had rated highly for diving localities generally, even though coral diversity was low at the Jamaican locations where they had been diving (Williams & Polunin, unpublished data).

We concluded that the fish attributes were the most important aspects that management might enhance in marine protected areas, and this study therefore aimed to compare densities of large fishes ('big fishes'), fish species richness ('variety of fishes'), unusual fishes and fish density and biomass ('abundance of fishes'), between protected and unprotected reef areas in each locality.

Habitat characteristics

No differences in habitat data were discerned between protected and unprotected areas at either depth in Montego Bay, on Cayman reefs, on shallow Belize reefs, or on deep Belize reefs, when, in the last case, the data from one outlier site were removed from each area (Table 4). The Isle of Youth, Cuba was the only location for which there were significant ANOSIM differences between management

Table 3 Mean rating of importance of reef attributes by diving tourists in Jamaica when asked what they preferred to see on dives (scale 0–5, $n = 195$). Divers were also asked to rate the condition of Jamaican dive sites for each attributes using the same scale. Differences between rating of 'importance' and 'condition' for each attribute is taken as an indication of 'disappointment' with conditions at Jamaican sites. Rank order of each attribute in square brackets.

Reef attribute	*Importance to divers*	*Rating of Condition*	*'Disappointment'*
Variety of fishes	4.3 [1]	3.4 [6 =]	0.9 [3]
Fish abundance	4.2 [2]	3.4 [6 =]	0.8 [5]
Variety of corals	4.1 [3]	3.8 [1]	0.3 [8]
Other large animals	4.0 [4]	2.4 [13]	1.6 [1]
Unusual fishes	3.9 [5]	3.0 [9]	0.9 [4]
Coral cover	3.7 [6]	3.1 [8]	0.6 [6]
Big fishes	3.6 [7]	2.5 [12]	1.1 [2]
Reef structure	3.5 [8]	3.8 [2]	−0.2 [11]
Unusual corals	3.5 [9]	3.7 [3]	−0.2 [9]
Large corals	3.3 [10]	3.4 [5]	−0.2 [10]
Crustaceans	3.2 [11]	2.7 [11]	0.5 [7]
Sponges	3.1 [12]	3.5 [4]	−0.4 [12]
Algae	2.3 [13]	2.8 [10]	−0.5 [13]

Table 4 Results of ANOVA and ANOSIM comparing habitat data between protected and unprotected areas at all locations. [1]% Sand was ln(x) transformed to meet requirement of homogeneity of variance.

Location		*ANOSIM p*	*Differences in individual habitat variables by 1-way ANOVA*
Montego Bay, Jamaica			
Shallow	(6m)	0.151	none
Mo Bay	(15m)	0.563	none
Ambergris Caye, Belize			
Shallow	(2m)	0.065	none[1]
Deep	(12m)	0.089	Rubble (p <0.05) range is from 6.7% (San Pedro) to 1.7% (Caye Caulker), Hol Chan is 3.8%
Deep with 1 site from each area removed		0.381	none
Grand Cayman			
	(12m)	0.077	nested ANOVA (areas within management level): none
Isle of Youth, Cuba			
	(12–15m)	<0.001	2-way ANOVA (reef type and management level): rugosity p <0.001 mean range 2.3–4.1; coral cover p <0.001 mean range 4.8–11.6%; for both variables, unprotected sites < protected sites

Table 5 Results of correlation between abundance of all fish groups and both rugosity and coral cover at protected (n = 16) and unprotected (n = 12) sites in Cuba: * = $p < 0.05$, other comparisons not significant. Trophic groups as for Table 2.

	Rugosity		*Coral cover*	
Fish category	*Protected*	*Unprotected*	*Protected*	*Unprotected*
Trophic group				
PV	0.569*	0.294	0.171	−0.076
IV	−0.057	−0.051	0.436	0.224
HB	−0.166	0.408	−0.168	−0.005
Total abundance	0.012	0.239	0.057	0.194
Big fish (>20cm)	−0.063	0.249	0.266	0.059
Big fish (>30cm)	0.401	0.144	0.477	−0.217
'Unusual' fish	0.235	0.089	0.090	0.182
Species richness	0.090	−0.087	0.483	0.433

levels, and two-way ANOVA indicated that mean coral cover and rugosity were both lower in the unprotected areas than the PNPF. Correlation analysis indicated that there was a significant positive association between piscivore density and rugosity, and between big fish (>30cm) and coral cover, among data from sites within the PNPF ($p < 0.05$, Table 5). Thus for the Cuban areas there were potential habitat effects confounding any management-level differences, particularly in any differences involving piscivorous fishes.

Differences between MPAs and reference areas in reef attributes important to dive tourists

A total of 40 species from the six censused fish families were recorded in the course of the study (Table 2); 23 of these species were found in less than 25% of all survey sites and were classified as 'unusual'.

There were very large variations in MPA/non-MPA differences at the four locations. Cuban and Belizean MPAs tended to have greater mean fish abundance and numbers of 'big' fish than reference areas, but differences corresponding to management level were less striking, between Jamaican areas and marginal to non-existent among surveyed Caymanian areas (Figs 2 and 3). In fact, there were no significant differences in any of the censused reef attributes between protected and fished areas in Grand Cayman (Tables 6 and 7), nor was there a tendency for there to be a disparity in abundance of 'big' or 'unusual' fish between protected and fished areas (Figs 2 and 3).

At Montego Bay, the only significant difference between deep (15 m) MBMP and unprotected sites was in species richness, which was higher at protected sites ($p < 0.05$, Table 6). Very few 'big' fish were encountered at all at Montego Bay sites, even when 'big' fish were considered to be anything larger than 20cm (Fig. 3). The few 'unusual' fish counted in surveys at Montego Bay deep sites were almost exclusively found within the MBMP (Fig. 2). Among shallow areas (< 6 m), sites in the MBMP had greater abundance and biomass of all fishes combined, and greater abundance of herbivorous fishes (Table 6 and 7), and were the only sites at which piscivorous fishes were encountered.

Among deep sites (12 m) at Ambergris Caye, Belize, there was a tendency for there to be a greater abundance of 'big fishes', 'unusual' fishes and piscivorous fishes at protected

Table 6 Results of ANOVA on fish abundance data: * = $p < 0.05$;** = $p < 0.01$; *** = $p < 0.005$; – = insufficient data; ms = marginally significant (test has low power and $p < 0.1$); ns = $p > 0.05$. Belize and Jamaica data analysed by one-way ANOVA, Cayman data by nested two-way ANOVA (reef nested within protection status), and Cuban data by crossed two-way ANOVA (protection status crossed with reef type, fringing or barrier reef). For Ambergris Caye data, Tukey's studentized range test was used to determine which areas the difference was significant between (at $p < 0.05$, or $p < 0.1$ for marginally significant tests). P = protected area(s); U = unprotected area(s), except Ambergris Caye: P = Hol Chan MR; U_1 = San Pedro; U_2 = Mata Cut/Mexico Rocks; U_3 (deep only) = Caye Caulker. Trophic groups as for Table 2. [1]loge (x + 1) transformed;[2] $\sqrt{\sqrt{}}$ transformed.

	Trophic group			*All*	*'Unusual'*	*Species*	*Big fish*	
Location	*HB*	*IV*	*PV*	*fish*	*fish*	*richness*	*>20cm*	*>30cm*
Montego Bay, Jamaica								
Deep (15m)	ns	ns	ns	ns	–	*P > U	–	–
Shallow (6m)	*P > U	ns	P only	**P > U	-	ns	ns	–
Ambergris Caye, Belize								
Deep (12m)	*P, U_3 > U_2	ns	ms P > U_2	*P,U_3 > U_2	ns	*P,U_3 > U_1,U_2	*U_3 > U_1,U_2	ms P > U_1,U_2
Shallow (2m)	ns[1]	ns	ns	***P > U_1,U_2	ns	*P > U_1	***P > U_1,U_2[1]	–
Cayman (12m)								
Protection level	ns	ns	ns	ns	ns[2]	ns	ns	ns
Reef	ns	ns	ns	*	ns	ns	ns	ns
Punta Frances, Cuba (12–15m)								
Protection level	ns	*P > U	***P > U	***P > U	***P > U	***P > U	*P > U	**P > U
Reef type	ns	ns	*	ns	ns	ns	ns	ns
Protection × Reef type	ns	ns	ns	ns	ns	ns	ns	ns

Table 7 Results of ANOVA on fish biomass data: * = $p<0.05$; ** = $p<0.01$; *** = $p<0.005$; − = insufficient data; ms = marginally significant (test has low power and $p < 0.1$); ns = $p > 0.05$. Belize and Jamaica data analysed by one-way ANOVA, Cayman data by nested two-way ANOVA (reef nested within protection status), and Cuban data by crossed two-way ANOVA (protection status crossed with reef type, fringing or barrier reef). For Ambergris Caye data, Tukey's studentized range test was used to determine which areas the difference was significant between (at $p < 0.05$, or $p < 0.1$ for marginally significant tests). P = protected area(s); U = unprotected area(s) except Ambergris Caye: P = Hol Chan MR; U_1 = San Pedro; U_2 = Mata Cut/Mexico Rocks; U_3(deep only) = Caye Caulker. Trophic groups as for Table 2. [1]loge (x + 1) transformed.

	Trophic group			*All*	*'Unusual'*
Location	*HB*	*IV*	*PV*	*fish*	*fish*
Montego Bay, Jamaica					
Deep (15m)	ns	ns	ns	ns	–
Shallow (6m)	ns	ns	P only	* P > U	–
Ambergris Caye, Belize					
Deep (12m)	ns	ns	ms P > U_1	*P,U3 > U_2	*P > U_1,U_2
Shallow (2m)	***P > U_1,U_2[1]	***P >U_1,U_2[1]	ms P > U_1,U_2	***P > U_1,U_2	***P > U_1,U_2
Cayman (12m)					
Protection level	ns	ns	ns	ns	ns
Reef	ns	ns	ns	ns	ns
Punta Frances, Cuba (12–15m)					
Protection level	ns	ns	**P > U	***P > U	*P > U
Reef type	ns	ns	ns	ns	ns
Protection × Reef type	ns	ns	ns	ns	ns

compared to unprotected sites when data from all sites were pooled by management level (Figs 2 and 3). There was not, however, a consistent difference between the protected and the three unprotected areas, rather it was the case that two of the unprotected areas (San Pedro and Mexico Rocks) generally had lower density of fishes than both of the other two areas (the protected area, Hol Chan, and the other unprotected area, Caye Caulker). Abundance or biomass of herbivorous fishes, all fishes, and 'unusual' fishes, and species richness were all greater at both Hol Chan and Caye Caulker

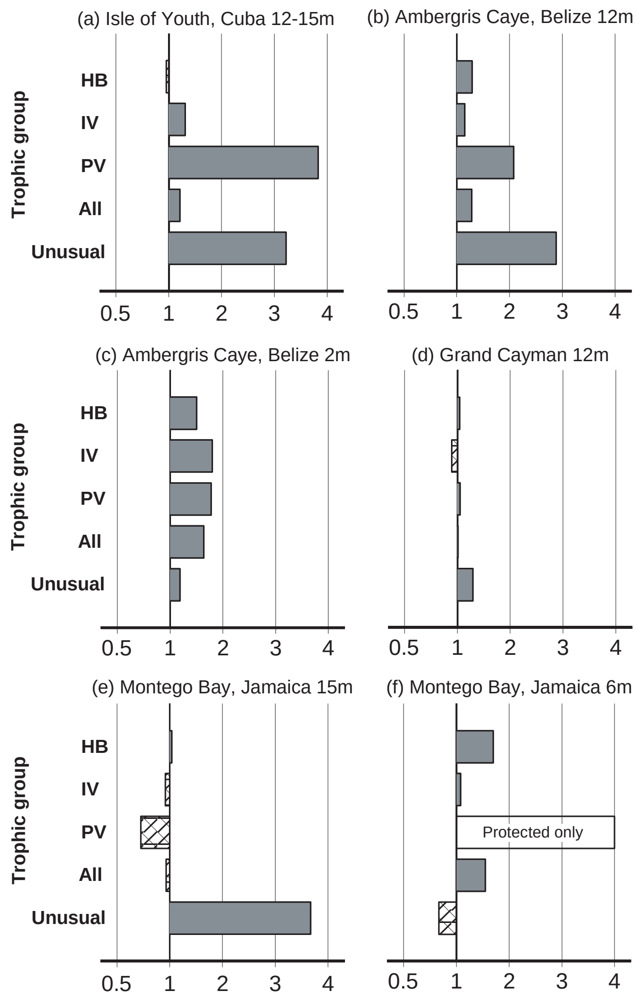

Figure 2 Ratios of mean fish abundance in MPAs compared to unprotected areas. In each case, fish abundance data have been pooled by protection status ('Protected' or 'Unprotected'). Solid bars indicate greater mean abundance at protected sites, hatched bars indicate greater mean abundance at unprotected sites. 'HB' denotes herbivores: 'IV' invertebrate-feeders/generalized carnivores; 'PV', piscivores; 'All' is total abundance of all censused fishes; 'Unusual' is total abundance of all fishes categorized as unusual. Note that no piscivorous fishes were recorded in censuses of unprotected shallow sites in Montego Bay.

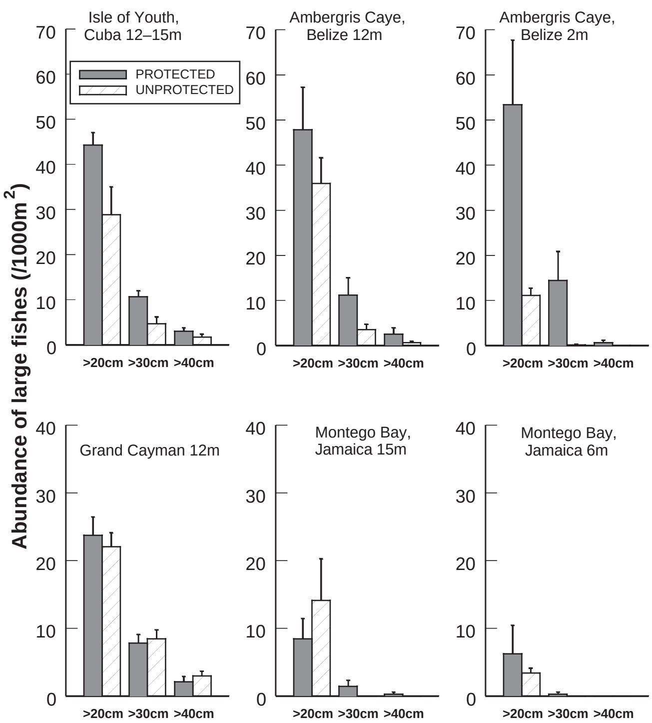

Figure 3 Numerical density of 'large' fishes in MPAs and reference areas. Data from each location is pooled by protection status ('Protected' or 'Unprotected'). Error bars indicate 1 standard error.

than one or both of the other two areas (Tables 6 and 7). For the marginally-significant cases ($p < 0.1$) of piscivorous fishes and number of fishes larger than 30cm, density was greater at sites in Hol Chan than San Pedro and Mexico Rocks, but there was no difference between Hol Chan and Caye Caulker (Tables 6 and 7). In shallow water, where lack of suitable shallow habitat meant that no sites were surveyed at Caye Caulker, there were substantial differences between the protected area and the two unprotected areas. Species richness, total abundance of fishes and number of fishes larger than 20 cm, were all greater at protected compared to unprotected sites (Table 6), and differences among areas were even stronger in terms of biomass: herbivorous fishes, piscivorous fishes, all fishes, and 'unusual' fishes all showed very significantly greater biomass within the protected area than at both of the unprotected areas ($p < 0.005$, Table 7). Few piscivorous fishes were recorded at Belize shallow sites, so variability was high and tests had low power, but the difference in biomass was marginally significant, with density greater at Hol Chan than at the two unprotected areas ($p < 0.1$, Table 7). Density of 'big' fishes tended to be much higher within the protected area, especially among >30 cm fish which were virtually absent from unprotected sites (Fig. 3).

At the Isle of Youth, Cuba, abundance or biomass was higher on PNPF than unprotected reefs for all categories of fishes other than herbivores (i.e. invertebrates, piscivores, all fishes, 'unusual' fish, big fish >20 cm, and big fish >30 cm). Species richness was also higher on PNPF reefs (Tables 6 and 7). The proportional differences in abundance were particularly large for piscivorous and 'unusual' fishes, both of which were more than three times as abundant in the PNPF than in reference areas (Fig. 2).

Discussion

The consistently high ratings given to all fish attributes (abundance, variety, number of 'large' and number of 'unusual' fishes, Table 3) strongly suggest that management measures which enhance these would increase the attractiveness of an area to dive tourists. Apart from the present study, such effects of protection have been indicated widely to occur (Polunin & Roberts 1993; McClanahan 1994; Jennings *et al.* 1996; Rakitin & Kramer 1996). The high average rating given by divers to another reef attribute, namely 'other large animals' (Table 3) also indicates that management which increased local abundance of animals such as sea turtles would also be advantageous to dive tourism.

It appears that very little survey work has been done of the kind that we conducted of diver preferences in Jamaica. One study in Zanzibar has indicated that 'variety of fish' was the most appreciated attribute of those suggested to tourists in a questionnaire (Andersson 1998). However, a comprehensive survey on the Great Barrier Reef indicated that coral attributes on average have more influence than those of fish on tourists' underwater experience (Shafer *et al.* 1998). Diver surveys at other times and places in the Caribbean might have indicated different preferences to those indicated by the present study. A particular question is how representative the surveyed dive tourists are likely to be of dive tourists generally. Jamaican reefs, being heavily overfished and having recently experienced two major hurricanes, are probably among the most degraded in the Caribbean (Munro 1983; Koslow *et al.* 1988, 1994; Hughes 1994). It seems unlikely therefore that reef condition was an important factor motivating the choice of holiday destination for many of the dive tourists we surveyed. Possibly, divers visiting more pristine locations, such as Belize and the Cayman Islands would have different preferences. There is clearly scope for further preference surveys of this type at other locations, and also greater understanding of whether these preferences and perceptions might be important factors motivating divers to visit or revisit certain locations.

Since we found time greatly constrained the number of divers responding properly to our survey, we kept some of the attributes that we asked divers about in Jamaica simple and ill-defined. 'Large' and 'unusual' fishes were such cases, and to some degree we also interpreted these categories rather loosely in our own survey: >20 cm may be a rather small size at which to consider fishes to be 'big', and, by 'unusual', divers could have meant very rare or cryptic species that we did not census. However, as we interpreted them, 'big' and 'unusual' appeared to be among the best indicators of fishing/protection effects (Figs 2 and 3). We also did not census the whole fish community, instead focusing only on fishery-target species, as impacts of fishing on non-target species have scarcely been detected on coral reefs (Bohnsack 1982; Jennings *et al*. 1995; Jennings & Polunin 1997; Russ & Alcala 1998). We did, however, census most of the larger non-cryptic species that will be most frequently encountered by divers.

Where we found differences between MPAs and unprotected areas, we can not unequivocally conclude that protection from fishing alone is responsible for those differences, as several factors other than variation in fishing pressure, including physical structure of reef habitat (Roberts & Ormond 1987), variable recruitment (Doherty & Williams 1988), and post-recruitment factors such as food-availability, competition, disturbance and predation (Jones 1991) have been shown to influence fish density and species richness, and may vary locally. The results from Isle of Youth (Cuba) in particular should be treated with caution; not only were protected and reference areas quite far apart (approximately 70 km), but also sites within the Parque National Punta Frances (PNPF) had significantly greater structural complexity (Table 4). There are, however, a number of reasons to believe that protection was an important factor generally in the differences we found between PNPF and reference areas. Firstly, there was no attribute at any location for which density or richness tended to be higher in unprotected areas than the PNPF (Tables 6 and 7), so observed differences are unlikely to be purely random. Secondly, where there were differences associated with protection level, the pattern was similar in all cases, namely greater species richness and total abundance in MPAs, but particularly large differences in the abundance of piscivorous and 'big' fishes (Figs 2 and 3, Tables 6 and 7), which are most indicative of fishing pressure. Thirdly, these patterns are consistent with other studies from tropical MPAs (Polunin & Roberts 1993; McClanahan 1994; Jennings *et al.* 1996; McClanahan & Kaunda-Arara 1996; Rakitin and Kramer 1996; Russ & Alcala 1996; Wantiez *et al*. 1997).

Reefs around the Montego Bay Marine Park (MBMP) are believed to be among the most heavily fished in the Caribbean (Hughes 1994), and so it might also be expected that there is considerable scope for building of fish populations within the protected areas. However, at the time of our survey, fishing was restricted but not banned within the MBMP, and enforcement of even these limited restrictions had been hampered by lack of finance in the year immediately preceding our work (Maldon Miller, personal communication April 1997). Given that background, it is perhaps surprising that we found any differences between the MBMP and adjacent unprotected areas. However, while our results suggest that reefs in the MBMP might tend to appeal more to dive tourists than reefs outside of the MPA, fish populations at all Jamaican sites were evidently depleted in comparison to other survey locations; densities of all categories of fishes were low, and 'big' and piscivorous fishes were almost absent from surveys there (Fig. 3; Williams & Polunin, unpublished data). Therefore, it is probable that considerable further improvement would be necessary for differences to be perceived by divers.

The fact that we could find no differences between Cayman 'marine park' areas (in which fishing was completely banned) and 'replenishment' areas (in which line fishing is permitted) raises the question of whether low levels of fishing reduce the appeal of coral reef areas to tourists. Although minor poaching and fishing concessions within a Seychelles MPA had significantly depleted fishery-target species, Jennings *et al.* (1996) believed that the appeal of the park to tourists had not been seriously affected, as exploitation had not substantially reduced total fish biomass or species richness, and those were the factors they supposed to be most important to tourist visitors. We found some support for that view as 'abundance' and 'variety of fishes' were the two factors rated highest by dive tourists in our survey (Table 3).

However, although we found no evidence of this among the Cayman areas we surveyed, large piscivorous fishes that are important elements of the 'big' and 'unusual' fish categories (Table 2) have generally been shown to be depleted rapidly by even low levels of fishing (Jennings & Lock 1996). Since our survey indicated that these are also among the features most important to dive tourists, it appears that, where it can be achieved, total prohibition of fishing might be necessary for an area to achieve maximum appeal to divers.

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