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Assessing the ecological effects of human impacts on coral reefs in Bocas del Toro, Panama

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Abstract Environmental and biological reef monitoring was conducted in Almirante Bay (Bahía Almirante) in Bocas del Toro, Panama, to assess impacts from anthropogenic developments. An integrated monitoring investigated how seasonal temperature stress, turbidity, eutrophication and physical impacts threatened reef health and biodiversity throughout the region. Environmental parameters such as total suspended solids [TSS], carbon isotopes ($\delta^{13}C$), C/N ratios, chlorophyll *a*, irradiance, secchi depth, size fractions of the sediments and isotope composition of dissolved inorganic carbon [DIC] of the water were measured throughout the years 2010 and 2011 and were analysed in order to identify different impact sources. Compared to data from Collin et al. (Smithsonian Contributions to the Marine Sciences 38:324–334, 2009) chlorophyll *a* has doubled at sites close to the city and the port Almirante (from 0.46–0.49 to 0.78–0.97 μg l^{-1}) and suspension load increased, visible by a decrease in secchi depth values. Visibility decreased from 9-13 m down to 4 m at the bay inlet Boca del Drago, which is strongly exposed to river run off and dredging for the shipping traffic. Eutrophication and turbidity levels seemed to be the determining factor for the loss of hard coral diversity, most significant at chlorophyll *a* levels higher than 0.5 μg l^{-1} and TSS levels higher than 4.7 mg l^{-1}. Hard coral cover within the bay has also declined, at some sites down to <10 % with extremely low diversities (7 hard coral species). The hard coral species *Porites furcata* dominated the reefs in highly impacted areas and showed a strong recovery after bleaching and a higher tolerance to turbidity and eutrophication compared to other hard coral species in the bay. Serious overfishing was detected in the region by a lack of adult and carnivorous fish species, such as grunts, snappers and groupers. Study sites less impacted by anthropogenic activities and/or those with local protection showed a higher hard coral cover and fish abundance; however, an overall loss of hard coral diversity was observed.

Keywords Reef cover · Biodiversity · Environmental · Biological monitoring

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Introduction

The drastic degradation of coral reef communities due to an increase in anthropogenic impacts has been documented within Almirante Bay (Bahía Almirante) in Bocas del Toro, Panama (Guzmán and Jiménez 1992; Guzmán and García 2002; Guzmán 2003; Collin 2005; Guzmán et al. 2005; Collin et al. 2009). This semi-lagoon system has one main inlet at Boca del Drago and outlets between Isla Colón and Bastimentos, and another at the east of Isla Popa (Fig. 1). It is bordered by large coastal swamps and mangrove forests (Collin 2005). The bay has an approximate surface area of 446 km^2 (D'Croz et al. 2005) with maximum depths in coastal areas reaching 20–50 m (Guzmán and Guevara 1998a) and a tidal amplitude below 0.5 m (Guzmán et al. 2005). It is exposed to several rivers and creeks (Fig. 1) and an oceanic inlet that transports sediment plumes from the rivers Sixaola (Costa Rica) and Changuinola into the bay (Saric 2005).

Coral reefs within the bay are exposed to various human impacts from land based changes as well as effluences into the marine environment. Banana plantations and export have grown since 1915 (Greb et al. 1996), when the port of Almirante was enlarged. Shipping traffic from Almirante port through Boca del Drago results in heavy metal pollution (Berry et al. 2013) and sedimentation from dredging (Burke et al. 2004). Deforestation for banana plantations, pasture land and teak plantations continues on the mainland and larger islands (Collin 2005), resulting in increased erosion, sedimentation, nutrification and pollution leading to a fundamental change of the marine bay systems within the past 20 years (Saric 2005). Nutrients (D'Croz et al. 2005) and heavy metals from fertilizer, herbicide and pesticide application (Guzmán and Jiménez 1992) are flushed into the bay. In addition, population size and tourism have increased since 1993 (Guerrón-Montero 2005). Furthermore, coastal developments, overfishing and use of destructive fishing methods have physically damaged coral reefs.

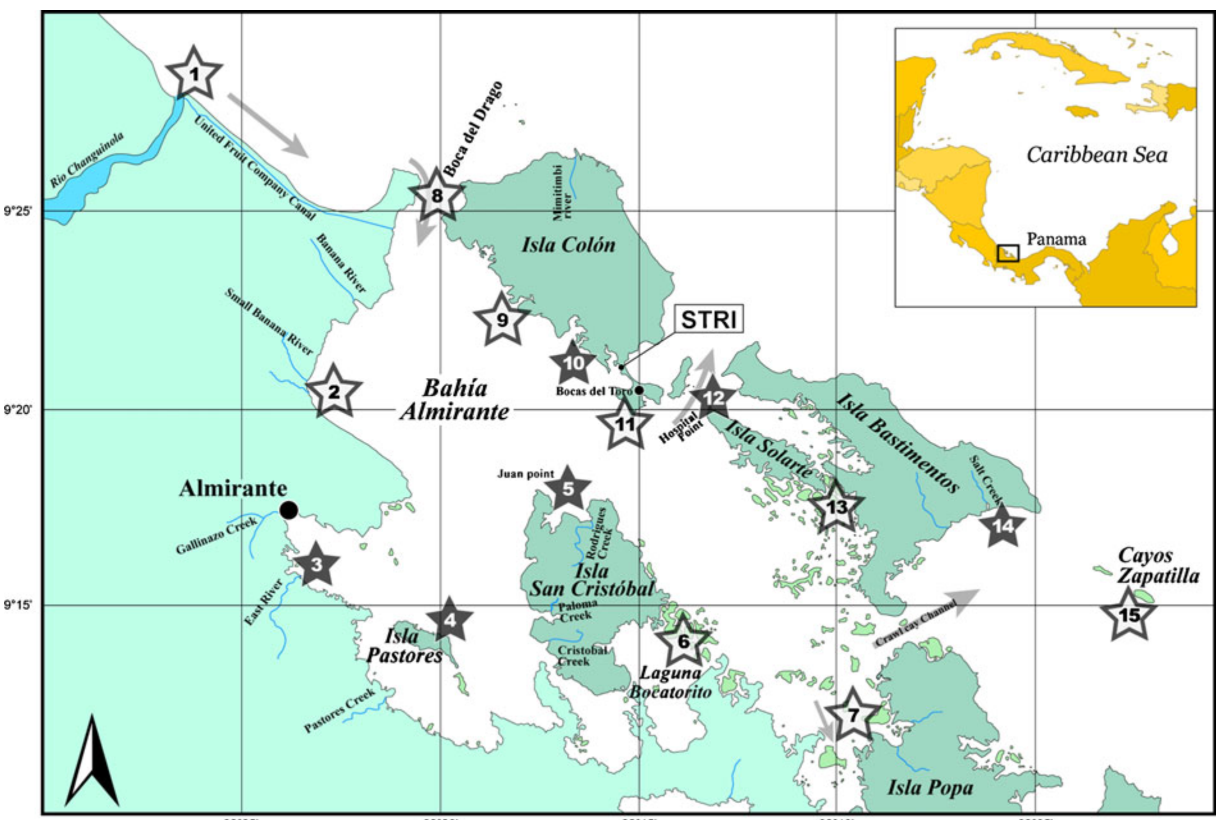


Fig. 1 Map of Almirante Bay with 15 sampling sites (*stars*, Table 1). Six sites were selected for detailed reef monitoring studies (*black stars*). *Arrows* indicate how the water is circulated within the bay system (Saric 2005)

As a result of high temperatures, fresh water input from high seasonal rain fall, oxygen depletion from a lack in water exchange and the building of thermoclines (Kaufmann and Thompson 2005), small scale bleaching events are frequent at reef patches within the bay. In September 2010, an intensive bleaching event resulted in the mass mortality and degradation of large areas of coral reefs in this region and worldwide (NOAA 2010).

Previous studies by Guzmán and Guevara (1998a; b; 1999; 2001) provided detailed information about reef community structure (cover, species diversity, zonation) within the Bocas del Toro archipelago. Another study from Guzmán et al. (2005) described CARICOMP sites (a Caribbean-wide program to monitor the productivity of coral reefs, mangroves and seagrass) that were monitored periodically, starting in 1999 and included meteorological and oceanographic data (air and water temperature, rainfall, salinity, solar radiation, wind speed) that are published in Kaufmann and Thompson (2005). Further environmental parameters such as chlorophyll *a*, secchi depth and oxygen were documented from 1999 until 2008 (Collin et al. 2009). Furthermore, an identification guide for invertebrates was developed for the most common species in the Bocas del Toro region (Collin et al. 2005).

The objectives of the present study were to qualify and quantify specific anthropogenic impacts and to relate this data to the current state of coral reef health. In addition, it aimed to quantify reef degradation processes such as coral bleaching and coral mortality within the Almirante Bay.

Materials and method

During July 2010, an environmental survey was conducted at 15 different coral reef sites (Table 1, Fig. 1) within and outside Almirante Bay. The first survey measured temperature, pH values, oxygen, salinity, $\delta^{13}C_{DIC}$ (from dissolved inorganic carbon), TSS (total suspended solids), secchi depth and irradiance (PAR—photosynthetic active radiation).

From November 2010 to February 2011 and from June 2011 to September 2011, physical environmental data acquisition was repeated for temperature, pH, oxygen, salinity, TSS, carbon (C) isotopes, C/N ratios, secchi depth and irradiance. Furthermore, water chlorophyll *a* content was measured as well as the size fractions of reef sediments. A biological reef monitoring was conducted regularly to obtain environmental data at six selected coral reef sites: Almirante [3] and Pastores [4] (close to the port), Casa Blanca [10] (near Isla Colon, exposed to Boca del Drago), Juan Point [5] (near Isla San Cristobal, exposed to Boca del Drago), Hospital Point [12] (near Isla Solarte, bay outlet), which are all located in Almirante Bay, plus one site outside the bay, and Salt Creek [14] (near Isla Bastimentos; Fig. 1).

Table 1 Sampling sites with coordinates

No.	Site name	Lat (N)	Lon (W)
1	Changuinola river outlet	09° 27′ 29″	82° 26′ 47″
2	Banana River	09° 21′ 18″	82° 22′ 10″
3	*Almirante	09° 16′ 16″	82° 23′ 24″
4	*Pastores	09° 14′ 25″	82° 14′ 25″
5	*Juan Point	09° 18′ 21″	82° 16′ 24″
6	Bocarito Bay	09° 14′ 09″	82° 13′ 57″
7	Popa Island	09° 12′ 25″	82° 09′ 40″
8	Boca del Drago	09° 25′ 25″	82° 19′ 24″
9	Punta Caracol	09° 22′ 37″	82° 18′ 08″
10	*Casa Blanca	09° 21′ 34″	82° 16′ 36″
11	Mangrove Point	09° 19′ 47″	82° 15′ 17″
12	*Hospital Point	09° 20′ 03″	82° 13′ 06″
13	Solarte Island	09° 17′ 18″	82° 10′ 00″
14	*Salt Creek	09° 16′ 50″	82° 06′ 05″
15	Zapatilla Islands	09° 15′ 07″	82° 02′ 30″

Six sites (asterisk) are the selected reef monitoring sites

Environmental survey

At all 15 sampling sites, water samples were taken at a depth of 3 m using a 'Niskin bottle'. To minimize handling errors, sampling was repeated three times per site. However, there is a variation in light and water movement due to the different hours of sampling. Water temperature, pH, oxygen and salinity were directly measured with a WTW Multiline P4–Probe, which was calibrated before each sampling period (accuracy pH 0.01, oxygen ±0.5 %, salinity ±1 % of value). Furthermore, sub-samples were taken for the isotope ratio of dissolved inorganic carbon [DIC] to assess organic matter input and primary production (Mook 2001). DIC analysis aliquots were poisoned with mercury chloride (50 μl $HgCl_2$) to kill all organisms. $\delta^{13}C_{DIC}$ analyses were done in Germany with a Thermo Finnigan GASBENCH II coupled with a Thermo DELTA *V* isotope ratio mass spectrometer.

Aliquots of each water sample were stored in an ice filled cooler and transported to the Smithsonian Tropical Research Station Bocas del Toro for immediate processing. To assess turbidity, water samples with a known volume were vacuum filtered through twice pre-combusted (450 °C, 8 h) and a pre-weighed Whatman GF/F filter (0.7 μm pore size). These filters were oven dried (60 °C, 24 h) and weighed for total suspended solids [TSS]. To estimate wastewater and fertilizer input, primary production and organic matter input and suspended sediment (Macko and Ostrom 1994; Lapointe 1997; Gartner et al. 2002) filters were analysed in Germany. After the decalcification (removing the inorganic carbon) of the filter-samples with hydrochloride acid (1 N HCl), samples were measured for $\delta^{13}C$ using stable isotope mass spectrometry (IRMS, DELTA V Advantage) with an elemental analyser (Thermo Flash EA 1112). Molecular weights (mg sample^{-1}) of C_{org} and N were used to calculate C/N ratios (instrumental error derived from Peptone standards is 3 %).

A third filter was frozen (−20 °C) for chlorophyll *a* analysis as a measure for eutrophication seen in the phytoplankton density (Smith 2003). Using a method adapted from Aminot and Rey (2000), the filter was ground and chlorophyll was extracted for 6 h in 90 % acetone solution. After, the samples were centrifugated to remove residuals of the filters and measured fluorometrically (TD 700 Turner Design) at the Bocas del Toro field station. The fluorometer was calibrated with a pigment standard of known value. To minimize analytical errors, a blank (90 % acetone) was used to correct shifts every 10 samples. The measurement was conducted under low light condition as well as constant room temperatures.

To assess the turbidity two methods were applied: LiCor (LI-192SA quantum sensor) was used to measure irradiance through the water body, expressed in PAR (photosynthetic active rate [$\mu mol\ m^{-2}\ s^{-1}$]) and a secchi disk was used to assess water clarity and visibility (accuracy ±5 %). LiCor measurements were only applied at noon on cloudless days.

Furthermore, sediment cores were taken from the upper 10 cm. Sediments were oven dried (60 °C for 72 h) and sieved to categorize grain sizes (2–1 mm, <1–>0.5 mm, 0.5–>0.25 mm, 0.25–>0.125 mm, 0.125–>63 μg, <63 μg). After grain size separation, the proportions of different fractions were determined based on dry weight.

Reef monitoring

Biological reef monitoring was conducted at the six selected sites (Fig. 1, Table 1) based on international Reef Check guidelines (Hodgson 2000; Hodgson et al. 2004). A 20 m line transect was conducted in replicates of four per reef at two depths of 1–5 and 6–10 m. Reef cover, live coral cover and the proportion of bleached colonies were recorded every 0.5 m within transects. The most abundant hard corals were quantified by identifying the species of each hard coral at every data collection point. All hard coral data points were summarized (100 %) and the relative coverage of each hard corals family is presented in Fig. 4.

Qualitative estimates of hard coral species diversity were recorded in a radius of 50 m using an observation method adapted from Guzmán and Guevara (1998a). An existing STRI field guide from Collin et al. (2005) and a new field guide (Supplementary material), which was developed for the surveys (Carballo-Bolaños et al. 2012), were used to ensure correct identification of species.

Additionally, fish abundance was estimated by counting specified indicator fish within a 20-m long and 5 m wide (5 m high) belt transect at the same two depths (4 replicates). Further indicator species for human impacts such as lobsters and triton shells as well as physical damage were recorded.

One researcher participated in all monitoring and validated the reasonability of data to prevent biased data collected by different people.

Data analysis

To identify the determining factors for site-specific differences and to find interdependences each environmental parameter and each type of reef cover was analysed with a *t* test. Statistical means were compared and significant differences between sites were identified. To explore possible interdependences between parameters linear regression analysis was applied in a multiple regression analysis. The software JMP 9.0.2 (SAS Institute) was used for these analyses. All values are presented as means±standard errors (when there were at least three replicates).

To investigate similarities between survey sites all environmental and biological parameters (reef cover, hard coral species composition, indicator species (reef check), reef damage and bleaching) were combined and analysed using a multivariate cluster analysis using the software Past (Bray–Curtis similarities). Before analysis all values were transformed to relative numbers (% of total value).

Results

Environmental survey

Water temperature measurements at 3 m depth differed as expected between seasons. In July 2010, temperatures were higher (30.2±0.2 °C) than the seasonal mean temperature all over the bay (28.3 °C; Kaufmann and Thompson 2005) that caused a severe coral bleaching event in September 2010 (NOAA 2010). The highest temperature was found at the site Almirante [3] (31.1±0.2 °C), while water at the Changuinola river outlet [1] (29.4°±0.1 °C) and the Boca del Drago inlet [8] (29.5±0.4 °C) were the lowest. Temperature values from Nov 2010 to Jan 2011 (26.6°±2.1 °C) went back to the normal seasonal average (Kaufmann and Thompson 2005). PH values within the bay were 8.0 (±0.3).

Oxygen saturation within the bay at a depth of 3 m depth had mean values of 83.5 % (±27). Water salinity throughout the bay was influenced by oceanic and fresh water sources. Salinity was highest (>33 ppm) at the two survey sites situated outside the bay (Salt Creek [14] and Zapatilla [15]), while salinity at sites situated near to the bay inlets/outlets (Hospital Point [12] and Popa Island [7]) was<32 ppm. The Boca del Drago inlet [8] had the highest salinity level (>32.5 ppm).

Values for $\delta^{13}C_{DIC}$ differed at the bay inlets/outlets and the river mouths. The outlet of the Changuinola river [1] was characterized by low values (−3.73±0.13; n=3). The outlet at Isla Popa [7] had values of 0.20 (±0.2, n=7). Almirante [3] showed a layering from surface water to 7 m depth (from 0.48±0.09 to 0.91±0.04). Highest values were found at the Boca del Drago inlet [8] (0.77±0.1, n=6) and Juan Point [5] (0.60±0.09, Table 2).

The suspension load and eutrophication regime showed seasonal patterns. TSS values were lower in Nov 2010–Feb 2011 (2.9 mg±1.2) than in July 2010 (5.3 mg±2.0) and Jun 2011–Sept 2011 (9.4 mg±2.6; Fig. 2). Water discharged from the Changuinola river outlet [1] (TSS 124 mg l^{-1}, July 2010) transports sediments into the bay.

$\delta^{13}C$ Isotope ratios of the particulate organic carbon [POC] within the TSS were lowest at the monitoring sites Almirante [3], Pastores [4] and Juan Point [5] (Table 2).

Chlorophyll *a* was higher Nov 2010–Jan 2011 (0.89±0.58 μg l^{-1}) than in Jun 2011–Sept 2011 (0.52±0.11 μg l^{-1}), along to what was found for secchi depth values (6.4±1.6 and 8.8±2.2 m, respectively) and photosynthetic active radiation at 3 m depth (388±145 and 850±229 μmol m^{-2} s^{-1}, respectively). The lowest secchi depth was found at Boca del Drago [8] (3.9 m±3).

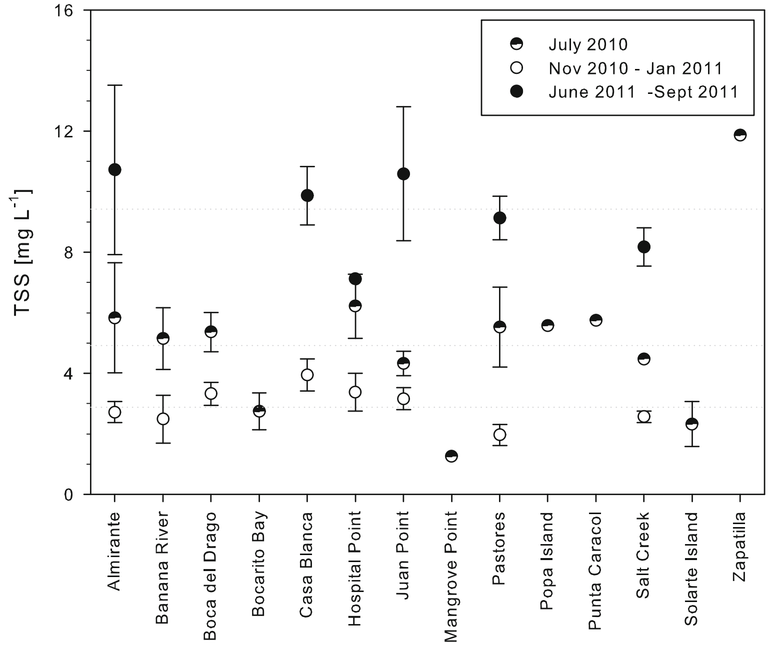
The size fractioning of the sediments sampled from the six studied reef monitoring sites: Almirante [3], Pastores [4], Casa Blanca [10], Juan Point [5], Hospital Point [12] and Salt Creek [14] indicated which sites contained higher amounts of smaller silt- and clay-sized sediment fractions, which are more likely to be resuspended than larger particles (Van Duin et al. 2001). Almirante, the site closest to the port, contained the highest amount of the smallest sediment fractions <63 μm–0.25 mm (Fig. 3). The largest grain sizes (>1 and >0.5 mm) were significantly lower at Almirante

Table 2 Environmental parameters at the 6 reef study sites from water samples at 3 m depths sampled between July 2010 and September 2011

	Almirante [3]	Pastores [4]	Casa Blanca [10]	Juan Point [5]	Hospital Point [12]	Salt Creek [14]
TSS [mg l^{-1}] (n=14)	4.21±3.27	3.65±3.10	4.93±2.78	4.74±3.27	4.91±2.10	4.00±2.52
$\delta^{13}C$ from POM (n=7)	−20.7±0.5	−20.7±0.5	−20.4±.0.5	−21.2±0.6	−19.6±2.0	−20.2±0.5
C/N from POM (n=7)	9.2±0.5	9.6±0.3	9.4±0.5	9.6±0.5	9.6±0.2	9.8±0.4
$\delta^{13}C_{DIC}$ (n=8)	0.34±0.09	0.43±0.07	−1.50±0.09	0.60±0.09	0.44±0.07	
Chlorophyll *a* [μg l^{-1}] (n=7)	0.88±0.29	0.97±0.86	0.78±0.34	0.52±0.36	0.51±0.34	0.58±0.27
PAR [μmol m^{-2} s^{-1}] (n=7)	507±252	537±274	403±229	457±261	793±132	540±296
Secchi Depth [m] (n=7)	5.9±1.4	7.5±2.7	7.4±1.5	7.3±2.9	6.8±3.2	7.4±1.6

$\delta^{13}C$ and C/N were sampled between November 2010 and September 2011. $\delta^{13}C_{DIC}$ was sampled in July 2010 along a depth profile (0–7 m, average value) next to the reef slope

Fig. 2 Total suspended solids (TSS) at three different seasons. *Dotted lines* are showing the mean value for each season



(9.7±3.6 and 17.2±7.8 %, respectively) than at Salt Creek (19.8±7.3 and 28.0±10.0 %, respectively).

Reef monitoring

The biological reef monitoring at the six sites showed differences in reef cover and species composition. Hard coral cover was significantly higher at the ocean exposed sites Salt Creek [14] (44 %±5) and Hospital Point [12] (43 %±15) than at Casa Blanca [10] (27 %±23), Pastores [4] (23 %±19) and Almirante [3] (23 %±11). Shallow transects generally showed a higher coral cover (Table 3) than deeper ones.

A comparison of soft corals, sponges and nutrient indicating algae (soft cover) between sites showed a significantly higher cover (38±14 %) at Almirante [3],

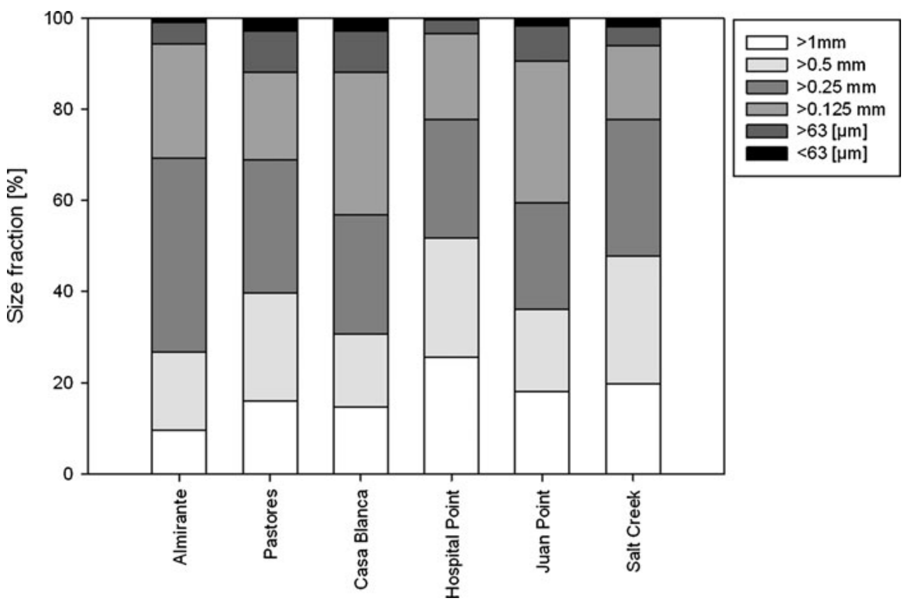


Fig. 3 Mean sediment size fractions from 10 cm sediment cores taken within the sites: Almirante [3] (n=7), Pastores [4] (n=6), Casa Blanca [10] (n=3), Juan Point [5] (n=6), Hospital Point [12] (n=1) and Salt Creek [14] (n=6)

whereby Hospital Point [12] had the lowest soft cover all over the bay (9±5 %). Salt Creek [14] presented the highest amount of nutrient indicating algae (10±3 %), which was lowest at Juan Point [5] (1±0.5 %).

The category "others" (zoanthids, gorgonians, calcifying algae, anemones) accounted for a large percentage of the total cover at some sites (Almirante 20 %, Salt Creek 13-14 % and Pastores 10-11 %). However, the composition of "others" differed between sites (Table 3). It was dominated by zoanthids at Almirante [3] (97.3 %±0.4; n=8) and Pastores [4] (94.4 %±0.2; n=8), and gorgonians (57.8 %±5.9) and calcifying algae (38.9 %±6.6) at Salt Creek [14] (n=12).

With regards to hard coral species diversity, Agariciidae and Poritidae (Fig. 4) were the most abundant families. Agariciidae species dominated reef cover at Casa Blanca [10], Hospital Point [12] and Salt Creek [14], while Poritidae species were most abundant at Almirante [3] and Pastores [4]. Agariciidae did not naturally occur at Almirante [3]. The deeper transects (6–10 m) were predominantly characterized by massive corals occurring in patches surrounded by silt and sand. Casa Blanca [10] and Juan Point [5] had few branching hard coral species in deeper regions compared to other sites (Fig. 4).

Species diversity was highest at Salt Creek [14], where 35 of the 58 hard coral species known for this region were found (Guzmán and Guevara 1998a) (Table 4). Juan Point [5] and Hospital Point [12] contained similar species diversity (23 and 22 species, respectively). The sites closest to the port Almirante [3] and Pastores [4] were dominated by *Porites furcata* (Fig. 4) and *Agaricia tenuifolia*. *A. tenuifolia* did not naturally occur at the site Almirante [3].

The first reef monitoring was conducted 2 months after the severe bleaching event in September 2010. A comparison of total bleached coral cover showed variable susceptibilities and recovery to bleaching between sites. Almirante [3] no longer showed signs of bleaching and Salt Creek [14] only exhibited slight bleaching (~1 %). Casa Blanca [10] was still severely bleached (~95 %), especially in a depth of more than 6 m depth. Pastores [4] and Juan Point [5] were ~55 % bleached, while Hospital point (bay outlet) was 40 % bleached.

Abundance of indicator fish was characterized by small sized juvenile fish. Site specific differences were found for fish abundance, which was in general very low (Tables 5).

Table 3 Mean cover of 9 different substrate types (% mean±SE) at all study sites

Site	Almirante [3]	Pastores [4]		Casa Blanca [10]		Juan Point [5]		Hospital Point [12]		Salt Creek [14]	
	1 m	1–5 m	6–10 m	1–5 m	6–10 m	1–5 m	6–10 m	1–5 m	6–10 m	1–5 m	6–10 m
Cover	n=21	n=24	n=16	n=16	n=16	n=16	n=16	n=16	n=16	n=24	n=20
Hard Coral	23±4	32±8	9±2	38±14	16±5	39±4	22±3	56±4	31±2	47±1	40±2
Recently killed Coral	1±1	11±7	7±7	4±3	9±9	2±1	13±11	10±6	7±7	4±2	1±0
Rock	2±1	17±6	15±6	12±9	32±10	13±6	12 ±4	16±10	23±6	12±3	14±3
Soft Coral	10±6	5±3	1±1	1±1	1±0	8±8	1±0	0±0	2±1	6±2	12±5
Sponge	26±4	11±1	6±1	14±3	5±1	14±2	11±4	5±1	7±2	2±1	4±1
Others	20±7	11±5	10±5	2±2	0±0	7±6	1±1	3±1	2±1	14±3	13±4
Nutrient indicator algae	2±0	2±2	0±0	0±0	2±2	0±0	2±1	3±1	1±1	11±2	9±3
Rubble	4±1	6±3	25±5	5±2	13±4	11±5	18±6	6±4	9±4	2±1	4±1
Sand	7±2	5±2	26±4	21±8	13±4	5±1	17±5	1±1	9±4	2±1	3±1
Silt	5±2	0±0	2±1	4±4	8±4	1±1	4±2	0±0	9±3	0±0	2±1

Transects in shallow (1–5 m) and medium depth (6–10 m) pooled, except Almirante (1 m)

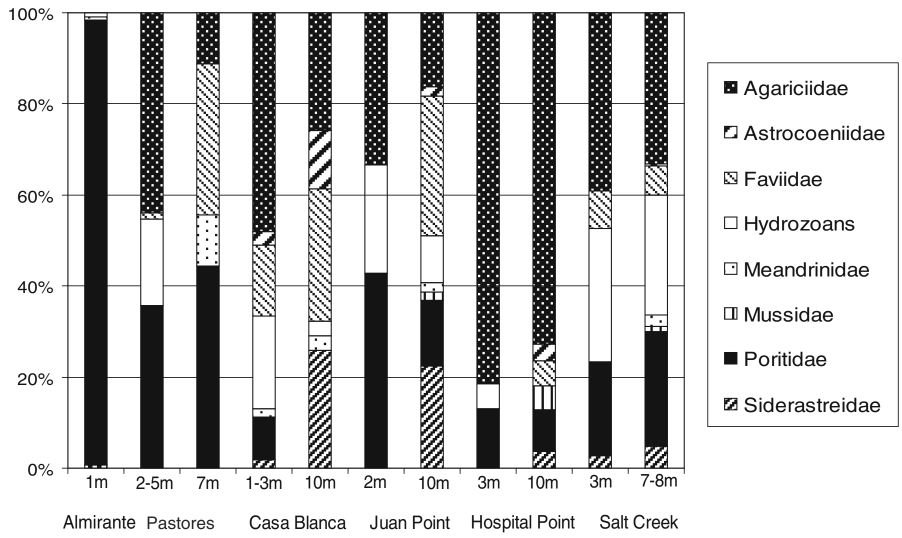


Fig. 4 Hard coral composition (Anthozoans and Hydrozoans) at 6 study sites at two different depths (1–5 and 6–10 m) with the different families contributing more than 10 % of hard coral coverage. The most abundant species were: *Agaricia tenuifolia* (Agariciidae), *Stephanacea intersepta* (Astrocoeniidae), *Montastrea (Orbicella) annularis* (Faviidae), *Millepora alcicornis* (Hydrozoans), *Meandrina meandrites* (Meandrinidae), *Mycetophyllia danaena* (Mussidae), *Porites furcata* (Poritidae) and *Siderastrea siderea* (Siderastreidae)

Invertebrate indicator monitoring showed a high abundance (per 20 m transect) of Diadema at Juan Point [5] (11.9±3.8) and Salt Creek [14] (10.7±3.2). Gorgonians were only abundant at Salt Creek (14.5±12), which was also most abundant in lobster (0.5±0.3). Other indicator species such as banded coral shrimp, pencil urchin, collector urchin, triton and flamingo tongue had extremely low counts or were not found.

Human induced damage from boat anchoring was observed at Hospital Point [12] (1.4±0.5 per 20 m) and Juan Point [5] (1.4±0.6). Marine debris was highest at Pastores [4] (0.4±0.2 per 20 m).

Cluster analysis revealed a similarity pattern. Salt Creek [14] (outside the bay) was shown to be least similar (30 %) to all other sites. The sites Pastores [4], Casa Blanca [10] and Juan Point [5] (similarity >40 %) build one cluster, whereby the site Almirante [3] (close to the city and the port) is apart from the other bay sites, thus with different characteristics (Figs. 5 and 6).

Discussion

As seen from the environmental data, Almirante Bay does not represent typical oligotrophic coral reef conditions (comparison Table 2 with oligotrophic conditions represented by TSS <2 mg l^{-1}, C/N ratios <4, chlorophyll *a* <0.4 μg l^{-1}, secchi depth >20 m; Edinger et al. 2000; Cooper et al. 2007; Sawall et al. 2011). They rather indicate natural and anthropogenic stress from particle run off and eutrophication. Over the last two decades anthropogenic activities within and surrounding Almirante Bay have resulted in increased turbidity within the bay. Secchi depth values decreased from 9-13 m in 2006–2008 (Collin et al. 2009) to 5-8 m. Besides, seasonal average chlorophyll*a* values all over the bay have increased compared to values from 2006 to 2008 (Collin et al. 2009). Values at Pastores [4] and Casa Blanca/STRI [10] have nearly doubled (from 0.46–0.49 to 0.78–0.97 μg l^{-1}), while coral reefs typically do not exceed values of 0.4 μg l^{-1} (Edinger et al. 2000; Cooper et al. 2007; Sawall et al. 2011). Furthermore, physical damages are a problem for the reefs of Almirante Bay. High physical damage from boat anchoring or from fishing with explosives created large-scale destructions of the reefs (personal observation).

The perceptible environmental changes of the Almirante Bay within the last decade were paralleled by a decline of hard coral cover and diversity. Hard coral cover declined down to values of <10 % (Table 3). That has been reported for reefs all over the Caribbean which declined from ~50 % coral cover to ~10 % within the last three decades (Gardner et al. 2003). In contrast, healthy reefs of the Caribbean have hard coral

Table 4 Hard coral species List (Anthozoans and Hydrozoans) from Guzmán and Guevara (1998a, 2001)

	Almirante [3]	Pastores [4]	Casa Blanca [10]	Juan Point [5]	Hospital Point [12]	Salt Creek [14]
Acropora cervicornis						x
**Acropora palmata*						x
Agaricia agaricites				x		x
Agaricia fragilis		x	x	x	x	x
Agaricia humilis				x	x	
Agaricia lamarcki			x	x	x	x
**Agaricia tenuifolia*		x	x	x	x	x
**Colpophyllia natans*	x	x	x		x	x
**Diploria clivosa*						x
Diploria labyrinthiformis				x		x
**Diploria strigosa*				x		x
Favia fragum			x			x
Isophyllastrea rigida						x
**Leptoseris cucullata*					x	x
Madracis decactis			x	x	x	
**Madracis mirabilis*				x		x
Meandrina brasiliensis	x		x	x	x	x
Meandrina meandrites		x	x	x	x	x
**Millepora alcicornis*	x	x	x	x	x	x
**Millepora complanata*					x	x
Millepora striata						x
Montastraea (Orbicella) annularis			x	x	x	x
Montastraea cavernosa		x	x	x	x	x
Montastraea (Orbicella) faveolata		x	x	x		
Mussa angulosa						x
**Mycetophyllia aliciae*				x	x	x
Mycetophyllia danaena		x				x
Mycetophyllia ferox						x
Mycetophyllia lamarckiana				x		
Oculina diffusa	x					
**Porites asteroides*	x	x	x	x	x	x
Porites colonensis					x	x
Porites divaricata				x		x
**Porites furcata*	x	x	x	x	x	x
Porites porites						x
Scolymia cubensis					x	x
Scolymia lacera					x	x
Siderastrea radians				x		x
**Siderastrea siderea*	x		x	x	x	x
Solenastrea hyades			x			
Stephanacoenia intersepta		x	x	x	x	
Stylaster roseus					x	x
Sum	7	11	17	23	22	35

Forty-two hard coral species found in total. Most abundant species (Guzmán and Guevara 1998a, 2001) with asterisk

Table 5 Indicator fish per 20 m of fish belt transect (mean±SE)

Fish	Almirante [3]	Pastores [4]	Casa Blanca [10]	Juan Point (Dominici-Arosemena and Wolff 2005)	Juan Point [5]	Hospital Point (Dominici-Arosemena and Wolff 2005)	Hospital Point [12]	Salt Creek (Dominici-Arosemena and Wolff 2005)	Salt Creek [14]
	n=12	*n*=24	*n*=20	*n*=48	*n*=24	*n*=48	*n*=20	*n*=48	*n*=20
Chaetodontidae (Butterflyfish)	3.4±2.0	8.4±1.6	7.8±2.0	3.0±0.3	8.6±0.9	0.7	2.9±0.8	1.7±1..0	6.5±1.5
Scaridae (Parrotfish)	1.3±1.0	0.7±0.3	2.3±0.8	9.7±5.2	2.3±0.9	3.1	5.7±3.2	2.8±0.3	2.2±1.3
Muraenidae (Moray eel)	0.0±0.0	0.0±0.0	0.0±0.0	N/A	0.0±0.0	N/A	0.1±0.1	N/A	0.0±0.0
Haemulidae (Grunt)	6.5±4.9	4.3±1.7	5.2±3.6	1.5±1.2	5.8±1.2	15.0	13.0±11.2	0.5±0.2	1.6±0.5
Lutjanidae (Snapper)	1.0±0.7	5.3±2.2	7.1±3.8	N/A	2.4±1.3	N/A	2.5±1.1	N/A	2.0±0.7
Serranidae (Grouper)	0.0±0.0	0.0±0.0	0.2±0.1	8.1±6.6	0.0±0.0	0.0	0.1±0.1	0.5±0.3	0.1±0.1
Serranidae (Nassau grouper, *Epinephelus striatus*)	0.0±0.0	0.0±0.0	0.1±0.1	N/A	0.0±0.0	N/A	0.0±0.0	N/A	0.0±0.0

Data were transformed to number of fish 100 m^{-2} and compared to the data from Dominici-Arosemena and Wolff (2005)

cover of >70 % (Hughes 1994; Hawkins et al. 1998). Also, hard coral species richness has declined from 60 species reported for the Caribbean (Hughes 1994) and 58 species reported for the Bocas del Toro area (Collin 2005) to 42 species (Table 4). The loss of the hard coral biodiversity is characteristic for the Almirante Bay even in reefs where hard coral coverage increased as observed for Casa Blanca (from 15 %±2 to 27 %±9; Guzmán and Guevara 1998b). This led to a dominance of a low diverse reef environment all over the bay, most distinct at the site Almirante [3]. A loss of biodiversity caused a loss of functional redundancy and biological niches, thus a loss of resilience and resistance of the reef systems (Hughes et al. 2003; Grimsditch and Salm 2006). Eventually, reef ecosystems within the Almirante Bay are becoming less stable and more sensitive to perturbations in particular to eutrophication and increased sediment run off (McCann 2000; Bellwood et al. 2003). However, compared to other studies throughout the Caribbean the Bocas del Toro Archipelago still represents one of the most biodiverse reefs: Barbados, 29 species (Oxenford et al. 2008); Santa Marta in Colombia, 12 species (Zea 1993).

Another human impact factor changing the reef systems of Almirante Bay were caused by a severe overfishing. This was indicated by the dominance of juvenile fish and the low abundance of larger predatory species as Haemulida (grunts), Lutjanidae (snappers) and Serranidae (groupers). Haemulida had abundances <13 100 m^{-2}, much lower than they can have in an undisturbed system (>50 100 m^{-2}). Lutjanidae had numbers of <7 100 m^{-2} instead of abundances >10 100 m^{-2} and Serranidae numbers of <0.5 100 m^{-2} instead of >3 N 100 m^{-2} in pristine reefs (Hodgson 1999). This threat has also been reported for other regions in the Caribbean and worldwide (Rodríguez and Villamizar 2000) (Mejía and Garzón-Ferreira 2000). The loss of fish might cause additional reef degradation, e.g. due to the lack of herbivores, which regulate algae abundance (Hughes 1994; Aronson et al. 2003; Hughes et al. 2007).

The coral sites within the bay were influenced by the sediment plume entering at the Boca del Drago inlet [8]. This plume is result of a high sediment run off from the Changuinola river [1] further north along the coast as well as river run off from the Sixaola river in Costa Rica (Saric 2005). Besides particulate matter, the riverine waters from the Changuinola river [1]

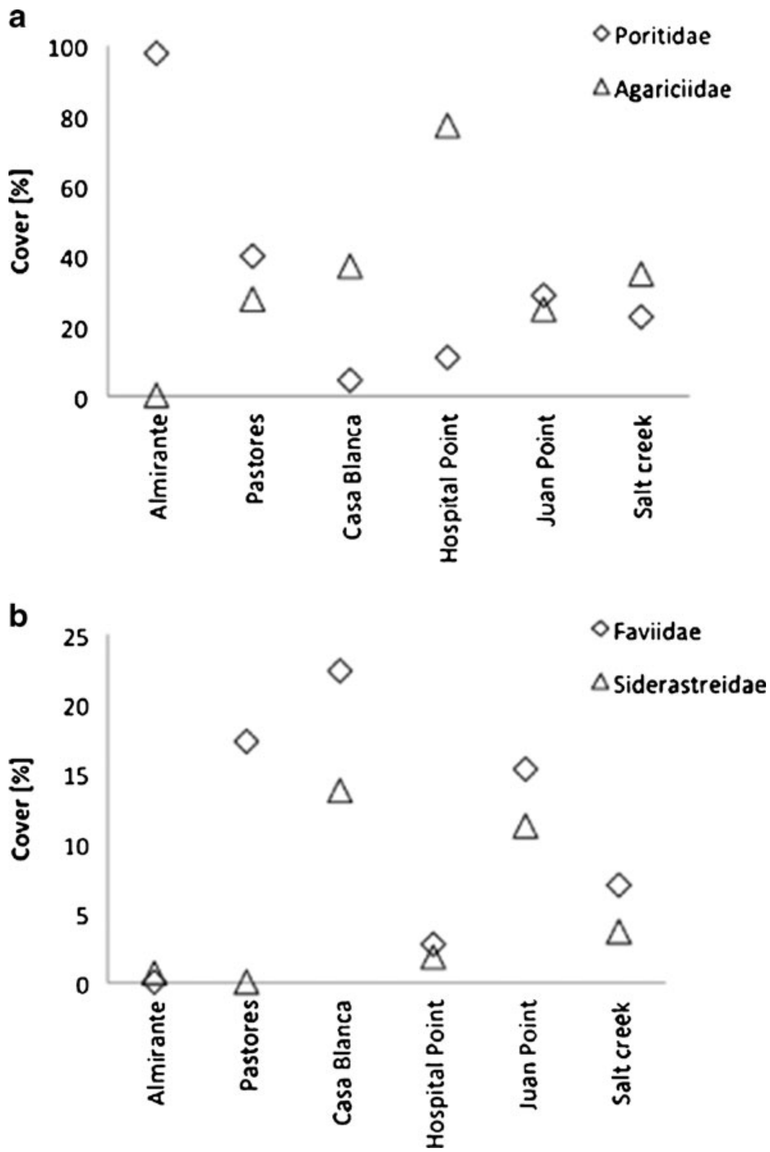


Fig. 5 Hard coral species dependences. **a** Poritidae and Agariciidae were found to prefer reef sites with apposed reef conditions. Sites with high abundance of Poritidae (e.g. Pastores) were found to have lower abundances of Agariciidae and vice versa (e.g. Hospital Point). **b** Corals from the families Faviidae and Siderastreidae (massive corals) inhabited reefs with similar conditions

carried carbon in dissolved inorganic form [DIC] from weathering indicated from low $\delta^{13}C_{DIC}$ values at the river outlet (Mook 2001). Considering, that the Changuinola river transports high amounts of nutrients (D'Croz et al. 2005), the carbon additionally enhanced primary production (phytoplankton growth), which might be the reason for the carbon isotope fractionation, thus an increase of the $\delta^{13}C_{DIC}$ value at the Boca del Drago inlet [8] (Fry and Sherr 1984; Mook 2001). Another influence is the intensified dredging at the shipping channel at Boca del Drago, which led to an additional re-suspension of less stable sediments and also contributed to high turbidity levels within the bay. This is another potential source for the elevated TSS values all over the bay (Table 3). The combination of both, increased sediment run-off and dredging, is one of the most potential reasons for the ongoing reef degradation within this area (Rogers 1990).

The survey site most impacted from the plume entering the Almirante Bay and the dredging at Boca del Drago [8] was Casa Blanca [10] close to Isla Colón (Fig. 1) visible in highest TSS values and high contents of small sand particles (>63 μm–0.25 mm) and silt (<63 μm; Fig. 3). Small size sediments are more likely to be resuspended than larger particles (Van Duin et al.

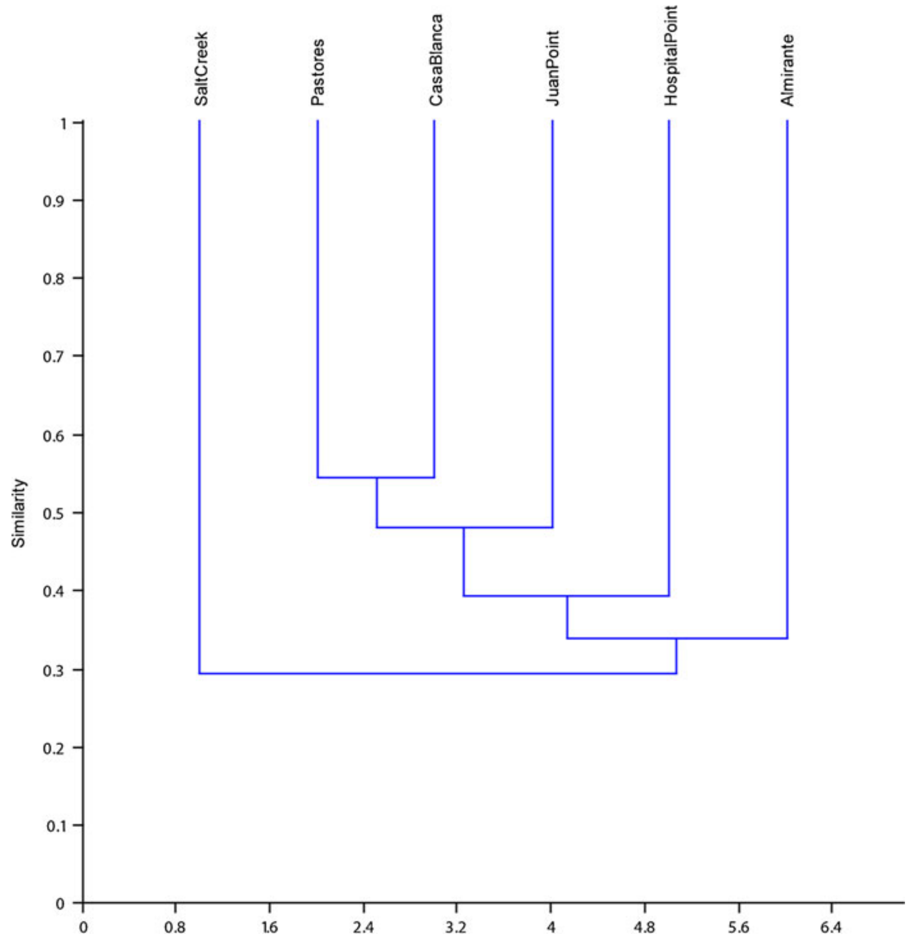


Fig. 6 Clusteranalysis (Bray–Curtis) between sites considering all physical and biological parameters

2001), thus they increase the turbidity. Additionally, silt i.a. can lead to damages in the photosynthetic system and bind more nutrients and contaminants (Weber et al. 2006). Also high turbidity has been linked to reductions in coral reef diversity in the Caribbean (Johannes 1975; Rogers 1990) and is likely one of the main factors contributing to the decline in coral diversity within the Almirante Bay. The biodiversity of hard corals at Casa Blanca was much smaller (17 species) than reported before (33 species). Opposite to what Guzmán and Guevara (1998b) reported, no big colonies of *Acropora cervicornis* were found in the Almirante bay and throughout the whole Caribbean (Greer et al. 2009). The paucity of *A. cervicornis* is considered an indicator for anthropogenic stress because the species is strongly susceptible to bleaching (Marshall and Baird 2000). In fact, Agariciidae and Hydrozoans and in deeper waters massive corals as Faviidae, Mussidae and Siderastreidae were most abundant at Casa Blanca [10]. Furthermore, Casa Blanca showed the highest coverage of sand (Table 3), suggesting that sedimentation could also be highest at this site. This would help to explain why Casa Blanca [10] showed the most severe bleaching (up to 95 %) and the slowest recovery during the bleaching event in 2010. One hundred percent recovery was not reported until September 2011.

The other site exposed to the sediment plume entering the bay was Juan Point [5]. It was characterized by a high sponge cover (Table 3) and a strong cover with sea urchins and brittle stars, which are associating to sponges (Henkel and Pawlik 2005). This indicated a combined input of nutrients and suspended particles, which have been identified as key factors for sponge growth (Wilkinson and

Cheshire 1990; Zea 1993; Fichez et al. 2005). In this area, sponges have become the major competitors for corals (Table 3) likely to eventually lead to their outgrowing (Jackson and Buss 1975). However, they are also valuable as a strong natural filter system cleaning the water from suspended particles, nutrients and even septic components and thus gaining importance in times of increased anthropogenic pollution (Diaz and Rützler 2001). Juan Point [4] showed few changes over the last decade, with regards to the reef structure, indicating a stable state of the reef despite the exposure to the sediment plume and eutrophication. Reef coverage and hard coral diversity reported by Guzmán and Guevara (Guzmán and Guevara 1999) was >30 % with 23 species, compared to 31 % cover and 26 species in the present study. Agariciidae and Poritidae dominated the shallow areas. However, they showed opposing trends (Fig. 5a), as also reported in Aronson et al. (2004) and Saric (2005). *Agaricia lamarcki* used to be the most abundant species in the deeper reef zone (Guzmán and Guevara 1999); however, in the present study, the massive corals Siderastreidae (18 %) and Faviidae (20 %) were dominant. They seem to have similar niche preferences (Fig. 5b). The decrease of *A. lamarcki* could be due to the observed susceptibility of Agariicidae to turbidity and low recovery after bleaching (Seemann et al. 2012b).

Another major impact factor within the bay can be considered the coastal erosion from deforestation. Deforestation of tropical forests at Hospital Point [12] and deforestation of peat-swamp forests at Pond Sock close to Almirante [3] was already reported in Guzmán and Guevara (1998b) and Collin (2005). Nevertheless, the coral reef at Hospital Point [12] showed a significant increase of its hard coral cover (from 29 %±4 to 44 %±3). The recovery rate is similar to what has been reported for reefs put under protection status ~10 % per 5 years (Selig and Bruno 2010). A correlative improvement in fish abundance was also observed. Chaetodontidae (butterflyfish) and Scaridae (parrotfish) increased (2.9±0.8 and 5.7±3.7 per 100 m^2, respectively) compared to numbers documented by Dominici-Arosemena and Wolff (2005). The abundances of Haemulidae (grunt) and Scaridae (parrotfish) were highest compared to all other sites (Table 5). The explanation could be the increased conservation effort from local dive stations to maintain this area as a dive location for tourists, whereby all other sites suffer from chronic overfishing and reef degradation.

In contrast, Almirante [3] was characterized by a loss of hard coral diversity to 7 species and a much lower fish abundance (Table 5). Additionally, a pronounced phytoplankton growth seen in the high chlorophyll *a* values (Table 2) indicated the increased eutrophication. Furthermore, during the bleaching event in 2010, the highest temperatures were measured at Almirante [3] suggesting that this site is influenced by a lower water flow rate than the other sites. Consequently, the reef is exposed to strong fluctuations in salinity in case of high levels of rainfall and river run off. The combination of these stressors resulted in a reef that is dominated by just one hard coral species (*P. furcata*), sponges and zoanthids. The latter are filter-feeding heterotrophs and bioindicators for elevated nutrient concentrations (Linton and Warner 2003) also indicating the exposure to eutrophication from anthropogenic activities. The dominance of *P. furcata* can be explained by its physiological tolerance to surface salinity fluctuations (Porter 1974) and a high competence for heterotrophy (Seemann et al. 2012a; Seemann 2013).

The eutrophication at Almirante [3] also reached Pastores [4]. High chlorophyll *a* values at Pastores (Table 2) were indicative of an eutrophied environment at Pastores, which were similar to the observations made by Collin et al. (2009). This elevated eutrophication might be the cause (Edinger et al. 1998; De'ath and Fabricius 2010) of the loss of hard coral coverage from >50 % (Guzmán and Guevara 1999) to 21 %±5, and for the decline of hard coral diversity from 18 reported species (Guzmán and Guevara 1999) to 11 in the present study. The dominant species in shallow waters remained Agariciidae (*A. tenuifolia*) and Poritidae (*P. furcata*; 42 % and 36 %, respectively; Guzmán and Guevara 1999). In contrast, species composition at deeper depths had changed within the last decade. Guzmán and Guevara (1999) claimed *Siderastrea siderea* as the most abundant species at Pastores however in the present study Faviidae (*22*%, *Montastrea cavernosa*) and Poritidae (44 %, *Porites asteroides* and *P. furcata*) were most abundant. *S. siderea* seemed to be more susceptible to the described eutrophication.

The sites outside the bay Salt Creek [14] and Zapatilla [15] (Fig. 1) did not increase as drastically in the eutrophication, respectively the chlorophyll *a* values over the last 5 years (from 0.46±0.22 to 0.58±0.27 μg l^{-1}). Besides, lower TSS values at Salt Creek [14] compared to the other study sites (Table 2) suggested that the impact from anthropogenic activities, such as increased suspension load and eutrophication is smaller, most likely due to its increased distance from the impact sources and its proximity to the open ocean. The main competitors for the hard corals were macro algae instead of sponges (Table 3), as described for Juan Point [5]. The higher amounts of suspended particles [TSS] within the bay seem to have enabled the expanded sponge growth (Wilkinson and Cheshire 1990; Zea 1993; Fichez et al. 2005). Salt Creeks coral reefs showed a superior health indicated by the highest hard coral cover, hard coral species diversity and a fast recovery after the bleaching event in 2010 (Grimsditch and Salm 2006). During the bleaching, the reefs in Salt Creek showed less bleaching and a recovery in less than 2 months (personal observation). Furthermore, the hard coral cover reported in Guzmán and Guevara (1998b) of 37 %±4 increased to 44 %±2. Species diversity remained similar with 37 species (Guzmán and Guevara 1998b) and 35 reported in this study. The high abundances of soft corals and gorgonians, also reported by Guzmán and Guevara (1998b), indicated an exposed exchange of water (Yoshioka and Yoshioka 1989). Although cover and diversity did not decrease over time, low fish abundance from overfishing was also observed at Salt Creek [14]. This is probably the reason for the high quantity of nutrient indicating algae and also high abundance of sea urchins, particularly Diadema, which feed on the algae (Lewis 1964; Hughes 1994).

In summary, the bay of Almirante underwent a serious change within the last twenty years. Turbidity from suspended particles and eutrophication has increased dramatically resulting in mortality of hard coral species, overgrowth by sponges and eventually the loss of hard coral biodiversity (Hughes 1994; Gardner et al. 2003). Reefs were not able to maintain hard coral diversity at mesotroph conditions (Cesar et al. 2003; Costa et al. 2008), since eutrophication levels seemed to be a determining factor for the loss of diversity of hard corals. It is most significant at chlorophyll *a* higher than 0.5 μg l^{-1}. Another main factor for the loss of hard coral diversity was the suspension load (TSS, threshold at 4.7 mg l^{-1}). Some hard corals seem to be adapted to high particle loads and turbidity (Anthony 1999; Sofonia and Anthony 2008; Seemann et al. 2012b), which allows partial recovery of degraded reefs, however just of some few species.

Nevertheless, the coral reefs less exposed to human influences remained in a better shape, especially in the case of temperature stress (Hoegh-Guldberg 1999) as observed for Salt Creek. These reefs recovered more quickly from bleaching compared to sites exposed to high turbidity levels, such as the site Casa Blanca (Glynn 1996).

It seems that the Almirante Bay undergoes a shift to reef systems with broader niche boundaries supporting species with a high tolerance to bleaching and heterotroph nutrition strategies to cope with the oversupply of suspended particles and plankton (Anthony and Fabricius 2000; Houlbrèque and Ferrier-Pagès 2009). The hard coral species living at sites most exposed to anthropogenic impacts, such as *Porites*, seem to represent the most robust species, which can cope with high particle loads and eutrophication. These "*Porites*" reefs still fulfil the role of a natural filter system, coastal protection and a habitat for fish and other reef organisms, which all together have a high economic value (Spurgeon 1992). Thus they should be focused for future protection efforts in the area. *P. furcata* appears to play a major role in maintaining reef structure in frequently disturbed environments (Lirman et al. 2003). It possesses an opportunistic life history (e.g. high recruitment, small colony size; Lirman et al. 2003) and strong trophic plasticity, allowing them to maintain energy demands through an increased heterotrophy (Aronson et al. 2005; Seemann et al. 2012a). Even though the reefs of Almirante Bay are not yet in a tipping point situation, where reefs suddenly shift into a new and irreversible state, dominated by fleshy algae or other soft cover (Leinfelder et al. 2012), further anthropogenic activity will lead to a continuous loss of hard structures (Hughes 1994; Gardner et al. 2003; Elmhirst et al. 2009). If turbidity and eutrophication increases, a further loss of hard coral species will be observed (Burke et al. 2004). The phase shift will be probably represented by sponges (Norström et al. 2009), since they seem to be less susceptible to suspension load and profit from eutrophication (Wilkinson and Cheshire 1990; Zea 1993; Fichez et al. 2005). An increased regularity of bleaching events will furthermore lead to the loss of slow growing massive species as *S. siderea* and also to a loss of organisms that are associated to this species. It will lead to a continuous loss of biodiversity of fish, of other invertebrates or even large umbrella species such as nurse sharks, which preferentially use big *S. siderea* colonies as a shelter (Wilson et al. 2006). Also, increased turbidity will intensify the general shift from communities dominated by the framework builders such as Acroporidae and Faviidae to non-framework builders, such as Agariciidae and Poritidae. With an increased turbidity the framework-building Acroporidae will not survive within the bay (Gardner et al. 2003).

A decrease in sediment loads and eutrophication is essential for the protection of coral reefs of the Almirante Bay. If protection efforts are not increased, coral mortality will continue resulting in a loss of biodiverse reef structures, fish sources and the economic value from tourism.

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