Environmental Conservation 31 (2): 111–121 © 2004 Foundation for Environmental Conservation DOI:10.1017/S0376892904001250

Distribution, diversity, and conservation of coral reefs and coral communities in the largest marine protected area of Pacific Panama (Coiba Island)

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Date submitted: 11 July 2003 Date accepted: 3 March 2004

SUMMARY

Sampling scale and lack of attention to taxa other than scleractinian corals have limited the capacity to protect coral reefs and coral communities in Pacific Panama. The distribution of coral habitats (live coral cover) and their species richness in the largest marine protected area of Panama, the Coiba National Park (270 125 ha), is described using quadrat transects and manta tows. The species richness of scleractinian corals and octocorals was lower in coral reefs than in coral communities, and a close relationship between richness and live coral cover was observed only in coral communities. The distribution of high live coral cover in coral communities overlapped with areas of high coral species richness. Average live coral cover in communities was 64%, compared to 28% in reefs, whereas algae cover was 30% and 49%, respectively. Twenty-two coral and 34 octocoral species were observed, many only now detected in Panama as endemic or new species. Analysis of satellite imagery showed 80% of terrestrial habitats were mostly primary forest, and coral reefs and coral communities covered 1700 ha, about 2% of marine habitats. Shallow marine environments (< 20 m) had up to 60% calcareous red algae cover (rhodolite beds). Based on the distribution of live coral cover and species richness, three conservation units were identified as priority, with the southern and northernmost sides of the marine protected area as the most significant. These three areas encompass most of the rare and endemic species or populations, as well as species previously regarded as endangered.

Keywords: Coiba Island, coral reef management, marine protected area, octocorals, Panama, scleractinian corals

INTRODUCTION

Marine biological diversity has been underestimated in comparison with land systems (Norse 1993). The analysis of marine ecosystems is complex, and efforts to understand the processes and patterns that characterize the distribution of their biological diversity have been approximate and incomplete (Jackson 1991, 1994; Norse 1993; NRC [National Research Council] 1995). To understand the most fundamental processes that create, maintain and regulate this biological diversity is a basic priority for the conservation of marine resources, as this will allow for their protection over the long term (NRC 1995, 2001). The accelerated demise of marine ecosystems, particularly coral reefs (NRC 1995), has increased scientific efforts to discern the structure and functioning of marine communities and the effects of this deterioration on the abundance and distribution of species observed today (Hughes 1994; Jackson 1994; Hughes *et al.* 1999; Roberts *et al.* 2001). These efforts should encompass distribution, composition and condition of the communities (Guzman & Guevara 1999; Hughes *et al.* 1999; Bellwood & Hughes 2001), adequately evaluate the diversity of species at different taxonomic levels (Knowlton & Jackson 1994; Sheppard 1998; Gladstone 2002) and apply remote survey techniques to increase spatial scale (Mumby 2001; Andréfouët *et al.* 2003). Without those approaches, we may be leaving highly sensitive conservation sites unprotected or maintaining protected areas that do not fulfil their mission (NRC 1995, 2001; Guzman & Guevara 1999).

The conservation of coral reefs in Panama has been particularly affected. There is copious scientific information available about biological processes and possible patterns for the already deteriorated reefs of Pacific Panama, but the prospects for long-term conservation of those reefs have been inadequately assessed, in spite of recent reviews of the country's reefs (Glynn & Maté 1997; Maté 2003). Most of these studies have been focused on small numbers of reefs, without adequate spatial scale with respect to diversity of habitats and species, and their distribution that would allow for sound management of resources at the local or regional level (Gladstone & Davis 2003). In consequence, many important habitats and taxa have been under sampled.

Here we describe the reefs and coral communities in the largest marine protected area of Panama, the Coiba National Park, which is also being considered as a World Heritage site by UNESCO. The protected area has no comprehensive management plan to date, and the purpose of this study is to inventory the biodiversity values of the coral systems

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and recommend locations or zones where, as a priority, management prescriptions should be applied. The specific goals include: (1) characterizing the alpha species richness of scleractinian and gorgonian corals, and their distributions; (2) quantitatively describing the live cover and relative abundance of corals and other sessile organisms, and their distribution; (3) producing a preliminary map of the distribution of coral reefs and communities and (4) defining priority conservation areas.

MATERIALS AND METHODS

Study area

The Coiba National Park (CNP) is located on the south-eastern border of the Gulf of Chiriquí, south-west Pacific of the Republic of Panama. It belongs to the Panamic Biogeographic Province, which extends from the Gulf of Guayaquil in Ecuador (3°S) to the Gulf of Tehuantepec in Mexico (16°N) (Glynn & Wellington 1983, Cortés 1997). The protected area was created in 1991 and, in 2002, it was included as part of a regional protected 'Pacific Biological Corridor', which includes the oceanic islands of Malpelo and Gorgona (Colombia), Galapagos (Ecuador) and Cocos (Costa Rica). The CNP has a surface area of 270 125 ha, of which 216 543 ha (80.2%) are marine (Cardiel *et al.* 1997). The CNP is made up of an archipelago of nine main islands and about 30 islets, the greatest of which are Coiba (50 314 ha) and Jicaron (2002 ha). An expansion of the marine protected area (MPA) has been proposed to include Montuosa Island, located 39 km west (264°) from Punta Hermosa (Coiba Island).

The climate of the region is humid-tropical monsoonic, with a rainfall of up to 3500 mm yr^{-1}, an average temperature of 25.9°C, and marked seasonality; it has dry (from mid-December to mid-April) and rainy seasons. The islands are covered by tropical rainforest, and they have several rivers with variable flows and hydrographic basin sizes. In particular, the hydrography of Coiba Island includes two large watershed areas (north and south) associated with the Central Fault of Coiba, which crosses the island diagonally from NW to SE, conditioned by the topography, rainfall and low-permeability soils (Kolarsky & Mann 1995; Cardiel *et al.* 1997). These islands were part of the continent until they were separated at the end of the last glacial period during the Late Pleistocene, between *c.* 18 000 and 12 000 years before present (Castroviejo & Ibáñez 2001). The protected area lies in the tropical eastern Pacific region, considered that with the greatest coral diversity (Glynn 1997). Coral reefs across the area are small in area, shallow (< 15 m) and structurally simple, and possess low scleractinian coral species richness (Glynn & Wellington 1983; Guzman & Cortés 1993; Cortés 1997). Reefs are affected by warming events associated with the El Niño Southern Oscillation, which brings environmental changes in the equatorial eastern Pacific every 2–7 years (Enfield 2001).

Distribution of species richness in coral reefs and coral communities

The development of species-area curves for checking optimum species richness may be considered standard procedure (see Beger *et al.* 2003; Gladstone & Davis 2003). However, due to the patchy distribution of coral and octocoral populations in the eastern Pacific (Glynn & Wellington 1983; Guzman & Cortés 1993; Cortés 1997), and the complexity of the shoreline within the CNP, we aimed to survey the entire coast. Accordingly, the shallow coastal zone (< 30 m deep) was arbitrarily divided every 2 km into 84 polygonal areas (defined and georeferenced a priori) to facilitate the survey in blocks and making of thematic maps using a geographical information system (GIS). This method allowed the survey of this large archipelago surrounded by shallow fringing coral communities and scattered coral reefs under different environmental and topographic conditions including those of current, tide and orography. Thus, the coast that comprises the CNP and its islands and islets (above 300 km) was assessed totally by 'manta' survey (Millar & Müller 1999) during five expeditions made to the CNP during 17 April–3 May, 1–10 August and 22–31August 2002, and 11–23 April and 1–7 May 2003. The overall information was primarily used to characterize the scleractinian and octocoral assemblages, to locate rare species, to identify areas of high species richness, to assess the distribution of coral reefs and coral communities, and to obtain a qualitative estimate of coral cover. In addition, species richness was further assessed at depths of up to 35 m at 56 randomly chosen sites, through 80-minute diving surveys with scuba equipment. Whenever necessary, organisms were collected for their subsequent classification. A comprehensive presence/absence list of species for scleractinian corals and octocorals was compiled using diversity manta and diving surveys, and a distribution map for species richness (number of species) was developed assigning each of the 84 polygons into one of the following four categories: high (>75%), moderate-high (50–75%), moderate (25–50%), and low (<25%). We evaluated species 'rareness' based on the percentage of polygons in which a species was found (75–100%: abundant, 50–75%: very common, 25–50%: common, 0–25%: rare).

Live coral cover status and distribution

Live coral cover and species composition were quantified at 24 sites (including Montuosa Island), using three 10-m long replicate transects placed parallel to the coast and at three different depths (Guzman & Guevara 1999). Coverage of corals, algae (frondose and turf species; mainly *Gelidiopsis* cf. *intricata*, *Hypnea* cf. *pannosa*, *Dictyota* spp. and *Amphiroa* cf. *beauvosii*) and sponges was visually estimated with a 1m^2 quadrat divided into 100 cells of 10 cm^2 each. Because vertical development of eastern Pacific coral reefs and communities is limited, it was not possible to sample 1, 3 and 8 m at all sites, however the same total area per site was always surveyed (a total of $90\,m^2$ per reef or community). Since coral communities are widely distributed along the coastline and usually have a higher diversity of corals than reefs, we developed a thematic map of the distribution of live coral cover only for these habitats based on the manta survey and grouped into the cover categories of high (> 40%), moderate (20–40%), and low (< 20%). The criterion to define these categories (percentages) visually at each of the 84 polygons in the field was based on the previous analysis and description of coral cover at the 24 sites.

Satellite image interpretation and cartography of terrestrial and marine environments

We aimed to produce maps that identified representative areas of several habitats that may be selected for protection and to support the creation of management zones. Mapping of terrestrial and marine environments was subject to the low spatial resolution and inherent limited definition and depth range imposed by the quality of the remote sensing imagery (Green *et al.* 1996; Andréfouët *et al.* 2003). The estimated area of the Park varied from previous estimates; the coastline was 29% (99 km) longer and habitats were 666 ha smaller in the present analysis than in Cardiel *et al.* (1997). These differences may relate to the use of old aerial photographs and maps at different scales to estimate area and/or the fact that the limits of the intertidal zone and of beaches with tidal ranges of up to 5 m were not defined in previous studies. In this survey, we defined beaches and rocky intertidal areas as coastal-marine environments and all islands and islets were included in the analysis.

We analysed habitats within the CNP through digital processing of a Landsat 7 ETM satellite image obtained on 27 January 2002. The satellite image was processed with ERDAS Imagine V.8.3.1 Professional, on a PC platform. The classified image was geo-referenced with localized points on maps from the Tommy Guardia National Geographic Institute (scale 1:50 000). Terrestrial environments were classified only to show the distribution of deforested areas as potential threats to coastal resources. Even though the supervised classification of the marine habitats was confirmed with 1377 coordinates or ground control points obtained in the field using a global positioning system, we were unable to unambiguously separate living from dead coral reefs (the 'spectral signature'). Similarly, the separation between coral reefs and coral communities was not clear in 40% of the cases, as the communities generally dominate subtidal rocky areas (0–15 m wide) that run parallel to the coast. Subsequently, habitat maps with scales of 1:60 000 and 1:180 000 were prepared with the ARCGIS 8.2 program.

Data analysis

Statistical techniques were used for multivariate analysis of marine communities using the PRIMER package (Clarke & Warwick 2001). Live coral cover and species richness of corals and octocorals (presence/absence of species) were compared in the 84 polygons into which the CNP was divided, using the Bray-Curtis similarity coefficient in non-transformed data. This information was sorted using non-metric multi-dimensional scaling (MDS). Each MDS analysis was performed 50 times as recommended. ANOSIM was used to test statistical differences in the presence/absence of species among sites. Pearson's parametric correlation test was used to assess the relationship between live coral cover and species richness of scleractinian corals, transformed taking into account normality and homoscedasticity.

RESULTS

Distribution of species richness in coral reefs and coral communities

We observed 56 hard coral species, 20 species of scleractinian corals and two species of hydrocorals (*Millepora* and *Distichopora*) (Table 1). The presence of *Pavona maldivensis* in Panama (Holst & Guzman 1993) was confirmed. In addition, we found *Pavona* cf. *duerdeni*, *P.* cf. *minuta* and *Pocillopora inflata*. There were 34 species of octocorals grouped in seven genera (Table 1).

The Bray-Curtis similarity analysis suggested four relatively well-defined groups of species (Fig. 1). The MDS indicated Groups 2 and 4 were different from Group 1, whereas Group 3 overlapped Groups 1 and 2 (Fig. 2*a*). Group 1 incorporated more than 50% of the species in 25% of the sites (dotted line in Fig. 2*b*), and the highest concentration of rare species (Fig. 2*c*).

The 56 species classified into four 'rareness' categories produced a new scattered spatial distribution for some species (Fig. 3). The species represented in 75% of the sites were spatially grouped together very closely (categories 1–3), whereas the rare species differed from the rest, and there was even a subgroup of rare species to very rare species (category 4). In 36% of the sites, at least one rare species was detected, whereas in 24% of the sites, 13 rare species were found.

In the archipelago, five priority regions were identified as having high species richness; in particular, these were the northernmost (Contreras Island) and southernmost (Jicarita Island) sides of the MPA (Fig. 4). Coiba Island had the most extensive area of low species richness, particularly on the eastern side, but it was intermingled with medium-high and medium species richness areas.

Live coral cover status and distribution

Overall, average ($n = 24$ reefs) live coral cover was 37.3% ± 4.5 (SE), ranging from 1.2–76.1% within the CNP (Table 2). Algae (frondose and turf) and crustose coralline algal cover were 44.9% ± 3.9 and 16.5% ± 3.5, respectively. In some areas, these algae covered 73.9% and 66%, respectively (Table 2). Live coral cover was higher in coral communities (58.4% ± 6.7, $n = 6$) than on reefs

Table 1 Checklist of hard coral (Stylasterina, Milleporina and Scleractinia) and soft coral (Octocorallia, Telestacea and Gorgonacea) species observed at the Coiba National Park. ID indicates the species number assigned for the Bray-Curtis similarity analysis (see Fig. 3).

ID	*Species: Stylasterina, Milleporina and Scleractinia*	*ID*	*Species: Octocorallia, Telestacea and Gorgonacea*
1	*Distichopora* sp.	23	*Carijoa riseii*
2	*Millepora intricata*	24	*Eugorgia daniana*
3	*Gardineroseris planulata*	25	*Eugorgia* sp. 2
4	*Pavona chiriquiensis*	26	*Heterogorgia* sp.
5	*Pavona clavus*	27	*Leptogorgia alba*
6	*Pavona* cf. *duerdeni*	28	*Leptogorgia cuspidata*
7	*Pavona frondifera*	29	*Leptogorgia* cf. *ramulus*
8	*Pavona gigantea*	30	*Leptogorgia* sp. 2
9	*Pavona maldivensis*	31	*Leptogorgia* sp. 3
10	*Pavona* cf. *minuta*	32	*Leptogorgia* sp. 4
11	*Pavona varians*	33	*Leptogorgia* sp. 1
12	*Pocillopora capitata*	34	*Muricea* cf. *austera*
13	*Pocillopora damicornis*	35	*Muricea* cf. *crassa*
14	*Pocillopora elegans*	36	*Muricea fruticosa*
15	*Pocillopora eydouxi*	37	*Muricea* sp. 3
16	*Pocillopora inflata*	38	*Muricea* sp. 2
17	*Pocillopora meandrina*	39	*Pacifigorgia adamsii*
18	*Porites lobata*	40	*Pacifigorgia bayeri*
19	*Porites panamensis*	41	*Pacifigorgia cairnsi*
20	*Psammocora stellata*	42	*Pacifigorgia eximia*
21	*Psammocora superficialis*	43	*Pacifigorgia firma*
22	*Tubastrea coccinea*	44	*Pacifigorgia* cf. *firma*
		45	*Pacifigorgia irene*
		46	*Pacifigorgia rubicunda*
		47	*Pacifigorgia rubinoffi*
		48	*Pacifigorgia senta*
		49	*Pacifigorgia stenobrochis*
		50	*Pacifigorgia* sp. 1
		51	*Pacifigorgia* sp. 2
		52	*Pacifigorgia ferruginea*
		53	*Psammogorgia arbuscula*
		54	*Psammogorgia* sp.
		55	*Psammogorgia* sp. 1
		56	*Psammogorgia* sp. 2

(28.9% ± 4.2, $n = 16$) (Table 2), and the reverse was the case for algae cover, with 32.5% ± 4.1 and 49.9% ± 5.1, respectively. Crustose coralline algae (CCA), as expected, were more abundant on reefs (19.9% ± 5.2) than in communities (8.9% ± 4.1). The reefs at Uva Island and the north-eastern side of Coiba Island had the highest live coral cover (>50%). To the east of Jicarita Island, there was also a reef with 45% cover (Table 2). The best coral communities were found in the north area of the Contreras Islands, with cover of >70% (Table 2). The newly proposed area of Montuosa Island had mean coral, algae and CCA covers of 37.6% ± 8.7, 46.7% ± 13.4 and 15.3% ± 5.8, respectively.

There was a significant positive relationship between cover and species richness of scleractinian corals in coral communities (Pearson's $r = 0.6866$, $p < 0.0001$). Among the 84 polygons, coral cover spatial distribution in coral communities coincided with sites of higher species richness (Fig. 2*b*), and 20% of the sites had a live coral cover > 40%. Although the spatial distribution of coral cover showed a clear distinction between several site groups, an overlap was observed between high-moderate and moderate-low categories (Fig. 2*b*), which the ANOSIM test hardly detected as different associations of species, and only when scleractinian species were analysed (ANOSIM Global $R = 0.16$). Cover categories were not distinguished from the sites when both scleractinians and octocorals were compared in the analysis (Global $R = 0.076$).

The northern Contreras Islands included the coral community areas with higher live coral cover, as well as the Jicaron and Jicarita Islands in the south, and the east side of the Canal de Afuera islands. Around Coiba Island, the northern area and south side of Rancheria Island (Fig. 5) were also of special importance. Coral cover in the communities was moderate (20–40%) in most of the coastal zone of Coiba Island. Coral composition for most reefs was typical of Panama, built up and dominated by *Pocillopora damicornis* (*sensu* Glynn *et al.* 1972). The few exceptions included the reefs at Islote Santa Cruz, Punta Baltasar and northern Montuosa Island,

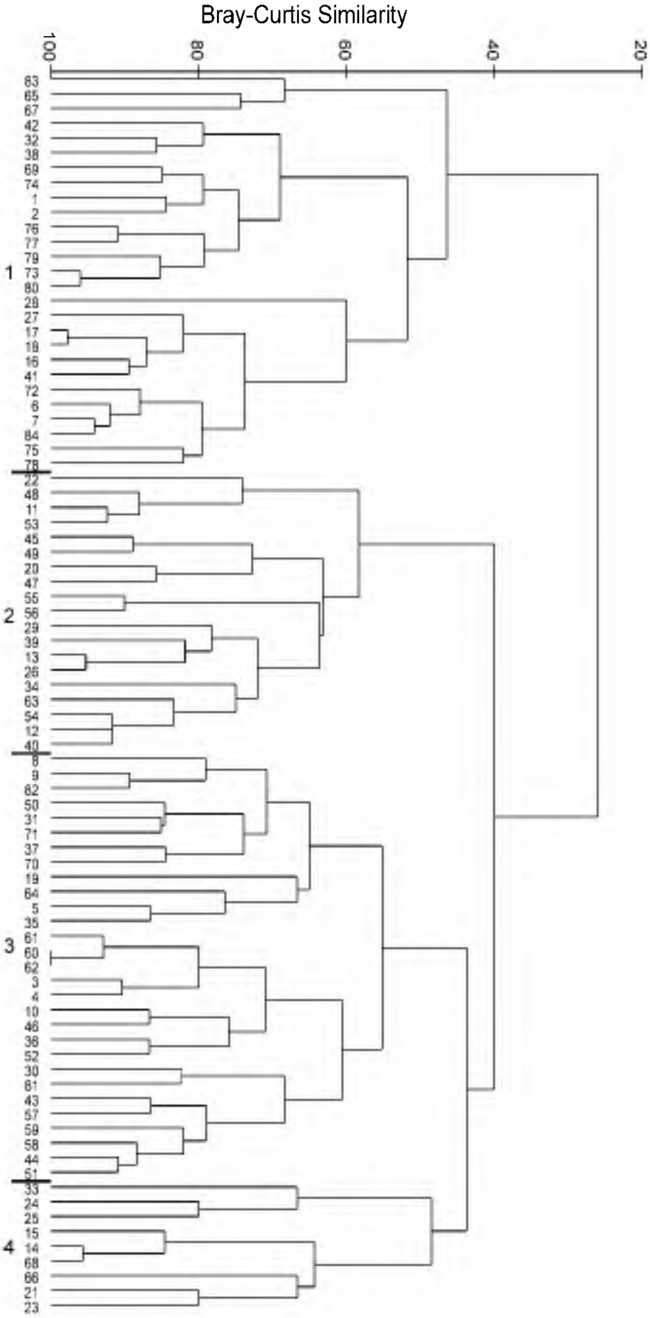

Figure 1 Bray-Curtis cluster analysis for 84 polygons of the Coiba National Park based on presence/absence of coral and octocoral species ($n = 56$ species).

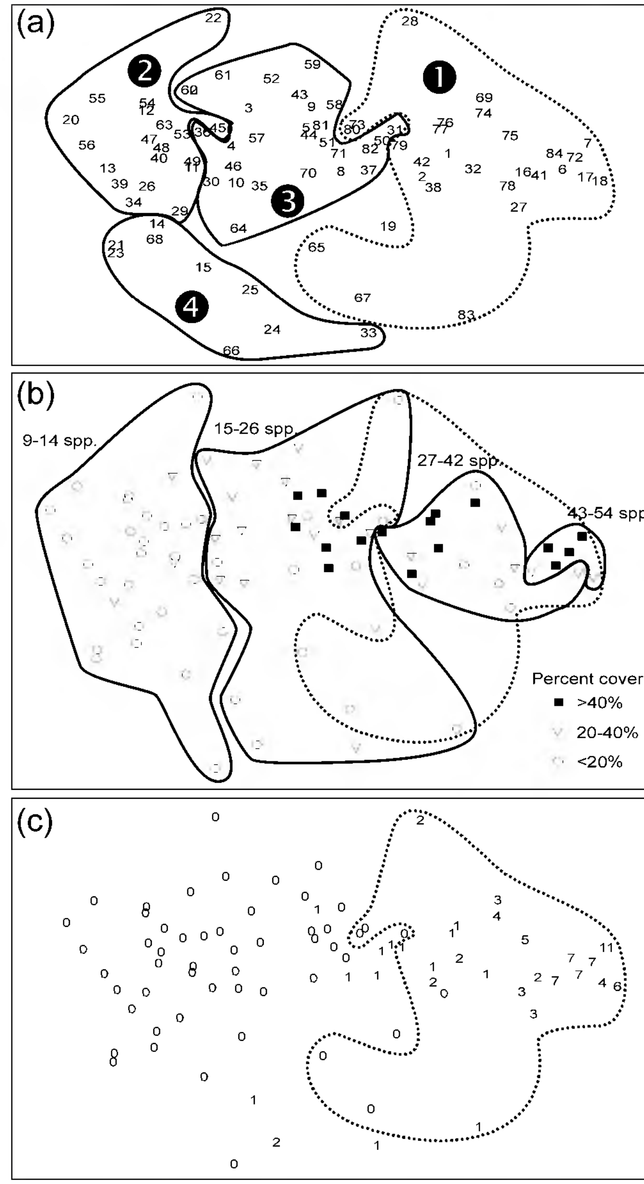

Figure 2 (*a*) MDS analysis of sites based on presence/absence of coral-octocoral species in the four groups in the Coiba National Park; (*b*) same MDS analysis classified into three categories of live coral cover for coral communities (high > 40%; moderate 20–40%; low < 20%). Number of species within sites was grouped (solid lines) into four richness categories (from right to left: high, moderate–high, moderate and low). (*c*) MDS analysis for the distribution of rare species. The dotted lines indicate sites containing relative high diversity, live cover, and rareness of species. Stress = 0.16.

completely built by massive *Porites lobata*, and those at Punta Cirilo, Jicaron Northwest, Jicarita East and Montuosa West, dominated by the massive species *P. lobata*, *Pavona clavus* and *P. gigantea* along the reef base (Table 2).

Satellite image interpretation and cartography of terrestrial and marine environments

The coasts of islands and islets that make up the Coiba National Park were *c.* 339 km long. Terrestrial environments encompassed a total area of approximately 52 865 ha, with 44 417 ha of primary forest, 4763 ha secondary forest and 1940 ha mangrove swamp. Deforested land, which included areas for livestock farming, crops and grassland, covered only 1745 ha. The largest deforested area was observed along the eastern side of Coiba Island (Bahía Damas) within 3 km of the coast (Fig. 6).

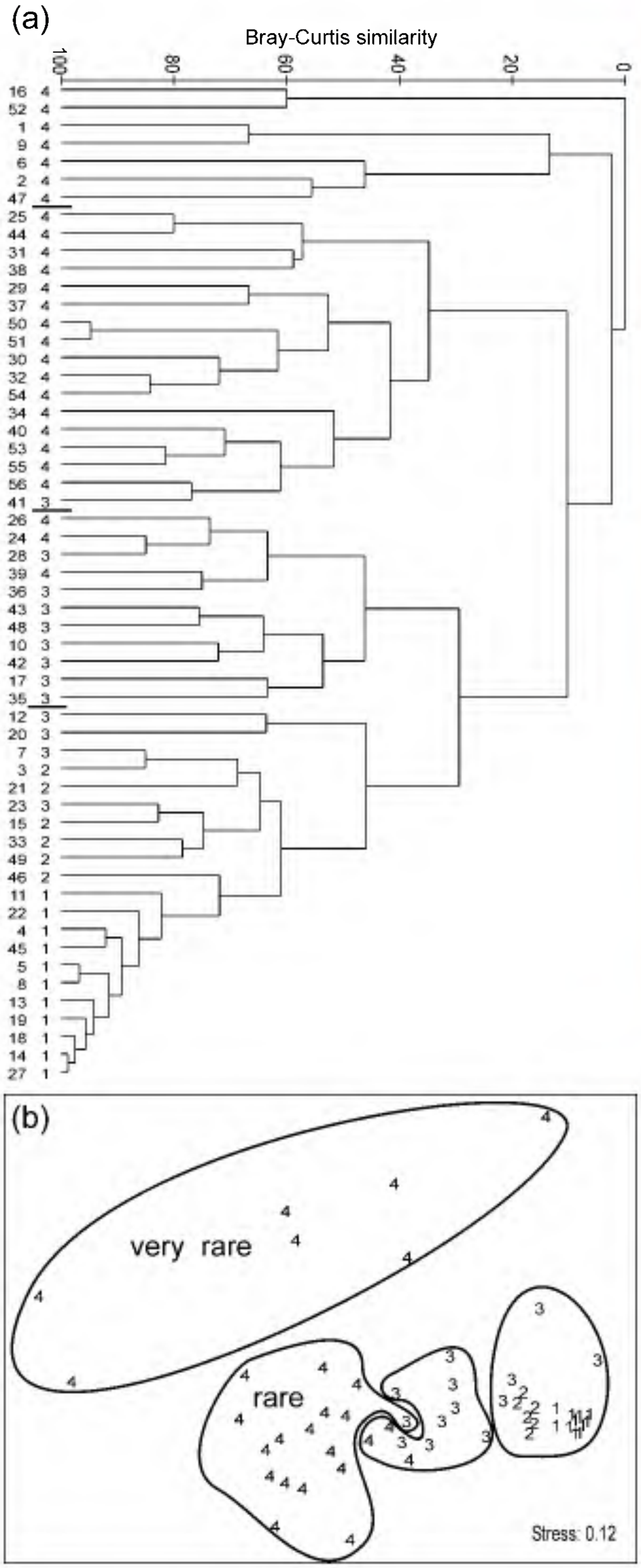

Figure 3 (*a*) Bray-Curtis similarity analysis of species commonness or rarity based on arbitrarily defined quartiles for percentages of sites: (1) abundant in 75–100% of sites, (2) very common (50–75%), (3) common (25–50%) and (4) rare (< 25%). Left axis indicates the species composition within the groups, as listed in Table 1. (*b*) MDS plot for the distribution of above categories and grouped by cluster analysis (solid lines). Stress = 0.12.

Figure 4 Distribution of species richness (coral and octocoral) in reefs and coral communities at Coiba National Park. The combined species richness is divided into four categories or quartiles: high (> 75%), moderate–high (50–75%), moderate (25–50%) and low (< 25%). Numbers indicate the sites given in Table 2.

We estimated approximately 24 901 ha of shallow marine habitats. Crustose coralline algae-building rhodolite communities were distributed widely and encompassed 60.5% (15 071 ha) of the total area (Fig. 6). Coral reefs were distributed along the eastern coast of Coiba Island and in patches surrounding the other islands of the archipelago. The area of reefs and coral communities was estimated to be 1703 ha (Fig. 6). Coral communities surrounded all the islands and islets, and were considered different from consolidated rocky beds (1499 ha). In Bahía Damas, we observed the largest subtidal rocky area, formed by scattered and semi-consolidated rocks (494 ha). The shallow sandy beds were divided into two categories, fine silt sand areas and coarse or calcareous sand areas with fragments of dead coral, with 4619 ha and 1063 ha, respectively (Fig. 6).

Table 2 Mean per cent cover (SE) of scleractinian corals, algae (frondose, turf) and crustose coralline algae at 24 sites in the Coiba National Park. Site names include those where only species richness was assessed (DS = diversity survey only). Coral reefs indicated without asterisk; *coral communities; and **coral reef monitoring sites. Site locations shown in Figures 4 and 5 (see later).

Site	*Site name*	*Coral*	*Algae*	*CCA*
1	Isla Pájaro*	71.3 (1.8)	24.1 (1.7)	2.9 (0.5)
2	Isla Brincanco Este*	48.9 (2.2)	45.5 (2.3)	5.2 (0.7)
3	Bajo Urracá	DS	DS	DS
4	Isla Brincanco Suroeste	DS	DS	DS
5	Isla Brincanco Suroeste	DS	DS	DS
6	Isla Sin Nombre Este*	64.0 (1.7)	27.9 (1.8)	6.3 (0.8)
7	Isla Uvita Arriba*	58.4 (2.4)	36.2 (2.4)	5.0 (0.6)
8	Isla Uvita Media*	76.1 (1.7)	18.9 (1.7)	4.2 (0.6)
9	Piedra Triple	DS	DS	DS
10	Piedra Bajo Triángulo	DS	DS	DS
11	Islote Almohada	DS	DS	DS
12–13	Isla Uva**	53.9 (4.0)	45.1 (4.0)	0.6 (0.2)
14	Roca Prosper	DS	DS	DS
15	Isla Canal Afuera Sureste**	1.2 (0.4)	55.1 (4.8)	42.9 (4.7)
16	Isla Canal Afuera Sureste	2.2 (0.5)	30.5 (3.8)	66.1 (3.9)
17	Isla Canal Afuera Norte	38.9 (2.3)	44.0 (2.4)	16.7 (2.0)
18	Bajo Canal Afuera	DS	DS	DS
19	Bajo La Viuda	DS	DS	DS
20	Islote Coibita	DS	DS	DS
21	Islote Aron	DS	DS	DS
22	Islote Pelado	DS	DS	DS
23	Islote Frijol	DS	DS	DS
24	Isla Ranchería Suroeste	31.9 (2.5)	65.1 (2.5)	2.0 (0.4)
25	Isla Coco Noreste	DS	DS	DS
26	Isla Granito de Oro	26.4 (2.9)	54.9 (3.6)	17.7 (2.1)
27	Isla Coiba Noreste	54.4 (2.6)	19.5 (2.1)	22.0 (2.5)
28	Punta Damas	27.6 (2.7)	53.8 (3.9)	12.4 (1.6)
29	Punta Felipa (Damas)**	26.1 (4.1)	65.3 (4.5)	8.6 (2.2)
30	Ensenada Maria (Damas)	17.0 (2.7)	45.8 (4.2)	36.8 (4.2)
31	Bajo Hill Rock	DS	DS	DS
32	Isla Barca Sur	DS	DS	DS
33	Isla Barca	22.9 (2.9)	73.4 (3.3)	3.5 (1.0)
34	Islote Punta Soledad	DS	DS	DS
35	Islote Passage Rocks	DS	DS	DS
36	Islote Logan Rock	DS	DS	DS
37	Piedra Hacha	DS	DS	DS
38	Bajo Telesto	DS	DS	DS
39	Bajo Twins	DS	DS	DS
40	Punta Cirilo	DS	DS	DS
41	Punta Cirilo	40.2 (2.8)	51.3 (2.5)	8.5 (1.4)
42	Punta Baltasar	DS	DS	DS
43	Islote Santa Cruz	DS	DS	DS
44	Ensenada Baltazar	15.3 (1.9)	73.9 (2.0)	6.6 (0.8)
45	Bajo Joshy	DS	DS	DS
46	Isla Jicarón Este*	30.9 (2.4)	40.1 (3.5)	29.0 (2.7)
47	Isla Jicarita Noreste	DS	DS	DS
48	Isla Jicarita Este	44.9 (2.4)	3.5 (0.9)	51.5 (2.7)
49	Isla Jicarita Sureste	DS	DS	DS
50	Bajo La Catedral	DS	DS	DS
51	Bajo Breaks	DS	DS	DS
52	Isla Jicarón Noroeste	30.5 (3.0)	63.9 (3.2)	2.6 (0.6)
53	Montuosa Norte*	20.4 (2.1)	73.4 (2.1)	5.3 (0.7)
54	Montuosa Sureste	43.4 (2.8)	35.8 (3.2)	15.4 (1.6)
55	Montuosa Oeste*	56.6 (2.7)	31.2 (2.3)	25.4 (2.2)
56	Bajo Montuosa Oeste	DS	DS	DS

DISCUSSION

This study suggests that a comprehensive survey designed to evaluate a coastal zone as complex as the CNP would not be possible without an increase in effort and sampling scale. The survey increased the chances to find rare species in habitats often not include in other studies and, therefore, to better identify high-diversity centres. In addition, an essential contribution to conservation was achieved through the first in-depth taxonomic account of the octocorals, a group that in addition to sponges remained ignored in the eastern Pacific for almost a century (Cortés 1997; Glynn & Maté 1997; Maté 2003).

The total reef area in Pacific Panama is unknown, but the Coiba Island reefs may be among the largest in the eastern Pacific with an area of up to 140 ha, if the reefs of Uva, Coiba (136 ha) and Canal de Afuera Islands are included (Glynn & Maté 1997; Maté 2003). Together with the localization of previously undescribed reef areas in the MPA, the satellite imagery allowed us to develop a map with the approximate distribution of coral reefs and coral communities in the Coiba archipelago. We report approximately 1700 ha of coral reefs and communities in the CNP. These areas include the oldest reefs in Panama, formed 5600 years before present, up to 12 m thick and dominated by *Pocillopora damicornis* (Glynn & Macintyre 1977).

The observed high coral cover and species richness were not evenly distributed across the coastal zone of the CNP and we identified the important areas based on the extensive distribution of coral communities (Figs 4 and 5). The maps show a spatial overlap of species richness and cover for 2–3 major proposed conservation units, namely the northernmost region (north Contreras Island and north-east Coiba Island) and the southernmost region (South Coiba Island/Jicarita Island). In addition, live coral cover observed in communities and reported here for the first time was surprisingly high relative to coral reefs, with an average of 60% coral cover, and up to 76% cover. Coral reefs with higher coral cover (> 30%) were located within the same area, which clearly demonstrates the need to protect the two areas mentioned above. These high species richness areas also contained species with large populations that were formerly classified as uncommon, such as *Gardineroseris planulata*, or common-endangered, such as *Millepora intricata* (Glynn & Ault 2000; Glynn *et al.* 2001; Maté 2003).

Coral reefs in these areas did not contain important populations of uncommon, rare or endangered species with locally restricted distributions, while coral communities sustained a higher species richness of scleractinian corals and octocorals than coral reefs (see also Glynn & Maté 1997; Maté 2003). Thus, we suggest that coral communities may be the source of larvae that are replenishing the populations of several species depleted by El Niño events, including common species like *Pocillopora* spp., *Gardineroseris planulata* and *Millepora intricata*. A particular reason for this is that these communities shelter higher habitat diversity than typical Panamanian coral reefs (Glynn & Wellington 1983; Colgan 1990; Guzman & Cortés 1993). On a regional scale, the availability and diversity of habitats might be factors that predict biodiversity of corals and reef-related species (Bellwood & Hughes 2001).

We suggest the sampling scale has limited understanding of the reefs and coral-community species distributions and abundances in the eastern Pacific for over 30 years and may have enhanced general perception that the species richness of the associated fauna is low (Colgan 1990, Cortés 1997; Glynn & Maté 1997) and its spatial distribution limited. We report four new undescribed species of *Pacifigorgia*; two are widely distributed in Panama, while two may be endemic to the Gulf of Chiriquí. The recently described octocoral *Pacifigorgia rubinoffi* is only known at eight sites in the Gulf of Chiriquí region (Breedy & Guzman 2003), four of which are in the CNP, and has a limited abundance of fewer than a dozen individuals. We confirm a new species of the hydrocoral *Distichopora* sp., mainly distributed on the southernmost side of the archipelago (reported as Stylasteridae in Maté 2003), and the second hydrocoral species for the eastern Pacific, after *D. laevigranulosa*, which is only known from the Galapagos Islands. Furthermore, the presence of *Pavona maldivensis* in the CNP (Jicarita Island) corroborates a previous report for Panama (Holst & Guzman 1993), which was doubted (Maté 2003), and for the first time we indicate the presence of *Pavona* cf. *duerdeni* and *P.* cf. *minuta*. We also confirm the presence of *Pocillopora inflata* in the area, previously confined in distribution to upwelling areas in the eastern Pacific (Maté 2003). It has been suggested that *Pocillopora eydouxi* is an uncommon species in Panama (Glynn & Ault 2000; Maté 2003), but we found colonies in coral communities all along the coast. In addition, important populations of *Millepora intricata* were present in shallow coral communities in the CNP and its surroundings. This indicates that these populations may have been abundantly present in other habitats, rather than exclusively found in shallow coral reefs (Glynn *et al.* 2001; Maté 2003). More thorough sampling may yet reveal populations of the two other species, *Millepora boschmai* and *M. platyphylla*, both considered extinct (Glynn & de Weerdt 1991; Glynn *et al.* 2001).

Threats to the integrity and management of the Coiba National Park

The selection process of marine protected areas must consider the identification of threats to diversity and its abundance (Done 2001; NRC 2001), including any type of risk related to unmanageable pressures such as anomalous temperatures (Done 2001). Threats identified for the present MPA include natural and anthropogenic disturbances that are common to the region (Maté 2003).

Natural disturbances have caused the most quantified damage in Panama. The region has suffered the consequences of warming events in 1982/1983 and 1997/1998 (Glynn *et al.* 1988, 2001) and, to a lesser extent, of red tides (Guzman *et al.* 1990). The 1982/1983 mortality apparently affected

Figure 5 Distribution of live coral cover in coral communities at Coiba National Park. Cover is divided into three categories: high (> 40%), moderate (20–40%) and low (< 20%). Numbers indicate the sites given in Table 2.

Figure 6 Distribution and surface area (ha) of marine and terrestrial habitats at the Coiba National Park, Panama. Map is based on preliminary analysis and interpretation of a LANDSAT 7 ETM image from 27 January 2002.

reefs regardless of whether they were to windward or leeward of the islands, and whether they were close or far from continental influence (Glynn 1984). However, during the 1997–1998 warming, greater bleaching and mortality pattern were observed at islands far away from the mainland than close to it, and it was suggested that some indicator species could be more susceptible, such as *Millepora intricata*, *Gardineroseris planulata* and *Porites panamensis* (Glynn *et al.* 2001). Although most Panamanian reefs suffered an estimated mortality of 50–100% (Glynn 1984; Glynn *et al.* 1988), there were areas where the integrity of the reef was maintained, perhaps associated with selective mortality of colonies (genotypes) that were less tolerant of thermal stress or the variety of orographic, hydrographic and oceanographic conditions affecting the protected area. This is evident today in the CNP, where mortality did not occur evenly across species, either within (depth, habitat) or between reefs separated by short distances (for example sites 1, 8, 17, 24, 26, 27, 41, 48 in Table 2; Fig. 5). *Millepora intricata*, *Gardineroseris planulata* and *Porites panamensis* are widely distributed and are currently abundant in the Gulf of Chiriquí. We conclude that the CNP has sustained large previously undescribed populations and coral species with genotypes probably resistant to some stressors; this may have mitigated the main unmanageable climate-change risk and aided the persistence of reefs and coral communities for the last decades (Done 2001).

There are three manageable anthropogenic factors currently affecting the integrity of the CNP. Overfishing occurs in spite of existing regulations. Secondly, sedimentation mainly affects the north-eastern drainage area of Coiba Island. This drainage encompasses at least eight of the rivers with the highest lengths and elevations in the basin (Cardiel *et al.* 1997) and the largest deforested area, which is close to the largest reef tract within the MPA. Finally, tourism is the largest threat to the Park, because any inadequate planning and unruly development of infrastructures would increase sedimentation and pollution in general, thus wasting the social, economic and environmental values of the region (Hall 2001; NRC 2001; Gell & Roberts 2003; Maté 2003).

We recognize that the MPA was created for its terrestrial attributes and not the status or diversity of marine habitats. This was appropriate given the selection of any MPA should consider the status of adjacent land habitats (NRC 2001). This indirect benefit has allowed managers and scientists to focus temporarily on designing priority conservation units within the MPA, based on the large-scale distribution of healthy reefs and coral communities and their diversity. The high cover of primary forest observed at most of the islands (> 84%), represents the best value added for the immediate protection of the CNP marine resources, particularly coral reefs. Hence, we provide three main recommendations for the conservation of the protected area considering potential threats and the landscape value of the terrestrial and marine environments as a whole. Firstly, three core zones of absolute protection should be created, restricting intrusive activities including fishing and extraction of sand and corals, and allowing regulated tourism. The three core zones, which include the northernmost area (Contreras Islands), north-eastern area (Canal de Afuera, Rancheria, north-east Coiba Island) and the southernmost area (Barca Island, Jicaron Island, Jicarita Island), might benefit neighbouring depleted fishing grounds (NRC 2001; Gell & Roberts 2003). Secondly, restoration and reforestation of grasslands on the eastern side of Coiba Island (Bahía Damas) could mitigate sedimentation in the coastal zone. Thirdly, tourist facilities should be developed outside of the MPA and on the mainland, which is less than 10 km from the north-eastern boundary.

ACKNOWLEDGEMENTS

We thank the crew of R/V Urracá and A. Lam for logistical field support. We are grateful to C. Muñoz for the analysis of satellite imagery and production of GIS maps. I. Hernández and K. Kaufman provided support on data management and analyses. The project was partially sponsored by Fundación AVINA and the Smithsonian Tropical Research Institute.

References

Andréfouët, S., Kramer, P., Torres-Pulliza, D., Joyce, K.E., Hochberg, E.J., Garza-Perez, R., Mumby, P.J., Riegl, B., Yamano, H., White, W.H., Zubia, M., Brock, J.C., Phinn, S.R., Naseer, A., Hatcher, B.G. & Muller-Karger, F.E. (2003) Multi-sites evaluation of Ikonos data for classification of tropical coral reef environments. *Remote Sensing Environment* (in press).

Beger, M., Jones, G.P. & Munday, P.L. (2003) Conservation of coral reef biodiversity: a comparison of reserve selection procedures for corals and fishes. *Biological Conservation* **111**: 53–62.

Bellwood, D.R. & Hughes, T.P. (2001) Regional-scale assembly rules and biodiversity of coral reefs. *Science* **292**: 1532–1534.

Breedy, O. & Guzman, H.M. (2003) A new species of *Pacifigorgia* (Coelenterata: Octocorallia: Gorgoniidae) from Panamá. *Zootaxa* **128**: 1–10.

Cardiel, J.M., Castroviejo, S. & Velayos, M. (1997) El Parque Nacional Coiba: El Medio Físico. In: *Flora y Fauna del Parque Nacional de Coiba (Panama)*, ed. S. Castroviejo, pp. 11–30. Madrid, Spain: Serviprint Press.

Castroviejo, S. & Ibañez, A. (2001) Origen y análisis de la diversidad biológica de la isla de Coiba. *Quercus* **188**: 29–32.

Clarke, K.R. & Warwick, R.M. (2001) *Changes in Marine Communities: an Approach to Statistical Analysis and Interpretation*, Second edition. Plymouth, UK: PRIMER-E Ltd.

Colgan, M.W. (1990) El Niño and the history of eastern Pacific reef building. In: *Global Ecological Consequence of the 1982–83 El Niño-Southern Oscillation*, ed. P.W. Glynn, pp. 183–232. Amsterdam, the Netherlands: Elsevier.

Cortés, J. (1997) Biology and geology of coral reefs of the eastern Pacific. *Coral Reefs* **16**: S39–S46.

Done, T. (2001) Scientific principles for establishing MPAs to alleviate coral bleaching and promote recovery. In: *Coral Bleaching and Marine Protected Areas*, ed. R.V. Salm & S.L. Coles, pp. 53–59. Honolulu, Hawaii, USA: The Nature Conservancy.

Enfield, D.B. (2001) Evolution and historical perspective of the 1997–1998 El Niño-Southern Oscillation event. *Bulletin Marine Science* **69**: 7–25.

Gell, F.R. & Roberts, C.M. (2003) *The Fishery Effects of Marine Reserves and Fishery Closures*. Washington, DC, USA: World Wildlife Fund.

Gladstone, W. (2002) The potential value of indicator groups in the selection of marine reserves. *Biological Conservation* **104**: 211–220.

Gladstone, W. & Davis, J. (2003) Reduced survey intensity and its consequences for marine reserve selection. *Biodiversity and Conservation* **12**: 1525–1536.

Glynn, P.W. (1984) Widespread coral mortality and 1982–83 El Niño warming event. *Environmental Conservation* **11**: 133–146.

Glynn, P.W. (1997) Eastern Pacific reef coral biogeography and faunal influx: Durham's dilemma revisited. In: *Proceedings 8th International Coral Reef Symposium, Volume 1*, ed. H.A. Lessios & I.G. Macintyre, pp. 371–378. Balboa, Panama: Smithsonian Tropical Research Institute.

Glynn P.W. & Ault, J.S. (2000) A biogeographic analysis and review of the far eastern Pacific coral reef region. *Coral Reefs* **19**: 1–23.

Glynn, P.W. & de Weerdt, W.H. (1991) Elimination of two reef-building hydrocorals following the1982–83 El Niño warming event. *Science* **253**: 69–71.

Glynn, P.W. & Macintyre, I.G. (1977) Growth rate and age of coral reefs on the Pacific coast of Panama. *Proceedings 3rd International Coral Reef Symposium, Volume 2*, ed. D.H. Taylor, pp. 251–259. Miami, USA: University of Miami Press.

Glynn, P.W. & Maté, J.L. (1997) Field guide to the Pacific coral reefs of Panama. In: *Proceedings 8th International Coral Reef Symposium, Volume 1*, ed. H.A. Lessios & I.G. Macintyre, pp. 145–166. Balboa, Panama: Smithsonian Tropical Research Institute.

Glynn, P.W. & Wellington, G.M. (1983) *Corals and Coral Reefs of the Galápagos Islands*. Berkeley, USA: University of California Press.

Glynn, P.W., Cortés, J., Guzman, H.M. & Richmond, R.H. (1988) El Niño (1982–1983) associated coral mortality and relationship to sea surface temperature deviations in the tropical eastern Pacific. *Proceedings 6th International Coral Reef Symposium, Volume 3*, ed. J.H. Choat *et al*., pp. 237–243. Townsville, Australia: 6th International Coral Reef Symposium Executive Committee.

Glynn, P.W., Maté J.L., Baker, A.C. & Calderon, M.O. (2001) Coral bleaching and mortality in Panama and Ecuador during the 1997–98 El Niño-Southern Oscillation event: spatial/temporal patterns and comparisons with the1982–1983 event. *Bulletin Marine Sciences* **69**: 79–109.

Glynn, P.W., Stewart, R.H. & McCosker, J.E. (1972) Pacific coral reefs of Panama: structure, distribution and predators. *Geologische Rundschau Stuggart* **61**: 483–519.

Green, E.P., Mumby, P.J., Edwards, A.J. & Clark, C.D. (1996) A review of remote sensing for the assessment and management of tropical coastal resources. *Coastal Management* **24**: 1–40.

Guzman, H.M. & Cortés, J. (1993) Los arrecifes coralinos del Pacífico oriental ecuatorial: revisión y perspectivas. *Revista Biologia Tropical* **41**: 535–557.

Guzman, H.M. & Guevara, C.A. (1999) Arrecifes coralinos de Bocas del Toro, Panamá: III. Distribución, estructura y estado de conservación de los arrecifes de las islas Pastores, Cristóbal, Popa y Cayo Agua. *Revista Biologia Tropical* **47**: 659–675.

Guzman, H.M., Cortés, J., Glynn, P.W. & Richmond, R.H. (1990) Coral mortality associated with dinoflagellate blooms in the eastern Pacific. *Marine Ecology Progress Series* **60**: 299–303.

Hall, C.M. (2001) Trends in ocean and coastal tourism: the end of the last frontier? *Ocean and Coastal Management* **44**: 601–618.

Holst, I. & Guzman, H.M. (1993) Lista de corales hermatípicos (Anthozoa: Scleractinia; Hydrozoa: Milleporina) a ambos lados del istmo de Panamá. *Revista Biologia Tropical* **41**: 871–875.

Hughes, T.P. (1994) Catastrophes, phase shifts, and large-scale degradation of a Caribbean coral reef. *Science* **265**: 1547–1551.

Hughes, T.P., Baird, A.H., Dinsdale, E.A., Moltschaniwskyj, N.A., Pratchett, M.S., Tanner, J.E. & Willis, B.L. (1999) Patterns of recruitment and abundance of corals along the Great Barrier Reef. *Nature* **397**: 59–63.

Jackson, J.B.C. (1991) Adaptation and diversity of reef corals. *BioScience* **41**: 475–482.

Jackson, J.B.C. (1994) Constancy and change of life in the sea. *Philosophical Transactions of the Royal Society London* **44**: 55–60.

Knowlton, N. & Jackson, J.B.C. (1994) New taxonomy and niche partitioning of coral reefs: jack of all trades or master of some. *Trends in Ecology Evolution* **9**: 7–9.

Kolarsky, R.A. & Mann, P. (1995) Structure and neotectonics of an oblique-subduction margin, southwestern Panama. *Geological Society America Special Paper* **265**: 131–157.

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

Miller, I. & Müller, R. (1999) Validity and reproducibility of benthic cover estimates made during broadscale surveys of coral reefs by manta tow. *Coral Reefs* **18**: 353–356.

Mumby, P.J. (2001) Beta and habitat diversity in marine systems: a new approach to measurement, scaling and interpretation. *Oecologia* **128**: 274–280.

Norse, E.A., ed. (1993) *Global Marine Biological Strategy: a Strategy for Building Conservation into Decision Making*. Washington, DC, USA: Island Press.

NRC (1995) *Understanding Marine Biodiversity*. Washington, DC, USA: National Academy Press.

NRC (2001) *Marine Protected Areas: Tools for Sustaining Ocean Ecosystems*. Washington, DC, USA: National Academy Press.

Roberts, C.M., McClean, C.J.,Veron, J.E.N., Hawkins, J.P., Allen, G.R., McAllister, D.E., Mittermeier, C.G., Schueler, F.W., Spalding, M., Wells, F., Vynne, C. & Werneretal, T.B. (2001) Marine biodiversity hotspots and conservation priorities for tropical reefs. *Science* **295**: 1280–1284.

Sheppard, C.R.C. (1998) Biodiversity patterns in Indian Ocean corals, and effects of taxonomic error in data. *Biodiversity and Conservation* **7**: 847–868.