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REPORT

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Coral reef distribution, status and geomorphology–biodiversity relationship in Kuna Yala (San Blas) archipelago, Caribbean Panama

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Abstract Most of the knowledge of the reef geomorphology and benthic communities of Kuna Yala coral reefs (Caribbean Panama) comes from the western side of the archipelago, a few tens of kilometers around Punta San Blas (Porvenir). To bridge the gap between Porvenir and the Colombia–Panama border, we investigated with Landsat images the extent and geomorphological diversity of the entire Kuna Yala to provide geomorphologic maps of the archipelago in 12 classes. In addition to remote sensing data, in situ survey conducted in May–June 2001 provided a Kuna Yala-wide first synoptic vision of reef status, in terms of benthic diversity (number of species of coral, octocorals, and sponges) and reef health (coral versus algal cover). For a total reef system estimated to cover 638 km^2 along 480 km of coastline, 195 km^2 include coral dominated areas and only 35 km^2 can be considered covered by corals. A total of 69 scleractinian coral, 38 octocoral, and 82 sponge species were recorded on the outer slopes of reef formations, with a slightly higher diversity in the area presenting the most abundant and diverse reef formations (western Kuna Yala). Attempts to relate benthic diversity and geomorphological diversity provided only weak relationships regardless of the taxa, and suggest that habitat heterogeneity within geomorphological areas explain better the patterns of coral diversity. This study confirms the potential of combined remote sensing and in situ surveys for regional scale assessment, and we suggest that similar approaches should be generalized for reef mapping and assessment for other reef sites.

Keywords Landsat · Remote sensing · Geomorphology · Mapping · San Blas · Coral reef diversity

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Introduction

Coral reefs of Kuna Yala (San Blas) archipelago (Fig. 1), Republic of Panama, have been studied for several decades (Porter 1974) . However, most of the knowledge of reef geomorphology and benthic and fish communities comes from the western reefs of the archipelago (Dahl et al. 1974; Lessios et al. 1984; Lasker et al. 1984; Ogden and Ogden 1993; Shulman and Robertson 1996; Clifton et al. 1997; Macintyre et al. 2001), few tens kilometers around Punta San Blas (or Porvenir). As a consequence, there are serious gaps in knowledge of coral reef ecosystem extent, type of structure, benthic diversity and reef health throughout the entire archipelago which stretches along 480 km of coastline from Punta Porvenir till the Columbia–Panama border.

Recently, Guzman et al. (2003) reported on the consequences of mining in coral communities by indigenous Kuna people and the status of coral reef communities in Kuna Yala. Since 1938, Kuna people have autonomy and authority within the boundaries of Kuna Yala, their territory, which includes the islands and reefs of Kuna Yala archipelago. Demographic growth and limited space on reef-top islands resulted in extensive coral mining to create new land. Guzmán et al. (2003) investigated the present situation in terms of living coral

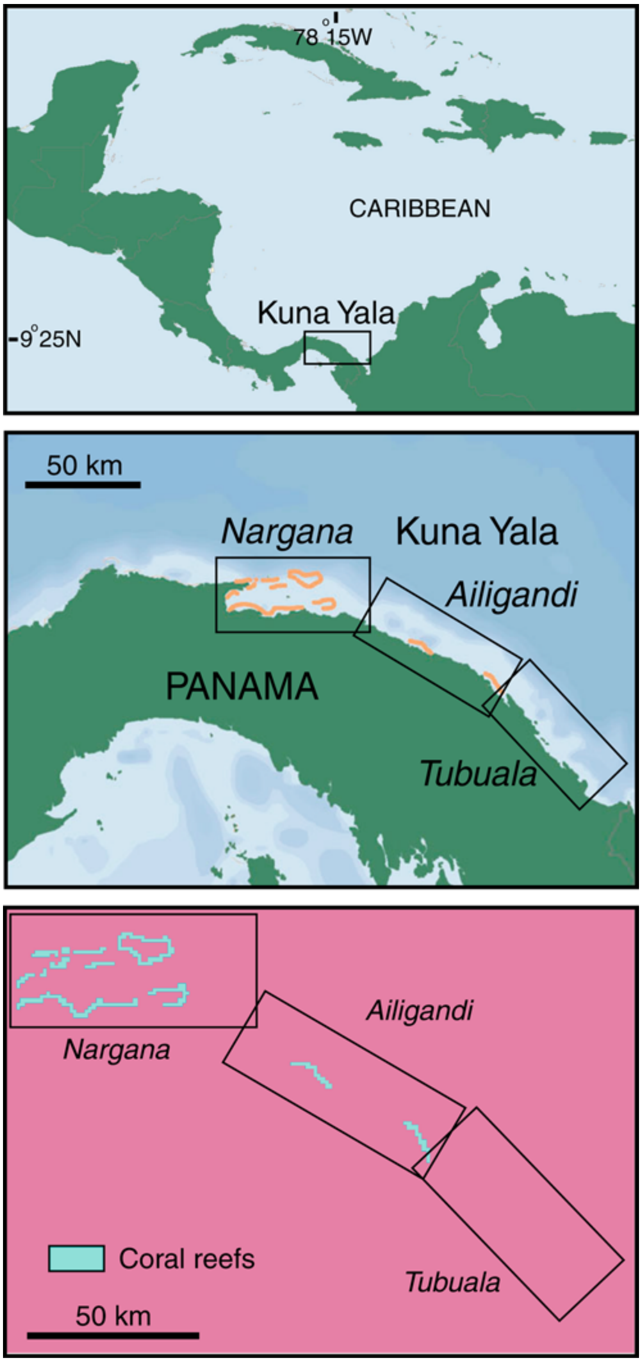


Fig. 1 Location of Kuna Yala archipelago (source: http://www.reefbase.org) and its three Corregimientos or political units (Nargana, Tubuala, and Ailigandi). The bottom panel highlights the current Caribbean Panama coral reef layer in ReefBase, also used in Spalding et al. (2001) for mapping and inventory of Kuna Yala reefs. Three discrete reef regions appear. Compare this map with Figs. 2 and 3

cover and compared with historical records. The data set describing the present situation was acquired mostly in May–June 2001 during a 6-weeks cruise spanning the entire archipelago from Punta Anachukuna to Punta Porvenir. Live cover and diversity of hard corals, soft corals, and sponges were assessed. Since the survey occurred mostly in *Terra Incognita* territory and during a limited time, several high-resolution Landsat images were used to plan the survey. In parallel with the benthic quantitative assessment, the images were also used to explore, survey, characterize, and inventory the different types of reef and island geomorphological formations. The multi-scale observations collected in 2001 allows us to present for the first time a complete overview of Kuna Yala reefs in terms of reef structures, reef extent, coral reef health, and coral diversity hot spots.

The creation of habitat or geomorphology maps is a critical step towards the assessment and management of reef ecosystems. Current applications of coral reef habitat maps include biogeochemical budgets (Andréfouët and Payri 2001) or resource assessment and exploitation planning (Long et al. 1993; Andréfouët et al. 2004). An interesting new application is to use remotely sensed habitat maps as indirect guides for assessing biological diversity in the context of marine conservation, or to identify the scale of processes that controls the structure of a mosaic of habitats (Mumby 2001). For marine conservation, the main goal is to predict the distribution of biodiversity in remote coral reef regions; and how this distribution can be inferred indirectly from broad-scale spatial patterns to avoid costly detailed surveys at the species level (Gaston 2000; Turner et al. 2003). Several examples of this approach already exist for coral reef environments, conducted at various spatial scales. However, in previous coral reef studies investigating diversity and spatial patterns (e.g., Galzin et al. 1994; Fabricius and De'ath 2001; Bellwood and Hughes 2001; Beger et al. 2003), remote sensing data have not been used and spatial information on reefs was consequently poorly estimated (e.g., surface area is crudely estimated by Bellwood and Hughes (2001)). These coral reef studies considered a limited number of positional (e.g., latitude, longitude, distance to center of diversity) or environmental predictors (e.g., surface areas, turbidity) while there is evidence that other local factors quantifiable from remote sensing images, such as presence of particular geomorphologic zones (e.g., pinnacles in lagoon), are also of importance (Adjeroud et al. 2000a). Indeed, if very general rules can be highlighted when considering very large geographic gradients (Bellwood and Hughes 2001), the effects of positional or environmental factors on biodiversity cannot be neglected for regional or archipelago-scale analysis (Gaston 2000; Cornell and Karlson 2000; Adjeroud et al. 2000a, Fabricius and De'ath 2001). Our Kuna Yala data set combining detailed coral reef geomorphology maps and benthic diversity censuses also enables us to explore if remote sensing maps can be used to predict coral diversity within a 480-km-long Caribbean reef track.

Material and methods

Nearly 600 field observations were collected by snorkeling in 2 weeks in May–June 2001 during a cruise on the R/V Urraca (Smithsonian Tropical Research Institute). These observations were made at various scales: geomorphology, habitat, community, and dominant species using a rapid assessment protocol (i.e., semi-quantitative description of benthic cover for habitat and community levels, and qualitative description for geomorphological and dominant species levels). For mapping purposes, we were constrained by the 30 m spatial resolution and limited spectral resolution (only the first three spectral bands are informative on underwater targets) of Landsat data. Therefore, a site consists of an area covering two to three Landsat pixels (1 pixel = 900 m^2), except in transitions. We conducted large-scale ‘‘transects’’ of several hundreds of meters or a few kilometers, in order to cross different sites of interest pre-selected on the images and georeferenced. Pre-selection intended to capture the highest diversity of sites in terms of color (due to bottom types and depth variations) and spatial structure. Spatial structure criteria include texture (related to two-dimensional patchiness of habitats), transition (mono-dimensional variation in color along sharp or large geomorphological gradients), and distance (e.g., distance to the shore). Each observation was georeferenced using hand-held GPS.

The same people who surveyed the reefs processed the images and designed the maps. For this project, four images were used, including three Landsat 7 Enhanced Thematic Mapper Plus (ETM+) and one Landsat 5 Thematic Mapper (TM) images. One ETM+ image of average quality (presence of clouds and atmospheric haze) acquired 19 August 2000 was used solely for the field survey conducted in May–June 2001, but not for mapping. To produce the final maps, two excellent recent ETM+ images acquired 3 June 2001 and 7 September 2001 were considered. The TM image (acquired 31 October 1986) came from the NASA Scientific Data Purchase program’s archive. It covers the Punta Porvenir area that was not optimal on the ETM+ image. It is of excellent quality, though it suffers from the standard TM problems (noise) and in our case from poorer geodetic accuracy (i.e., a 150-m offset compared to ETM+, which were at the precision of the pixel size). Overlap between ETM+ and TM data authorized the correct georeferencing of the TM image. A final mosaic was assembled by empirically correcting the at-sensor radiances using the 3rd June 2001 image as a reference. Bottom features were generally detectable to depths of 20–35 m depending on image quality and location.

To produce the geomorphological maps, the mosaic was processed using a combination of expert-driven segmentation, intra-segment classification, mathematical morphology operators, and final contextual editing. In short, it means that: (1) the analyst segments manually the image in broad zones of interest to avoid areas with different thematic meaning but with similar signatures. This stage could be called a priori contextual editing; (2) the resulting segments separately undergo a spectral supervised classification to discriminate areas thematically different but spectrally dissimilar within the segment, (3) each classification is processed to remove noise and correct misclassification by using morphological operators (e.g., to refine a contour) or a posteriori manual contextual editing (to reassign a group of misclassified pixels to a more adequate category).

This protocol, and the techniques we have developed, is very different than the typical habitat mapping exercise that can be found explained in the literature or handbooks (e.g., Green et al. 2000). Indeed, the constraints are different. Large spatial extent, variations in habitat types, and limited ground-truth data prevent using habitat mapping methods in an operational and accurate way. A recent study conducted in the southern Great Barrier Reef provides a clear demonstration that regional habitat mapping can produce results of doubtful value, with map overall accuracy ranging from 12 to 70% for reefs only few kilometers apart (Joyce et al. 2004). Another recent study confirmed on ten different sites worldwide that typical habitat mapping techniques seldom yield 90% accuracy, using Landsat 7 but also higher spatial resolution sensors such as IKONOS (Andréfouët et al. 2003a). In order to produce maps accurate at a rate higher than 90% (so that we can consider truly reliable for management decisions), large scale maps need to be conceived explicitly at geomorphological level, but with enough thematic complexity so that they intrinsically reflect the locations of key habitat zones. Such geomorphological maps, realized with a different protocol than ours, but with very similar outputs, have been recently released for Colombian reefs (Díaz et al. 2000).

Finally, and very importantly, the main difference between habitat mapping and our protocol lies in the accuracy assessment protocol. The accuracy of a habitat map is generally quantified using an error matrix that describes quantitatively how pixels of known habitat types have been misclassified (Foody 2002), but here, accuracy assessment is based on the respect of topological rules between classes. These rules are inherent to the description of each class. For instance, an ‘‘enclosed lagoon’’ is necessarily surrounded almost entirely by a ‘‘reef flat’’. A ‘‘fringing reef’’ is necessarily connected to the land. An ‘‘outer slope’’ is necessarily connected to the open deep water, a ‘‘crest’’ or a ‘‘reef flat’’. Although it is possible to automatize the computations of such topological rules (e.g., Suzuki et al. 2001 for atoll spillways and reef flats or Andréfouët et al. 2003b for atoll microbial mats), it is generally a complex and time-consuming challenge. Thus, here, consistency in topological rules is based on manual verification of the products. Moreover, human eyes detect immediately topological inconsistency while fully automatic processes are still imperfect (Suzuki et al. 2001), thus justifying our approach for the sake of efficiency. To conclude, according to our protocol, a map where geomorphological classes are topologically coherent is an accurate map.

Benthic community structure was quantitatively assessed by a separate team of SCUBA divers during the same cruise. They used previously implemented survey methods (*sensu* Guzman et al. 1991; Guzman and Guevara 2001). Species diversity (presence/absence) of hard corals (scleractinians and *Millepora*), soft corals (octocorals), and sponges were surveyed during 80-min dives on 56 reefs scattered along the archipelago (Table 1). The percent cover of major sessile organisms (e.g., corals, sponges, macro algae, and coral line algae) and density of sea urchins (*Diadema antillarum*) were visually estimated in 35 of the 56 reefs using a 1 m^2 quadrat subdivided into 100 grids of 100 cm^2. Three 8 m^2 transects separated by 10 m were randomly positioned parallel to the shore at four different depths (1–3, 10, 15, and 20 m).

To assess the linkages between geomorphology and benthic diversity we used a multi-scale approach based on simple indices of geormorphological diversity (O'Neill et al. 1988). The geomorphologic context of each benthic diversity site was characterized at three different scales by considering: (1) the geomorphological unit of the sampling zone (e.g., outer slope of fringing reefs, outer slope of patches, etc.), (2) the number of geomorphological zones in a 500×500 m window around the sampling site, (3) the number of geomorphological zones in a 1.5×1.5 km area around the sampling site. The 500 m and 1.5 km thresholds were selected by iteration with 100-m increment. Below 500 m, most of the time, only one or two geomorphologic zones were present in the moving window centered on the benthic sampling site, while above 1.5 km most of the geomorphological zones on large reef complexes (defined below) were included and most sampling sites reached the same value (five or six). Thus, we selected these thresholds of window sizes in order to span the widest range of geomorphological diversity (from one to six). Then, we compared the relationships between benthic diversity and geomorphological units and diversity for all taxa (corals, octocorals, and sponges).

Results

Kuna Yala reef classification

According to field and image observations, reef formations of Kuna Yala can be subdivided into four main classes. We described hereafter only the main sub-classes and their characteristics critical for this study. Further qualitative descriptions of the main benthic communities encountered in each geomorphological sub-class are available in Guzmán et al. (2002). The main reef types are fringing, coastal patches, reef complexes, and deep reefs.

Fringing reefs are structures physically connected with the mainland or connected to large islands in the East of the Kuna Yala system. Fringing reef flats were shallow (<1 m depth) and their outer delineation was derived from the limit of visibility in ETM+ Band 2 to integrate the upper section of the outer slopes to depths of approximately 10 m. Fringing reefs are the predominant reef type in the most eastern part and western part (from Punta Porvenir to Panama Canal) of the archipelago. Three sub-types of fringing reefs could be discriminated, related to three degrees of development of the outer crests as observed in situ. These were the no crest (sheltered reef), coral crest, and coralline algal crest types. Benthic diversity sampling sites were located on the outer slopes of the exposed fringing reefs, presenting coral or coralline crests.

Coastal patch reefs are isolated structures several hundreds of meters wide generally close to the shore, or at mid-distance between the shore and the outer reef complexes (defined below). They were frequently organized in fields or connected networks. Exposed patches showed differential growth patterns and clear, but narrow, zonations (live coral slope, crests, back-reef with dead structures and rubble, sand and seagrass) while sheltered patches did not. Outer slopes were generally steep. Very few patches presented extensive octocoral communities on sandy or pavement bottoms. These were not sub-surface patches, but had depths of 2–4 m and lacked crests.

In previous definitions (Guilcher 1988), reef complexes generally comprise several major reef types (e.g., fringing, barrier, and patch reefs) within an area. Here, Kuna Yala reef complexes are individual offshore structures organized around one or many cays, with reef flats, lagoons, channels, and patches. From east to west, reef complexes increase in numbers, size, and complexity, but they all belong to the same family of reef structures, thus we use the term reef complexes for all of them. On the eastern side of the archipelago, the complexes are few, of ellipsoidal shapes with none or only one single sand or vegetated cay. They are of simple complexity with a reef flat, crest, and outer slope. On the western side, the complexity increases with half-dozen sand cays connected by reef flats and patches or separated by enclosed lagoon and channels. These larger western reefs also have been named "bank barrier systems" (Macintyre et al. 2001). The main geomorphological sub-classes are cays (sandy or vegetated), crests, reef flats (sand, seagrass, coral, and heterogeneous flats), enclosed lagoons, networks of patches, passes, channels, and outer slopes. Finally, a particular reef complex is the Punta Porvenir area since this is the only complex connected to the mainland, with a fringing reef system. It deserves the term "complex" and not simply "fringing" because it presents most of the features of an offshore complex (cays, enclosed lagoon, reef flats, passes, and channels). This area has been the most intensively studied in Kuna Yala.

Reef complexes are connected by deep non-reefal areas, which are visible in ETM+ Band 1 or ETM+ Band 2, due to bright deep sand patches. This signature enables detection of envelopes around the reef complexes, which reveal how individual reef complexes are

Table 1 Sites investigated during the May–June 2001 survey for benthic diversity and cover

No.	Latitude (N)	Longitude (W)	Name	Sector	Diversity corals	Diversity octocorals	Diversity sponges	Geomorphological unit	Geomorphology index 1	Geomorphology index 2
1	8.745000	77.535556	Punta Anachukuna[a]	1	41	22	30	5	1	1
2	8.796944	77.521667	Bajo Yansidiuar	1	29	18	13	1	1	1
3	8.826111	77.601944	Isla Oro[a]	1	37	20	29	5	1	1
4	8.931389	77.688889	Isla Targantupo[a]	1	40	23	33	5	1	1
5	8.943333	77.739722	Mulatupo-Sasardi[a]	1	25	1	11	6	2	3
6	8.997222	77.746111	Isla Pino[a]	1	43	12	29	5	1	1
7	9.076389	77.761111	Bajo Isla Iguana	1	25	19	23	1	1	1
8	9.106111	77.858889	Punta Mosquito[a]	1	45	7	20	5	1	2
9	9.131389	77.872222	Bajo Isla Mosquito	1	32	9	25	1	1	1
10	9.141111	77.930556	Isla Ustupo[a]	2	39	4	21	5	3	4
11	9.211111	77.937500	Banco Mamitupo[a]	2	49	22	32	2	3	5
12	9.198333	77.980556	Achutupo[a]	2	45	17	26	1	3	5
13	9.249444	78.027222	Aligandi[a]	2	39	5	29	2	3	4
14	9.291111	78.066389	Bajo Aligandi	2	28	8	22	1	1	1
15	9.311389	78.153333	San Ignacio Tupile[a]	2	44	16	31	1	2	4
16	9.313333	78.169167	Bajo Cuitupo[a]	2	39	6	20	1	2	3
17	9.326389	78.231944	Isla Urbile	2	51	9	26	1	3	5
18	9.372778	78.261389	Cayo Ratones[a]	2	44	20	31	2	3	4
19	9.358333	78.235556	Cayo Ratones Este	2	44	13	20	2	3	4
20	9.310000	78.219167	Playon Chico Este[a]	2	35	12	16	7	2	3
21	9.413333	78.269444	Bajo Ratones Norte	2	26	14	19	3	2	2
22	9.319167	78.243056	Playon Chico Oeste[a]	2	23	1	13	7	2	6
23	9.422778	78.304444	Bajo Spokeshave Este	2	26	15	18	3	2	2
24	9.350000	78.304167	Bajo Irgandi	2	34	15	25	1	1	1
25	9.335833	78.170000	Tupile Norte[a]	2	42	14	29	1	3	4
26	9.415000	78.338611	Banco Spokeshave[a]	2	45	15	22	2	4	4
27	9.372222	78.354722	Roca Aguachichi[a]	2	44	18	27	7	1	2
28	9.395278	78.402222	Bajo Airdigandi	2	45	19	24	7	2	4
29	9.412222	78.452500	Punta Niadu[a]	2	32	18	31	5	1	1
30	9.469167	78.505556	Isla Puyada Este[a]	2	46	18	29	2	3	3
31	9.492778	78.465556	Bajo Puyada Este	2	26	14	32	3	2	2
32	9.433611	78.518333	Isla Tigre[a]	2	44	20	41	1	3	3
33	9.454722	78.546389	Isla Tupile	2	41	20	27	1	2	4
34	9.476944	78.591944	Isla Coco Oeste[a]	3	49	20	37	2	3	4
35	9.459444	78.607222	Isla Sugar	3	38	16	31	4	1	4
36	9.451944	78.659444	Isla Faro[a]	3	48	21	42	7	3	3
37	9.476667	78.657500	Isla Ubigantupo	3	37	21	41	4	3	5
38	9.517222	78.621667	Cayos Oldupuquip[a]	3	33	8	32	4	5	6
39	9.476111	78.691389	Cayos Mangles[a]	3	46	18	38	4	3	6
40	9.481389	78.720833	Cayos Morrotup Este	3	39	16	39	4	4	6
41	9.503889	78.809167	Cayos Morrotup Oest[a]	3	46	18	33	2	4	4
42	9.466667	78.781111	Bajo Punta Macolla	3	36	9	33	7	2	2
43	9.485000	78.819444	Cayo Moron[a]	3	46	17	41	2	3	3
44	9.506111	78.845556	Cayos Grullos	3	36	20	33	4	3	4
45	9.540833	78.897500	Cayos Limon Oeste[a]	3	58	22	39	4	3	4
46	9.563056	78.848889	Cayos Limon Este[a]	3	50	17	38	4	3	4
47	9.577500	78.726111	Cayos Maoki Sureste[a]	3	51	18	41	4	3	4
48	9.592778	78.765278	Cayos Maoki Oeste	3	34	15	25	4	3	4

Table 1 (Contd.)

No.	Latitude (N)	Longitude (W)	Name	Sector	Diversity corals	Diversity octocorals	Diversity sponges	Geomorphological unit	Geomorphology index 1	Geomorphology index 2
49	9.576111	78.685000	Cayos Maoki Este[a]	3	51	19	27	4	3	3
50	9.579444	78.733056	Cayos Maoki Suroeste	3	43	16	35	4	3	4
51	9.470556	78.927778	Bajo Carti Este[a]	3	44	1	35	7	2	2
52	9.494167	79.030278	Cayo Guardo[a]	3	48	6	36	7	2	2
53	9.545833	78.979444	Ulaksukum[a]	3	44	4	48	4	3	5
54	9.553611	78.944167	Aguadargana[a]	3	53	23	43	4	2	3
55	9.485833	78.984167	Bajo Carti Noroeste	3	39	15	47	7	2	2
56	9.534722	79.041389	Isla Gertie Norte	3	36	3	44	6	1	1

[a] Sites investigated in May–June 2001 survey

Sector: *1* Tubuala, *2* Ailigandi, *3* Nargana. Type of geomorphological units: *1* Reef complex slope Type 1 (low relief, high algal cover), *2* Reef complex slope Type 2 (high relief), *3* Reef complex slope Type 3 (wide exposed terraces), *4* Reef complex slope Type 4 (narrow protected walls), *5* Exposed fringing reefs slopes (moderate to low relief), *6* Protected fringing reef slopes (low relief), *7* Slopes of coastal patches (moderate to low relief). "Geomorphology Index 1" is the number of geomorphologic strata (see list in Table 2) present in a 0.5×0.5 km window around the sampling site. "Geomorphology Index 2" is the number of geomorphologic strata (Table 2) present in a 1.5×1.5 km window around the sampling site

interconnected by shallower seafloor. Comparisons with nautical charts suggest that these envelopes follow closely the 35-m isobath for clear water areas, and ~20-m where water is more turbid or the image noisy (TM data). On the southern side of reef complexes, envelopes are generally narrow and follow closely the outer slopes (see below) outlines, while they are more extended on the lateral and northern sides of reef complexes.

We describe hereafter in more detail the geomorphological sub-classes within a reef complex.

- Reef flats can be extensive and are always shallow in the limit of visibility of ETM+ Band 3. Coral flats usually consist of finger *Porites* spp. pavements, and display less commonly frameworks of small massive coral colonies. Seagrass flats typically include dense *Thalassia testudinum* beds grading to more scattered grass often mixed with sand, branching coral line algae (*Neogoniolithon* sp.), sponges, green algal communities, and coarse skeletal debris. Flats exposed to the south and protected by cays on their northern side are generally very narrow, less than 100 m wide, but present the highest density of *Acropora palmata* framework at their edges. Few of these *A. palmata* colonies were healthy.
- Crests on the exposed sides (North) of reef complexes are generally well-developed coralline crests associated with zoanthids and *Millepora*. There are coral crests (or no crests at all) on the protected sides (South). Some high energy crests are exceptionally wide and well visible on ETM+ imagery. Cores have shown that these crests are not built by calcareous algae, but by storm deposits coated by coralline algae (Macintyre et al. 2001).
- The different types of outer slopes can be categorized in four reefscapes, according to four architectures. Dahl et al. (1974) provide several drawings of profiles of outer slopes in Western San Blas that match our definitions. Type 1: wide gentle slopes, with poor structural complexity, dominated by brown algae communities. Large isolated individual *A. palmata* colonies are frequent, either healthy, dead, or covered by encrusting sponges. Type 2: wide slopes of high structural complexity presenting three facies, with coralline-cemented crests, well-defined spur-and-groves and deeper large bommies and coral heads (e.g., *Montastraea* spp.). Type 3: multiple-terraced slopes with sand channels. These are high exposure slopes, very wide, exclusively on the northern sides of the most northern outer reef complexes. They appear to have mostly rocky bottom with high algal cover. The widest Type 3 outer slopes are on Cayo Holandes (2 km wide) and north of Cayo Icacos, the last one presenting most likely intermediate coral escarpment between the terraces, according to visual image interpretation. Type 4: narrow steep coral slopes and coral walls, encountered along protected sides (South) of reef complexes and along few patch reefs. *Millepora* spp. is abundant in the shallows. Brown algae

communities were also abundant. Extensive octocoral communities are often present at the interface with the sand/seagrass zone at the bottom of the slope. A high diversity of hard corals was noted there in agreement with observations made three decades ago (Dahl et al. 1974).

Finally, deep reefs are also present in Kuna Yala. Indeed, images reveal large structures entirely submerged visible on both Band 1 and Band 2 but not Band 3. Image of lower quality can only outline the shape of the reefs in Band 1, at the limit of the noise. This suggests an average depth of 10–20 m. These submerged deeper reefs are aligned with modern reef complexes. They also have the same features and same complexity and topography as modern sub-surface reef complexes with remnants of reef flats, sand pools, enclosed lagoons, passes, and channels clearly visible on the images. Cover of the submerged flats is unknown, but spectral signatures suggest that the bottom is very similar to the reef complex Type 3 outer slope and that brown algae communities are dominant. The reason why these deep reefs did not catch-up with sea surface or why they have sunk is unknown.

Kuna Yala reef mapping and extent

We propose 12 thematic reef layers (Table 2) to map Kuna Yala reefs (Figs. 2, 3). Another layer is added for the small scattered clouds that could not be removed using multi-date imagery. Labeling is geomorphological (Table 2). The moderate-complexity map in 12 classes provides clear indication of the variation of reef structure throughout Kuna Yala and also highlights the specificities of this reef tract in the Caribbean context.

Table 2 reports the surface areas of each geomorphological class for the three political units of Kuna Yala: Tubuala, Nargana, and Ailigandi. Nargana is the region with by far the most diverse and abundant reef formations. The most eastern region, Tubuala, is the poorest. In terms of inventories of coral reefs, we need to keep in mind what the different classes imply in terms of cover. Total reef area is 638.66 km^2 considering all the classes (Table 2). However, coral-dominated areas are limited to some slopes and escarpments, and some sections of reef flats and top/crests of coastal patches and fringing reefs. Even on outer slopes of reef complexes, the large value for Nargana includes mostly wide terraces dominated by algae. This means that true coral area are around 4.63 (slopes of reef complex patches) + 60.67 (reef flats) + 51.24 (reef complex outer slopes) + 40.59 (coastal patches) +34.68 (fringing reefs) = 191 km^2. Moreover, assuming realistically that 1% of deep zones, 5% of reef flats, fringing reefs, and coastal patches, and 25% of slopes are live corals, we obtain 35 km^2 of coral-dominated areas. These figures can be compared to the previous reference, a 1-km resolution inventory based on digitized nautical charts (Spalding et al. 2001). The 1-km resolution raster database provides ~250 km^2 of coral reef areas for Kuna Yala (Fig. 1) (Spalding et al. 2001) and poorly reflects the actual continuous spatial distribution of the reefs (Figs. 2 and 3), with no reefs reported for Tubuala, for instance (Fig. 1). This number does not reflect accurately either the extent of the reef system (638 km^2) or the surface area likely covered by corals (35 km^2).

Table 2 Surface areas (km^2) per geomorphological class mapped in Figs. 3 and 4, for the three Kuna Yala political units

Geomorphologic class	Tubuala	Nargana	Ailigandi	Total
Fringing reefs	13.47	18.18	3.03	34.68
Coastal patches				
Summit	5.65	16.05	1.27	22.97
Slope	2.34	13.70	1.58	17.62
Deep reef complexes	12.14	34.52	28.61	75.27
Reef complexes				
Algal crest[a]	0.00	0.23	0.00	0.23
Patches	0.00	2.91	0.00	2.91
Slope of patches	0.00	4.63	0.00	4.63
Reef flats	0.71	53.35	6.61	60.67
Enclosed lagoon	0.43	16.50	0.70	17.63
Outer slopes	0.70	41.73	8.81	51.24
Envelop	58.01	179.67	102.59	340.27
Cays	0.34	7.33	2.88	10.55
Total	93.78	388.79	156.09	638.66

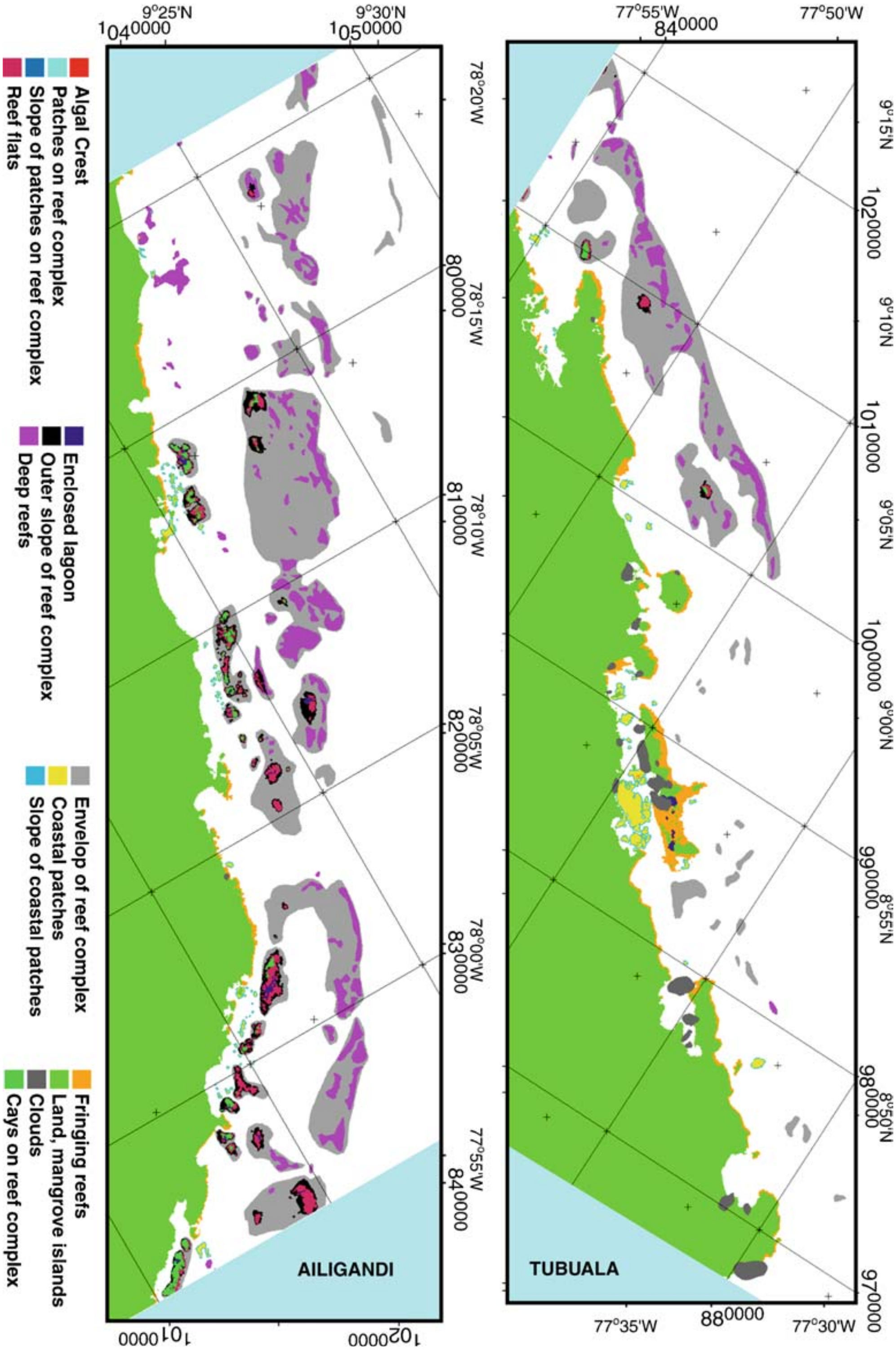
[a] Refers to the structure described in Macintyre et al. (2001)

Benthic diversity and cover

The results on benthic diversity and community structure are partially available elsewhere (Guzman et al. 2003) for the same three political units of Kuna Yala, including the detailed list of species records (Guzman et al. 2002). Here, we provide coral and algal cover for all the 35 sites where cover was measured (Fig. 4). All values are mean ± standard errors. Coral cover in Nargana ($29.4 \pm 0.54\%$, $n = 1368$ m^2) was significantly higher than in Tubuala ($21.4 \pm 0.80\%$, $n = 504$) and Ailigandi ($19.6 \pm 0.49\%$, $n = 1344$) (Kruskall–Wallis one-way ANOVA, $H = 19.184$, $P < 0.001$). Overall, compared to the historical data for western Kuna Yala, this suggests a significant decrease in coral cover in some areas from 60% down to 13% (Guzman et al. 2003). Coral cover was slightly lower in the shallow (<5 m depth) areas ($22.8 \pm 2.1\%$, $n = 34$ transects) compared to the 10, and 15 m depth sites ($26.5 \pm 1.9\%$, $n = 35$ and $27.4 \pm 2.3\%$, $n = 31$ respectively), but higher than at depth >20 m ($19.7 \pm 2.9\%$, $n = 28$). Macroalgae cover was always high and not significantly different between regions ($63 \pm 2.3\%$ considering all field stations) (Fig. 4). Differences with depth occur, with lower algal cover in the shallows ($58.9 \pm 2.6\%$, $n = 34$) than at deeper sites ($68.6 \pm 3.4\%$, $n = 28$).

For diversity, 69 scleractinian coral, 38 octocoral, and 82 sponge species were recorded throughout Kuna Yala. There is also a regional pattern for scleractinian

Fig. 2 Geomorphological maps of Tubuala and Ailigandi political units of Kuna Yala as derived from Landsat imagery. See Fig. 1 for panel location. Geographic grid in UTM WGS 84 (each square = 10 km)



and sponges. For scleractinia, we observed a higher diversity in Nargana (67 species) than in Tubuala (57) and Ailigandi (62). This increased the known diversity of the Caribbean Panama reefs, previously estimated to be 61 scleractinian species (Holst and Guzman 1993). For sponges, we also observed a higher diversity in Nargana (74 species) than in Tubuala (54) and Ailigandi (63). Although this also increased the number of recorded species, it is far below the total number of species recorded for the Caribbean (640) (van Soest 1984) and the Kuna Yala diversity is still likely underestimated. The total number of soft coral species was not different between regions (30, 34, and 33 for Tubuala, Ailigandi, and Nargana, respectively).

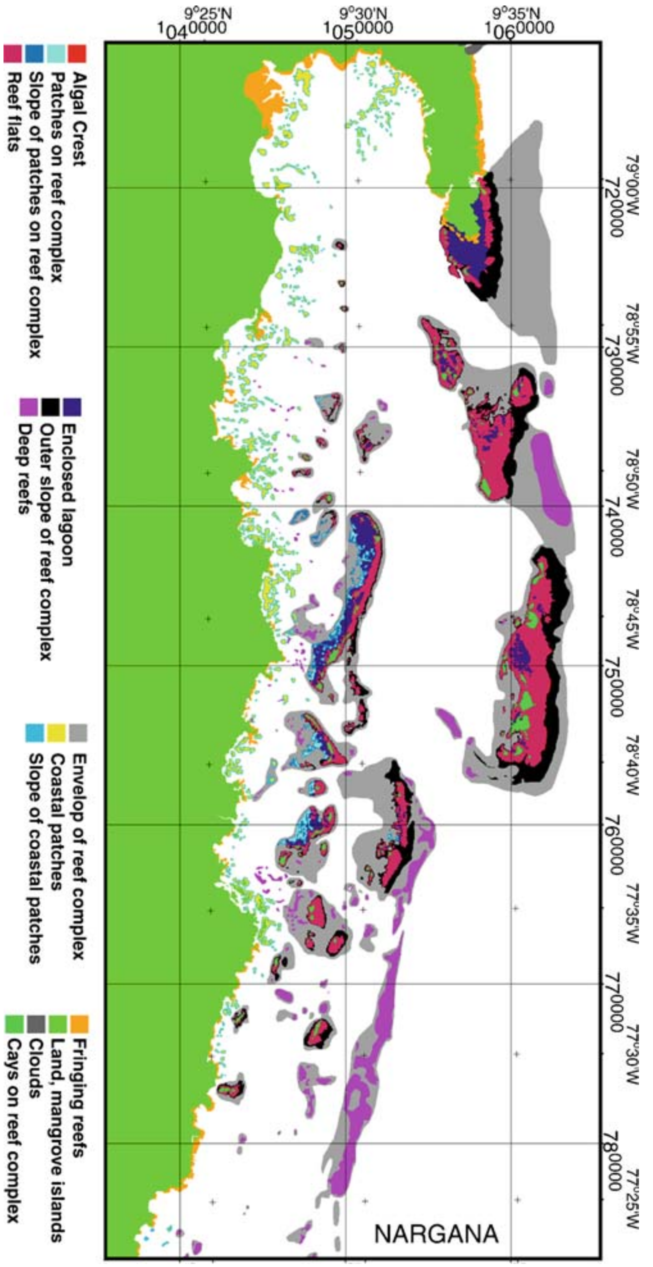


Fig. 3 Geomorphological map of Nargana political unit of Kuna Yala as derived from Landsat imagery. See Fig. 1 for panel location. Geographic grid in UTM WGS 84 (each square = 10 km)

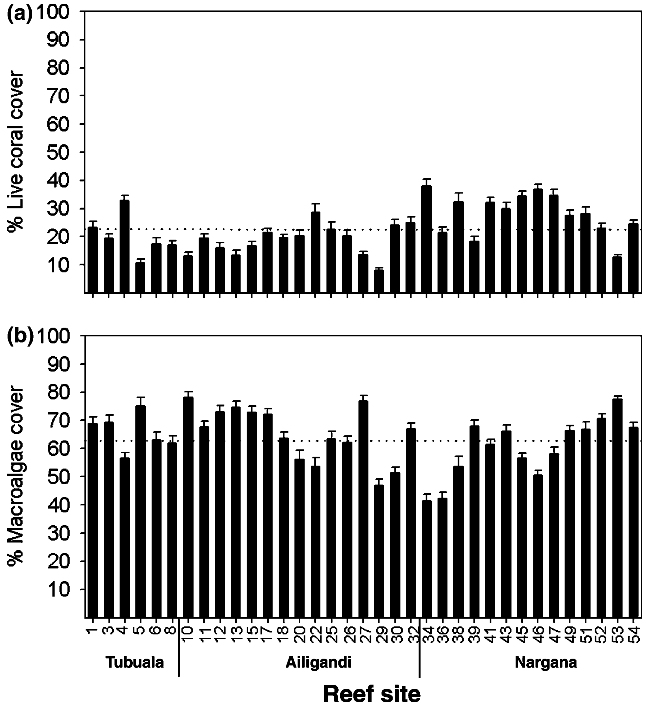


Fig. 4 Coral and algal cover for all the sites surveyed in May–June 2001. *Broken line* represents the mean, *error bars* are Standard Errors

Discussion

Geomorphology–benthos diversity relationships

In many land studies, remotely sensed indicators are used to develop and improve models of biodiversity (e.g., Stohlgren et al. 1997; Wagner and Edwards 2001; Luoto et al. 2002) to help management decisions and better understand the environmental factors controlling diversity at various spatial and biological scales (alpha-, beta-, or gamma-diversity) (Stoms and Estes 1991; Nagendra 2001). Biodiversity is generally defined in its organismal sense, referring mostly to species distribution and numbers within a given area (Turner et al. 2003). Remote sensing has been used for direct assessment of biodiversity (i.e., counting species of trees) but more generally indirectly (i.e., providing information on environmental proxies related to biodiversity patterns) (Turner et al. 2003). Few studies have tried to correlate directly the distribution of species diversity with habitat or geomorphology maps derived from remote sensing, even for land studies (Nagendra 2001).

At a large oceanic scale, in the Indo-Pacific, reef types did not seem to explain substantially biodiversity patterns (Bellwood and Hughes 2001), but reef types were only categorized as oceanic and continental reefs without further geomorphological details. Here, the Nargana area presented the highest number and density of reefs (Fig. 3) and the highest benthic biodiversity (Fig. 4), suggesting that at archipelago scale, number, and density of reefs are important factors to explain patterns of biodiversity (Gaston 2000). Diversity decreased eastward at both scales, geomorphological and biological. Diversity varied positively with increasing surface areas of coral reefs for corals and sponges for the three major structural (and political) zones of Kuna Yala. For scleractinian corals, we observed a higher diversity in Nargana (67 species, 388.79 km^2 of reefs) than Ailigandi (62 species, 156.09 km^2 of reefs) and Tubuala (57 for 93.78 km^2 of reefs). This is in general agreement with the fact that larger areas may support more species than smaller areas (Cornell and Karlson 2000).

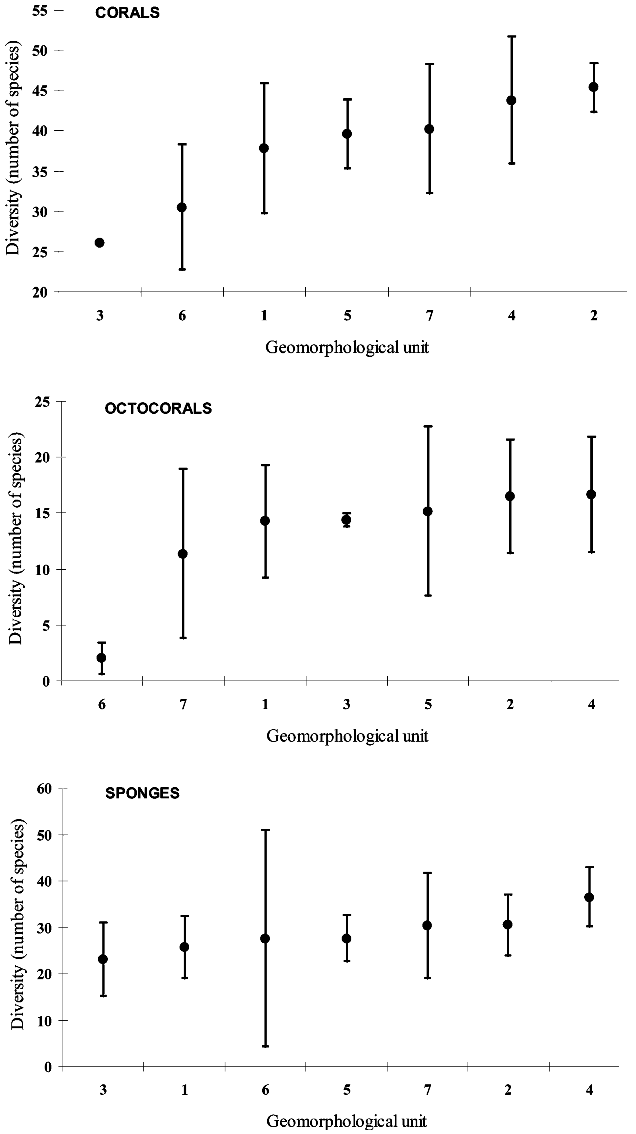


Fig. 5 Relationships between geomorphological unit and benthic diversity (mean ± standard deviation) for corals (*top*), octocorals (*middle*), and sponges (*bottom*). Geomorphological units are ranked by increasing average number of species. Type of geomorphological units: *1* reef complex slope Type 1 (low relief, high algal cover, $n=12$), *2* reef complex slope Type 2 (high relief, $n=9$), *3* reef complex slope Type 3 (wide exposed terraces, $n=3$), *4* reef complex slope Type 4 (narrow protected walls, $n=14$), *5* exposed fringing reefs slopes (moderate to low relief, $n=7$), *6* protected fringing reef slopes (low relief, $n=2$), *7* slopes of coastal patches (moderate to low relief, $n=9$)

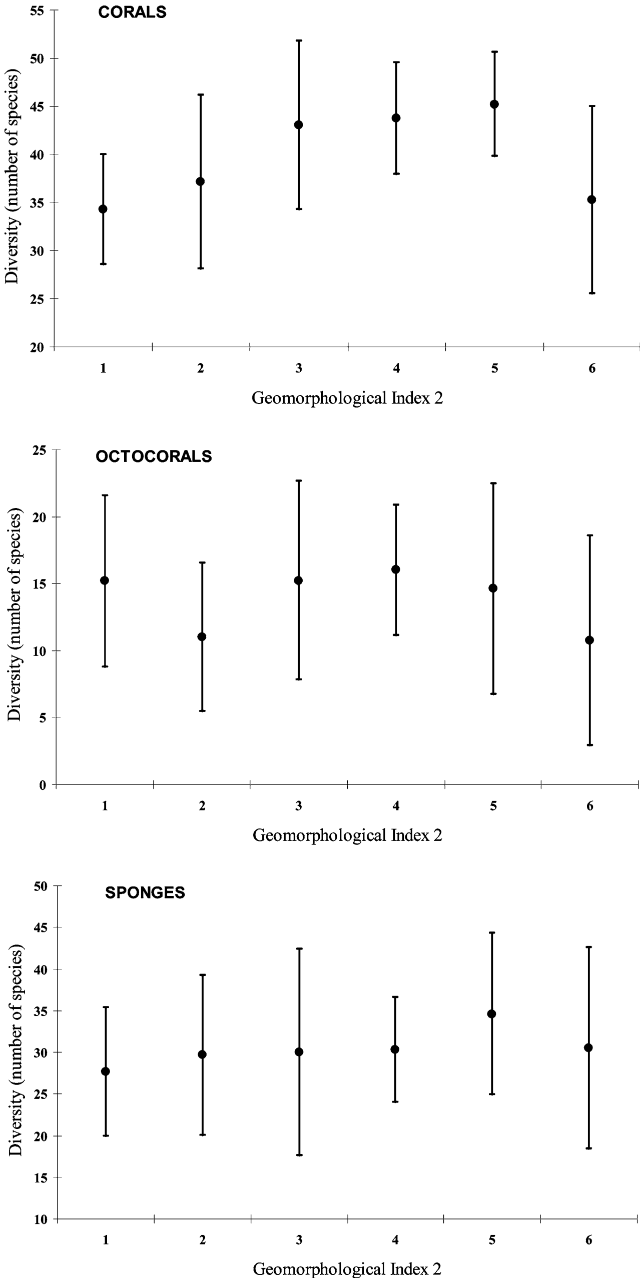


Fig. 6 Relationships between geomorphological diversity (index 2, computed with a 1.5×1.5 km window centered on each station detailed in Table 1) and benthic diversity (mean ± standard deviation) for corals (*top*), octocorals (*middle*), and sponges (*bottom*). Population number (n) = {11, 9, 9, 18, 5, 4} for Index 2 = {1, 2, 3, 4, 5, 6}, respectively

These patterns prompted us to check if geomorphological descriptors alone could be used to predict benthic diversity. We acknowledge that the survey and sampling design was not initially designed to fully address this question, since the diversity and community structure surveys addressed only the outer slopes of the reefs and few deep reefs. Shallow reef flats, patches, fringing reefs, or deep reefs were not sampled with the same effort because of the limited time during the May–June 2001 survey. However, to design marine protected areas within a region, the question of whether remote sensing products alone (habitat or geomorphology maps) can be used as surrogates for benthic or fish diversity is a key issue (Ward et al. 1999; Beger et al. 2003) and we investigate this aspect using only outer slopes data, which generally provides the highest coral diversity.

Here, we observe some linear trends, but they are weak (Figs. 5 and 6). Results suggest that coral diversity throughout Kuna Yala follows a trend at the level of the geomorphological unit (Fig. 5) and for the 1.5 km×1.5 km spatial scale (Fig. 6) but not at 500 m×500 m scale (not shown). Most differences are not significant. At the geomorphological unit level, we observe a linear increase in species number that can be explained by the degree of structural complexity of outer slopes of reef complexes. Since we have categorized the outer slopes of reef complexes in four reefscapes, this trend actually reveals the influence of habitat heterogeneity within the geomorphological strata.

No clear trends exist between geomorphology and sponge or octocorals diversities, except for octocorals at the geomorphological unit scale (Fig. 5). However, since sponges inventories are clearly underestimated, the question of a relationship geomorphology–sponge diversity remains open.

Our results suggest that geomorphologic diversity alone is a poor predictor of the biodiversity within Kuna Yala. The most convincing result (coral diversity versus geomorphological unit) rather confirms that habitat (or reefscape) heterogeneity is a more appropriate way to predict benthic diversity (Ward et al. 1999; Cornell and Karlson 2000; Mumby 2001). However, to fully assess the power of geomorphological predictors, we also suggest that more tests are necessary if the opportunity to combine high quality, high resolution data sets of large number of species over large area arises. The first reason for further tests is that, in our study, we explored one simple way to quantify the geomorphology–species diversity relationship, but we were limited in the options because the May–June 2001 survey was not conceived for this purpose. A beta-diversity analysis of geomorphology or habitat (sensu Mumby 2001) would not have been possible with our data set. The main drawback of the simple geomophologic diversity index that we used here is that differences between geomorphological units are hidden. For instance, a coral-rich outer slope of an exposed fringing reef is closer to a coral-algal outer slope of an exposed patch than a seagrass-rich reef flat but we did not consider so. All geomorphological units had the same level of dissimilarity.

The second reason is that even if spatial variations exist from one Kuna Yala region to another, the range of diversity between the poorest and richest area is not huge, with 67 coral species for Nargana and 57 for Tubuala. Thus, it may be difficult to highlight clear trends with so little variation. In comparisons, studies at the scale of the Indian and Pacific Ocean consider *quasi* an order of magnitude difference in biodiversity between sampling sites (e.g., for number of coral species) (Bellwood and Hughes 2001). Exploring and explaining the patterns of coral diversity in low diversity regions is possible but the regions previously considered were much larger than Kuna Yala so larger gradients of environmental factors or type of reefs were included (e.g., Eastern Pacific in Glynn and Ault (2000)). Including geomorphology maps in studies at the scale of the Indo-Pacific will likely be enlightening, especially considering the highest diversity of reef structures. For instance, Adjeroud et al. (2000b) have shown that the diversity of fish in Tuamotu atolls lagoons is well predicted by the size of the lagoon, but also by the type of geomorphological strata present in the atoll. Similar results were obtained for coral diversity in the same lagoons (Adjeroud et al. 2000a).

We suggest that our Kuna Yala test should be reproduced at the scale of the Caribbean after compilation of an adequate spatially explicit biodiversity data set and using a set of Landsat-derived geomorphology maps. It should be also possible to re-explore previous georeferenced benthic data sets in other regions of the world (e.g., Fabricius and De'ath 2001) even if they have been acquired several years ago, since reef geomorphology is not fast changing. Depending on the location, scale, and scope of these previous studies, several positional or environmental regional/local factors (depth, distance to the shore, riverine discharge, shoreline habitats, sea surface temperature, circulation, turbidity, human disturbances) explained the spatial patterns, but never entirely, since many processes occurring along the continuum of time and space scales control diversity (Cornell and Karlson 2000). Indicators of geomorphological (and reefscape) heterogeneity may provide residual explanations. We agree with Cornell and Karlson (2000) that "we suspect that (between-habitat area) heterogeneity (in medium to large areas) will be a dominant factor in the richness-area correlation because of its ubiquity on reefs". Since remote sensing maps such as those used here have become widely available even for very large areas, systematic inclusion of geomorphological, reefscape, or habitat data in multivariate statistical analysis is recommended.

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