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Status of Coral Reef Communities on the Caribbean Coast of Costa Rica: Are We Talking about Corals or Macroalgae Reefs?

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Abstract: In the past decades, one of the most widely reported phenomena on Caribbean reefs is the general fall in coral cover and rise in macroalgae. Reefs with low coral cover and high macroalgal abundances are often presumed to provide poorer ecosystem functions and services. In this study, we assessed the condition of coral reefs on the Caribbean Coast of Costa Rica and determined how eight key ecosystem metrics varied in response to different coral and fleshy macroalgae covers. Most reefs surveyed had high fleshy macroalgae and low live coral covers, with an average (±SD) of 31 ± 28% and 14 ± 13% per site. The value of many of the ecosystem metrics estimated for coral reefs of the region appears to be lower than what has been reported for other areas in the Caribbean. We found that the rugosity, urchin density, fish richness, total fish biomass, large fish density, and the potential fishery value of the reef were higher in sites with low fleshy macroalgae covers (<10%). Our results concur with the prevailing paradigm that an increase in macroalgae abundance could reduce the ecosystem services provided by coral reefs.

Keywords: coral reefs; macroalgae; ecosystem services; ecosystem functions; phase-shifts

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1. Introduction

Coral reefs are in decline worldwide due to the effects of multiple global and local stressors [1]. In the Caribbean, warming events, disease outbreaks, hurricanes, overfishing, and water pollution due to inadequate coastal development have severely impacted coral reefs [2–6]. As a result of these stressors, coral cover has declined and been replaced by a high abundance of macroalgae in many Caribbean reefs [6–10]. As coral cover declined, the structural complexity of many reefs also decreased, which caused significant changes in the associated fish communities [11–13]. As coral reefs shift towards macroalgae-dominated states, it is believed that their ability to support ecosystem services will be compromised [14–16]. Nonetheless, further studies are needed to understand the full implications of coral–algal phase shifts on the diverse range of ecosystem services provided by coral reefs, including food provision, coastal protection, tourism, recreational opportunities, and aesthetic and cultural values [17].

Recent evidence suggests that live coral cover may not be as important as previously thought in sustaining coral reef functionality [18,19]. In the Caribbean, Lester et al. [18] documented poor relationships between coral cover and several ecosystem metrics related to reef ecosystem functions and services and found numerous bright spots where the herbivorous fish biomass, large fish density, fishery value, and fish species richness were high despite the low coral cover. Thus, there appears to be high variability in the ability of low coral cover reefs to support important reef functions [18]. One factor that may be conditioning this variability is that different ecological states are possible in the absence of high coral cover, as the reef benthos could be dominated by fleshy macroalgae, filamentous turf algae, calcareous coralline algae, soft corals, sponges, and other organisms [16,18,20,21]. Variations in the structural complexity of the reefs may also condition this variability, as structural complexity is not strongly related to live coral cover in the Caribbean, and reefs that are structurally complex despite low coral cover may be able to support high fish richness and biomass [11,13,18,22]. Improving the state of knowledge of the ecosystem services provided by non-coral-dominated reefs may prove useful to foster effective management strategies to support reef resilience [18,23]. Especially considering that, as the impact of global stressors like climate change and ocean acidification increases, it is unrealistic to expect that coral reefs would recover to their past coral-dominated configurations [1].

Coral reefs in the Southwestern Caribbean (SWC), which includes the Caribbean coasts of southern Honduras, Nicaragua, Costa Rica, Panama and Colombia, have distinct coral assemblages that tend to be less diverse and complex than in other regions of the Caribbean [24,25]. The reefs of this region have historically been exposed to high levels of river discharge, which can limit the development of coral-dominated reefs [26–29]. Thus, the SWC represents an interesting area for studying the functionality of non-coral-dominated reefs, as many of the reefs found in this region have low coral and high algae covers [30–32].

In the Caribbean Coast of Costa Rica, three areas of reef development are recognized: (1) between Moín and Limón (1), (2) Cahuita, and (3) between Puerto Viejo and Punta Mona (Figure 1) [33]. The first reports on the status of coral reefs on the Caribbean coast of Costa Rica were conducted in the 1970s and early 1980s, which described the reef and associated organisms at Cahuita [34,35]. During the 1980s and 1990s, multiple natural and anthropogenic disturbances impacted the reefs, including warming events, disease outbreaks, earthquakes, water pollution, increased sediment loading, and tourism impacts [33,36–40]. As a result, coral cover on Cahuita reefs declined from 40% in the early 1980s to 10% in the early 1990s [36]. Coral cover increased from 13% in 1999 to 28% in 2003, but declined to about 17% over the next five years [41]. In contrast, macroalgae cover increased significantly from 37% in 2003 to 61% in 2008 [41]. The coral reefs of the Moín–Limón and Puerto Viejo–Punta Mona areas have historically been less studied than the Cahuita reefs, but the existing assessments have also reported low coral and high algae covers [30,33,42].

Since 2010, only a few reports have been published on the status of coral reefs along the Caribbean Coast of Costa Rica [43,44]. Williams et al. [44] compared the status of *Orbicella* reefs and gorgonian plains between multiple countries in the Caribbean, and recorded a mean coral cover of 7.7% in 2012 around Cahuita and Puerto Viejo–Punta Mona. Overall, there is a lack of monitoring records regarding the status of coral reefs on the Caribbean coast of Costa Rica, and the existing records mostly focus on Cahuita. Also, the existing assessments exhibit a spatial and methodological disparity, which complicates the identification of regional trends in the coverage of benthic organisms.

We report on the status of coral reefs of the Caribbean coast of Costa Rica based on reef survey data collected between 2019–2022. To our knowledge, this is the most spatially representative coral reef assessment ever recorded for the Caribbean coast of Costa Rica until now, as we surveyed 24 reef sites located among the three reefs areas. We examined how eight key ecosystem metrics—including the coral richness, substrate rugosity, urchin density, fish richness, total fish biomass, herbivore fish biomass, large fish density, and the potential fishery value of the reef—varied in response to differential coral and macroalgae cover.

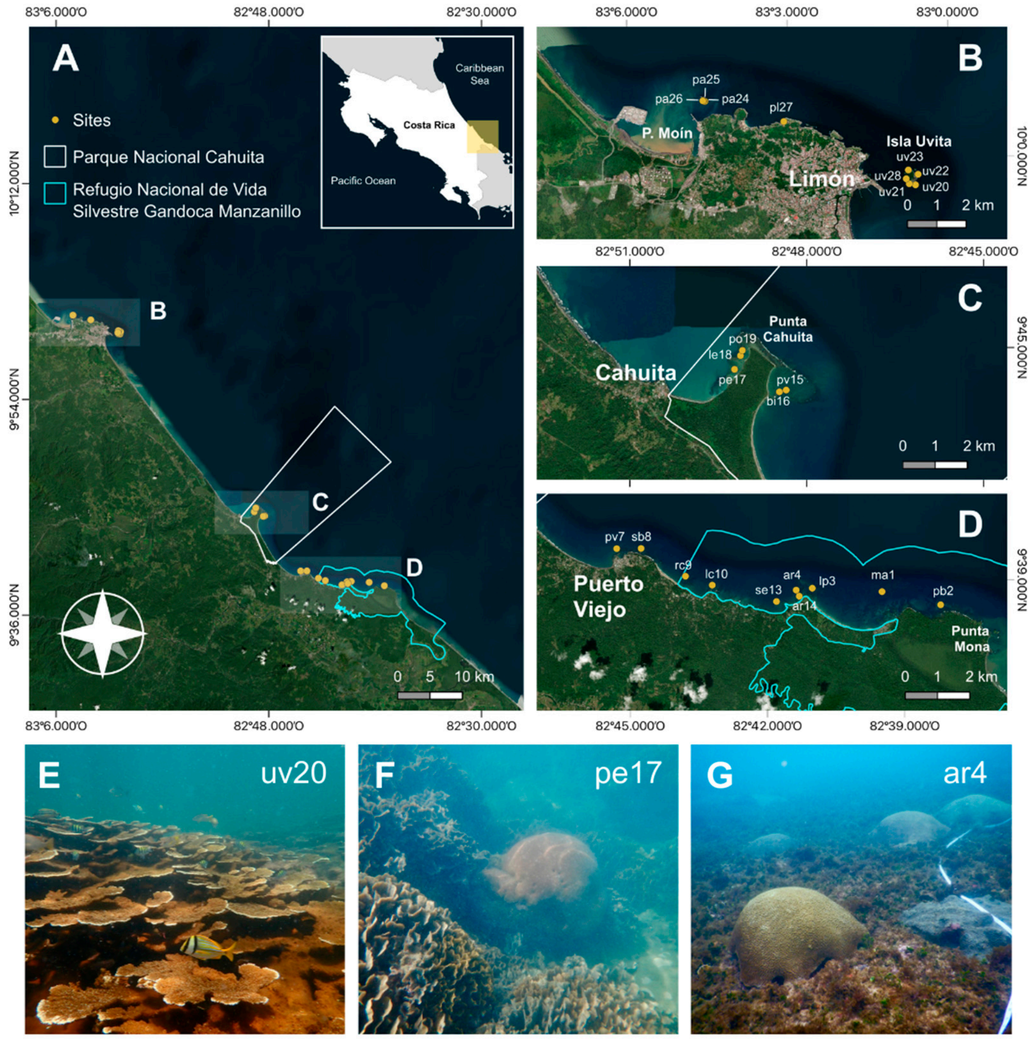

Figure 1. (**A**) Study area and survey sites across the regions of (**B**) Moín–Limón, (**C**) Cahuita, and (**D**) Puerto Viejo–Punta Mona. Survey site code can be found in the Supplementary Material Table S1. Photos of surveyed reefs in (**E**) Isla Uvita (Moín–Limón), (**F**) Perezoso (Cahuita), and (**G**) Punta Uva Arrecife (Puerto Viejo–Punta Mona).

2. Materials and Methods

2.1. Study Area

The Caribbean coast of Costa Rica consist of high-energy sandy beaches that are interrupted by carbonate promontories on the Southern section. Between Moín and Limón, carbonate platforms and small fringing and patch reefs are found along the coast, including Isla Uvita [33] (Figure 1B). Cahuita is the largest fringing reef, with three barriers: the outer barrier, stretching for 5 km from the Western side of Punta Cahuita; the inner barrier, which is about 500 m long and is located between the coast and the eastern part of outer barrier; and a 100 m long barrier located at the western end of the reef [33]. Between Puerto Viejo and Punta Mona, fringing reefs, patch reef, carbonate banks and algal ridges can be found [33]. Two marine protected areas (MPA) with coral reefs are in the Caribbean coast of Costa Rica: Cahuita National Park ("Parque Nacional Cahuita"), founded in 1978; and Gandoca-Manzanillo Wildlife Refuge ("Refugio Nacional de Vida Silvestre Gandoca-Manzanillo"), founded in 1982 (Figure 1). Within the protected areas, artisanal fishing and tourism activities are permitted following specific regulations.

2.2. Survey Sites and Data Collection

Between 2019 and 2022, we conducted reef surveys at 24 sites along the Caribbean Coast of Costa Rica. Survey sites were selected with an effort to span the regions from Moín to Punta Mona. We selected and identified the survey sites through consultations with local tour operators and fishermen who had extensive knowledge of the marine area. We only considered sites between 2 and 10 m that had a base structure of calcium carbonate. We surveyed nine sites between Moín and Limón, five in Cahuita National Park, and ten between Puerto Viejo and Punta Mona, eight of which were inside the Gandoca-Manzanillo Wildlife Refuge (Figure 1). The coordinates and mean depth of the survey sites can be found in the Supplementary Material Table S1.

On each reef survey, benthic, substrate rugosity, motile invertebrate, and fish community data were collected via SCUBA using standard methodologies. During every survey, three 10 m linear transects were arranged parallel to the cost. Benthic community data were collected using a photo-quadrat methodology. Ten 0.25 m^2 quadrats were placed at each meter of the transect line, accounting for a total surface area of 2.5 m^2 per transect. A photograph of each quadrat was taken at a 90° angle to the reef benthos. Photographs from all surveys were analyzed using the software photoQuad v1.4 [45] to quantify the cover percentage per benthic taxa and the coral species richness.

The substrate cover percentage was estimated by overlaying 50 stratified random points on each image and identifying the taxa that occurred under each point. We classified the organisms into ten functional groups: hard coral (all scleractinian taxa and the hydrozoan *Millepora*), soft coral, sponge, non-calcified Hexacorallia (anemones, zoanthids and corallimorphs), turf algae (defined in Smith et al. [16] as the "epilithic algal matrix" generally composed of a mixed community of filamentous algae and cyanobacteria usually less than 2 cm tall), fleshy macroalgae (*Dictyota*, *Dictyoteris*, *Sargassum*, *Laurencia*, *Lobophora*, etc.), calcareous macroalgae (*Halimeda*, *Amphiroa*, *Galaxaura*, etc.), crustose coralline algae or CCA (defined in Smith et al. [16] as all encrusting, non-geniculate members of the Corallinales), crustose non-coralline algae (*Peysonelia*), and non-biological substrate (sand, basalt). Hard corals were identified to species, fleshy and calcareous macroalgae to genus, and other organisms to their functional group. We estimated the coral richness per transect by counting the number of corals that appeared in the photographs of the ten quadrats surveyed. In total, we analyzed 820 photos from 82 transects.

To quantify the substrate rugosity, we fitted a 10 m long fine-linked chain (link length: 1 cm) to the contours of the reef substrate along each linear transect and measured the total distance in a straight line from the start to the end point of the chain [46]. We then calculated the rugosity index by subtracting one from the ratio of chain length to the linear distance between the chain ends; where a value of 0 indicates a flat surface and values >1 indicate greater rugosity [47,48]. Motile invertebrate data was collected by identifying and counting all the motile invertebrates found within one meter of each side of the 10 m transect line [48]. Motile invertebrates were defined as conspicuous animals larger than 2.5 cm in body size, and included echinoids, asteroids, gastropods, cephalopods, and crustaceans [48].

Fish community data was collected by counting and estimating the total length of each fish found within a 5 m wide and 10 m long belt transect [48]. Total fish length was estimated based on the following categories: <5, 5–10,10–15, 15–20, 20–25, 25–30, 30–40, 40–50, 50–100, >100 cm. Due to poor environmental conditions, we were only able to conduct fish community surveys in 15 of the 24 survey sites. For each transect, species-specific biomass was estimated according to their length to mass ratio [48].

2.3. Ecosystem Metrics

Based on the reef survey data, we quantified eight ecosystem metrics relating to reef functions and services, including coral richness, substrate rugosity, urchin density, fish richness, total fish biomass, herbivore fish biomass, large fish density, and potential fishery value of the reef. Metric selection was based on existing reviews of the ecosystem services provided by coral reefs, and empirical studies on coral reef functionality [15,17,18,49].

Many of the ecosystem metrics were selected following Lester et al. [18], who studied the relationship between coral cover and different ecosystem metrics relating to functions and ecosystem services provided by Caribbean coral reefs. Each of the ecosystem metrics considered is described in the following section:

1. Coral richness: Number of coral species encountered at each benthic transect (spp. 2.5 m^{-2}).
2. Substrate rugosity: Estimated rugosity index values for each transect.
3. Sea urchin density: Number of sea urchins encountered at each motile invertebrate transect per area (ind. m^{-2}).
4. Fish richness: Number of fish species encountered at each transect (spp. 50 m^{-2}).
5. Fish biomass: Summation of biomass estimates of all fishes counted at each fish transect per area (kg 100 m^{-2}).
6. Herbivore fish biomass: Summation of biomass estimates of fishes of the families Acanthuridae and Scaridae counted at each transect per area (kg 100 m^{-2}) [50].
7. Large fish density: Number of fishes greater than 20 cm in total length counted at each transect per area (ind 100 m^{-2}). Lester et al. [18] used a >40 cm cutoff to measure this metric. However, we did not count any individual with an estimated total length greater than 40 cm, so we decided to use the >20 cm cutoff.
8. Potential fishery value: To quantify the potential fishery value of the reef fish assemblage, we multiplied the species-specific biomass estimates for each transect by the species-specific price estimates reported by Lester et al. [18] (USD 100 m^{-2}). The price estimates are based on fishery statistics from Puerto Rico that provided an estimate of value in USD per pound of fish landed by species or by family (Lester et al. [18]). For species that did not appear in the Lester et al. [18] list, we first determined if they had or did not have a fishery value based on the information listed in FishBase under the human uses category [51]. If "commercial fisheries" was listed as a human use of the specific species, we then assigned it the price estimate of a similar species included in the Lester et al. [18] list (i.e., of the same genus or family). Of the total fish species encountered on the surveys, four species of commercial fishery importance were not listed in the species-specific price estimates reported by Lester et al. [18] (Supplementary Material Table S4).

2.4. Data Analysis

We estimated the general and per-site average cover of the ten benthic functional groups previously described, including hard corals, soft corals, sponges, non-calcified Hexacorallia, turf algae, fleshy macroalgae, calcareous macroalgae, CCA, crustose non-coralline algae, and non-biological substrate. The percentage contribution of each coral species to the total hard coral cover was determined by adding the estimated mean cover of the specific species at each site and dividing it by the summation of the total hard coral cover estimated for each site [48]. The percentage contribution of each macroalgae genus to the total fleshy macroalgae was also quantified.

Following Smith et al. [16], we used Pearson correlations to examine whether there was a negative relationship between mean fleshy macroalgal and coral cover, and between the cover of reef builders (hard corals + CCA) and that of fleshy algae (fleshy macroalgae + turf algae) among sites. Based on the mean cover of these benthic groups, we determined which of the 24 reef sites surveyed were dominated (>50% cover) by hard corals, fleshy macroalgae, reef builders, and fleshy algae. Also, to evaluate variations in the reef benthic composition between the Moín–Limón, Cahuita, and Puerto Viejo–Punta Mona areas, NMDS and PERMANOVA tests were performed. A SIMPER was performed to identify the benthic taxa that contributed most to the differences between regions.

We identified among the reefs surveyed "bright spots" and "dim spots" of coral cover, fleshy macroalgae cover, coral richness, substrate rugosity, urchin density, fish richness, total fish biomass, herbivore fish biomass, large fish density, and the potential fishery value of the reef. A site was identified as a bright spot or a dim spot when its mean was significantly higher or lower than the general mean estimated among all sites, respectively. To determine if the means were significantly different, we compared their 95% confidence intervals (CI); if the range of the CI did not overlap, then significant differences were assumed.

We examined whether the ecosystem metrics quantified per transect varied between reefs with different levels of coral and fleshy macroalgae covers. For the analysis, we binned the coral cover values into three categories following Lester et al. [18]: low (<10% cover), medium (10–20% cover), and high (>20% cover). We also binned fleshy macroalgae covers into three categories: low (<10% cover), medium (10–50% cover), and high (>50% cover). We determined these fleshy macroalgae cover categories based on the variation of our data and the literature information. The lower cover category was mostly based on reef health indicators for Caribbean Mesoamerican reefs, which consider reefs with fleshy macroalgae covers around 0 to 12% to be in a very good to regular state. While a >50% cutoff was used to define the higher cover category, as to only include reefs where fleshy macroalgae were the dominant benthic organisms. Kruskal–Wallis and Mann–Whitney tests were used to determine significant differences in the ecosystem metrics—including coral richness, substrate rugosity, urchin density, fish richness, total fish biomass, herbivore fish biomass, large fish density, and the potential fishery value of the reef—between the coral and fleshy macroalgae cover categories. All statistical tests were run using R (v.4.2.3) [52].

3. Results

The surveyed reefs were dominated by turf algae and fleshy macroalgae, with an average ($\pm$SD) cover of $42 \pm 19\%$ and $31 \pm 28\%$, respectively (Figure 1A). Brown macroalgae of the genus *Dictyota*/*Dictyopteris* were the predominant fleshy macroalgae species found on the reefs (Figure 2B). Hard live corals covered $14 \pm 13\%$ of the reef substrate on average (Figure 2A). We identified 14 species of reef-building corals among all survey sites (Supplementary Material, Table S2). The lettuce coral *Agaricia agaricites* and the fire coral *Millepora complanata* were the predominant coral species found on the reefs, followed by the elkhorn coral *Acropora palmata* (Figure 2C). These were the predominant coral species on reefs with high coral cover (>20%). In reefs with medium (10–20%) and low (<10%) coral cover, the predominant species were the massive starlet coral *Siderastrea siderea*, *Pseudodiploria* brain corals growing like thick crusts and mounds, and the fire coral *Millepora complanata*.

The fleshy macroalgae cover was higher than the coral cover in 15 of the 24 reefs surveyed, of which six presented fleshy macroalgae covers superior to 50%. None of the reefs surveyed presented covers of reef builders (hard corals + CCA) higher than 50%, and almost all were dominated by fleshy algae (fleshy macroalgae + turf algae) (Figure 3). We recorded significant negative relationships between coral and fleshy macroalgae cover (cor = -0.43, $p < 0.001$) and between reef builders and fleshy algae cover (cor = -0.83, $p < 0.001$).

The composition of the benthic community of the reefs varied significantly between the regions of Moín–Limón, Cahuita, and Puerto Viejo–Punta Mona (Figure 4, PERMANOVA, $p = 0.001$). According to SIMPER, the taxa that contributed the most to the dissimilarity between sites were the macroalgae of the genus *Dictyota/Dictyopteris*, which were more abundant in the reefs of the Puerto Viejo–Punta Mona area (Supplementary Material, Table S3). We recorded bright spots of high coral and low fleshy macroalgae cover in Cahuita and Moín–Limón, while most of the reefs of Puerto Viejo–Punta Mona were categorized as dim spots of high fleshy macroalgae cover (Figure 5A,B). The reef with the highest average coral cover was located near Punta Cahuita (pe17: 39% cover), where fire corals were the dominant coral species. We identified another bright spot of coral cover on Isla Uvita (uv20: 39% cover), where elkhorn corals were the main reef-forming species. On average, we recorded 3 ± 2 coral species per 2.5 m^2 of reef area. Despite their high macroalgae covers, many reefs in Puerto Viejo–Punta Mona appeared to be bright spots of coral richness (Figure 5C). Regarding substrate rugosity, the reefs were not very structurally complex and tended to be flat, with an average linear rugosity index of 0.2 ± 0.1. The two reef locations with the highest average coral covers were categorized as bright spots of substrate rugosity (Figure 5D).

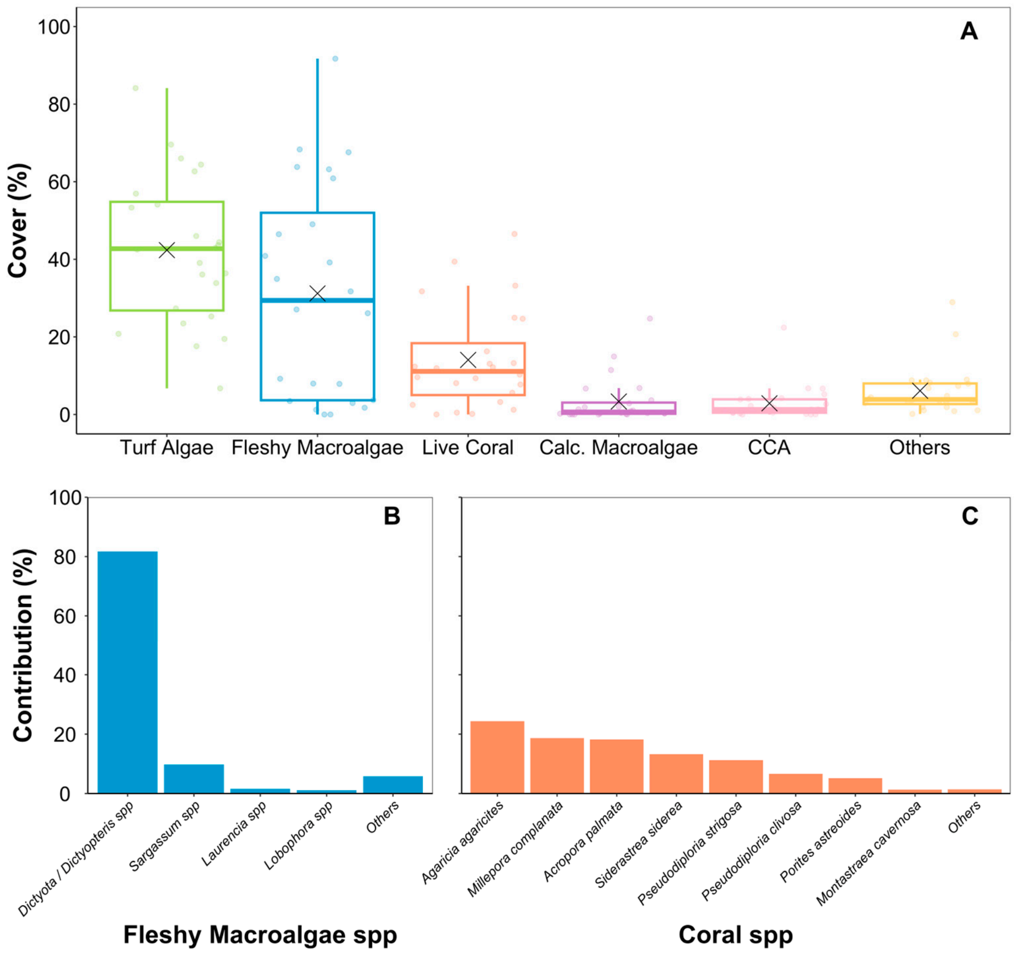

Figure 2. (**A**) Percentage cover of benthic organisms in the reefs surveyed on the Caribbean Coast of Costa Rica. Each point represents the mean cover estimated for a survey site. ✕ symbol represents the mean cover between all survey sites: Calcareous macroalgae (Calc. Macroalgae) and Crustose coralline algae (CCA). (**B**) Macroalgae species percentage contribution to the total fleshy macroalgae cover of the reefs surveyed. (**C**) Coral species percentage contribution to the total live coral cover of the reefs surveyed.

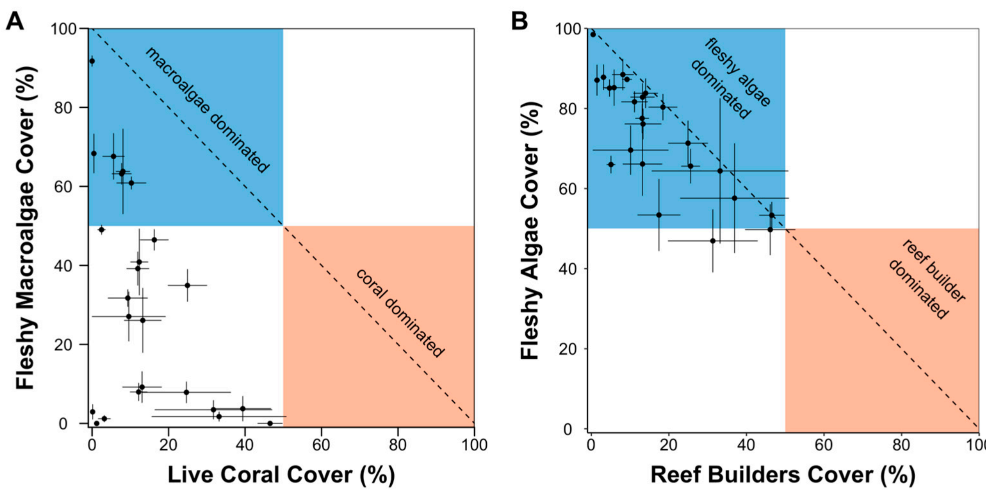

Figure 3. (**A**) Relationship between mean coral and fleshy macroalgal cover across all survey sites (± SE); (**B**) Relationship between mean reef builders (hard coral + CCA) and fleshy algae (turf algae + fleshy macroalgae) cover across all survey sites (±SE).

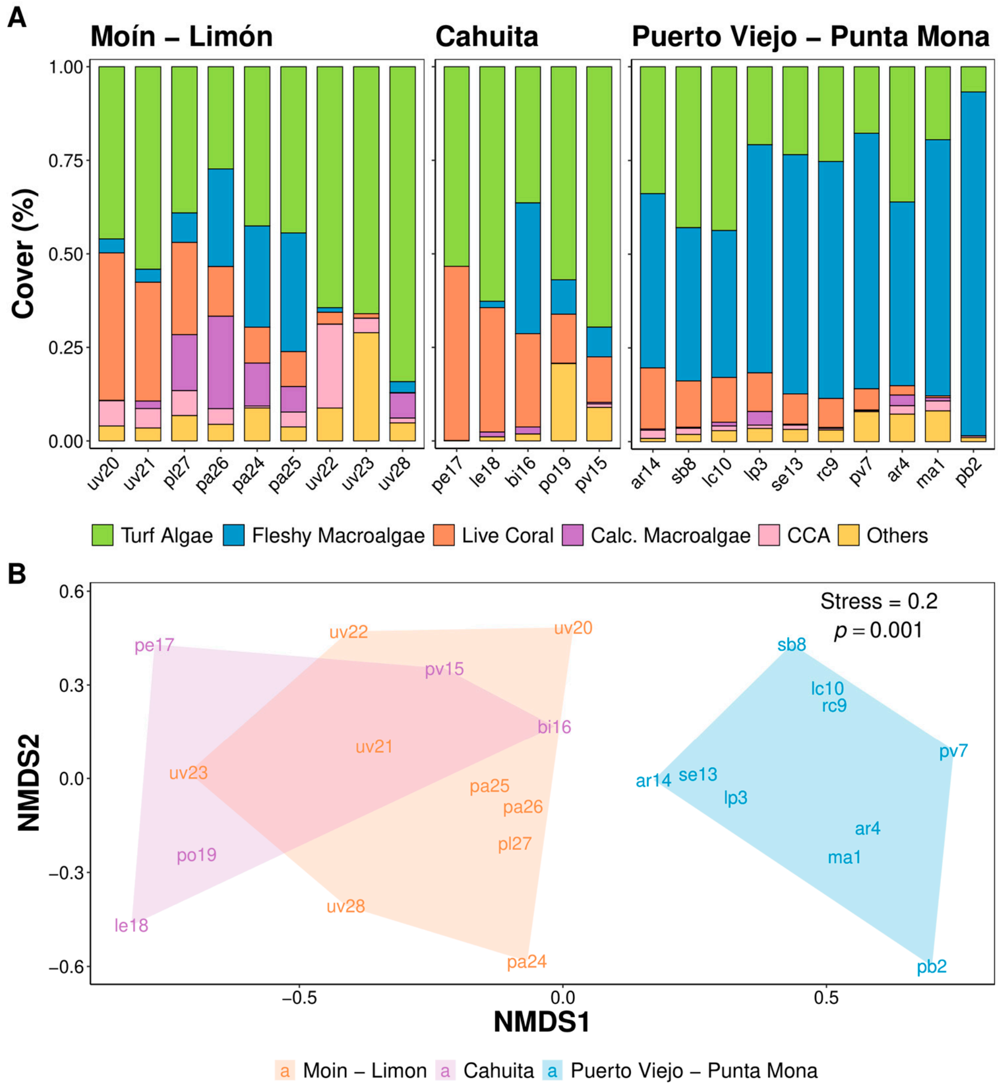

Figure 4. (**A**) Estimated average cover of benthic organisms by survey site: Calcareous macroalgae (Calc. Macroalgae) and Crustose coralline algae (CCA). (**B**) NMDS of the reef benthic communities on the three regions of reefs development in the Caribbean Coast of Costa Rica. Stress values and *p*-value of the PERMANOVA are shown.

Urchin density was low among the surveyed reefs, with an average of 0.7 ± 2.0 ind. m^{-2} (Figure 5E). The most common urchin species were *Echinometra lucunter*, *Echinometra viridis*, and *Diadema antillarum*, with average densities of 0.5, 0.1, and 0.05 ind. m^{-2}, respectively. Concerning the fish community, we recorded 56 species belonging to 11 families, which were among the 16 sites where fish surveys were conducted (Supplementary Material, Table S4). On average, we recorded only 5 ± 1 fish species per 50 m^2 of reef area (Figure 5F). The estimated values of the fish community metrics were low across the region's reefs, with an average biomass of 3.7 ± 7.3 kg 100 m^{-2}, herbivore biomass of 1.6 ± 5.6 kg 100 m^{-2}, large fish density (>20 cm) of 15 ± 34 ind 100 m^{-2}, and a fishery value of only 5.1 ± 9.6 kg 100 m^{-2} (Figure 5G–J). Overall, the fish families with the highest average biomass were Acanthuridae (surgeonfishes) and Pomacentridae (damselfishes), with 1.4 ± 5.2 and 0.7 ± 1.0 kg 100 m^{-2}, respectively. The reef with the highest mean fish biomass, herbivore fish biomass, and large fish density among all survey sites was the same reef on Isla Uvita categorized as a bright spot of high coral and low macroalgae cover (uv20).

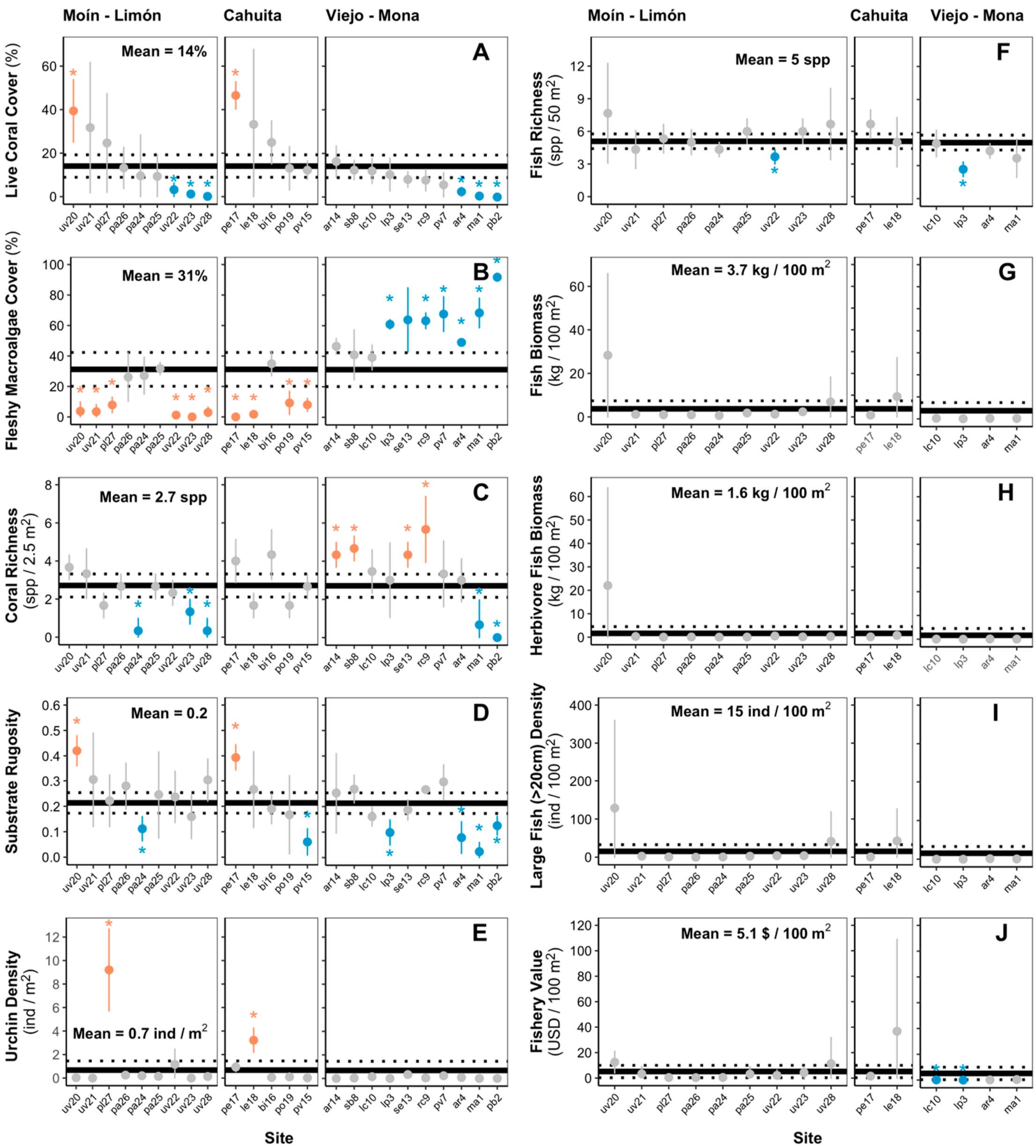

Figure 5. Mean ecosystem metrics by survey site (±95% CI). The horizontal solid black line represents the general mean among all sites and the dotted line the 95% confidence intervals. An asterisk (*) indicates that the site was categorized as either a bright or a dim spot, painted orange and blue respectively.

The estimated value of some ecosystem metrics relating to reef functions and ecosystem services varied between sites with different coral and macroalgae cover levels. Reefs with low coral covers (<10%) were associated with significantly lower coral richness per unit area (Figure 6A). Substrate rugosity was higher on reefs with high coral (>20%) and low macroalgae covers (<10%) (Figure 6B). Urchin density was also significantly higher on reefs with low macroalgae cover (<10%) (Figure 6C). Metrics relating to the fish community—fish species richness, biomass, large fish density (>20 cm), and fishery value—were significantly higher on reefs with low macroalgae cover (Figure 6D–H). Although not statistically significant, we also recorded a tendency of lower herbivore fish richness in reefs with higher macroalgae covers. Fish community metrics appeared higher on reefs with high coral cover; however, apart from fish biomass, we did not find statistically significant differences of the fish community metrics between the coral cover categories.

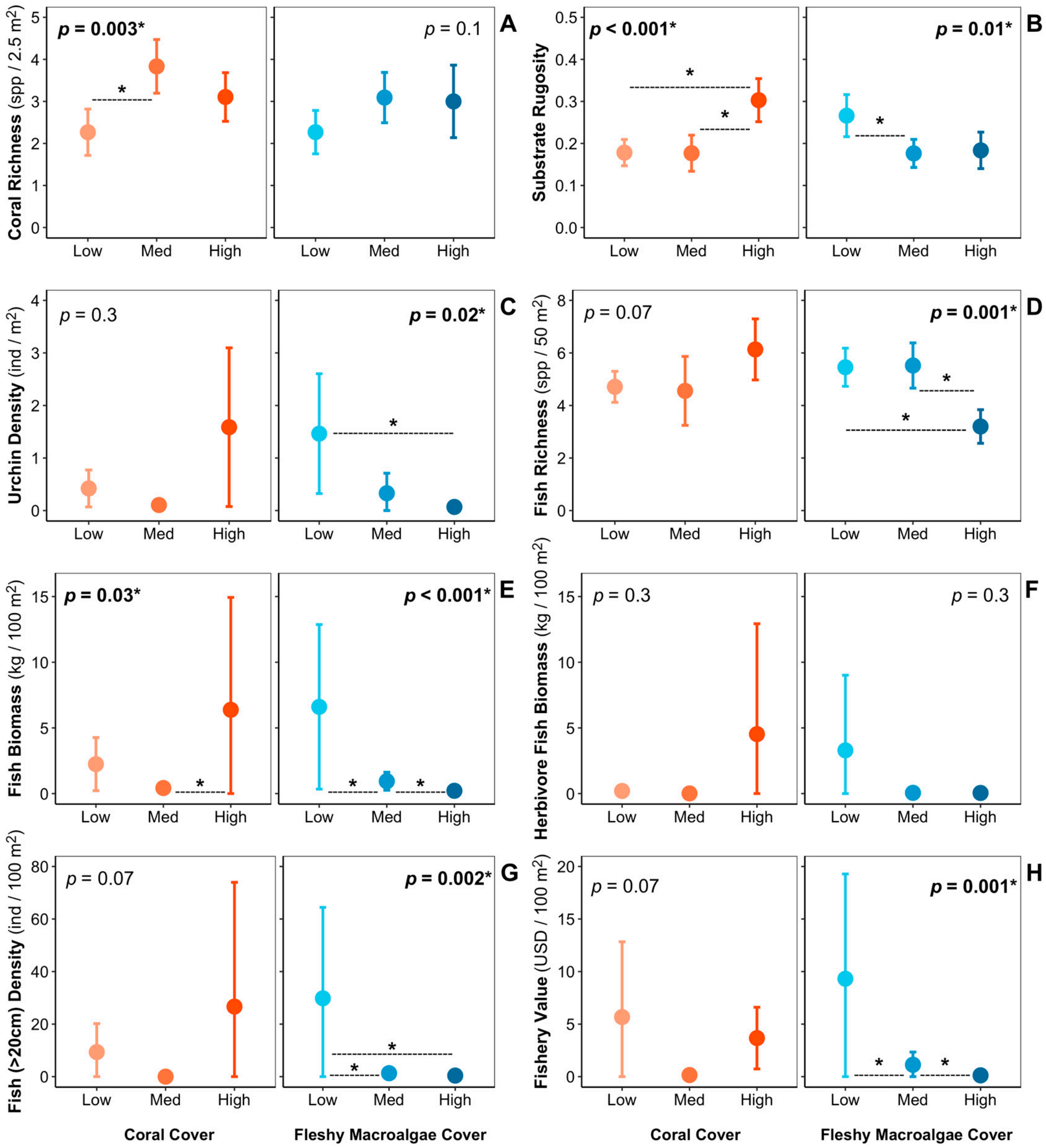

Figure 6. Mean ecosystem metrics (±95% CI) by three categories of coral and fleshy macroalgae cover. High coral cover is defined as >20%, medium is 10%–20%, and low is <10%. High fleshy macroalgae cover is defined as >50%, medium is 50–10%, and low is <10%. The *p*-value from Kruskall–Wallis tests comparing the mean of the three categories are shown in each panel. Asterisks (*) indicate significant differences ($p < 0.05$). Dotted lines between boxplots represent significant differences between the two cover categories based on Mann–Whitney tests.

4. Discussion

This study represents the first report on the status of coral reef communities on the Caribbean coast of Costa Rica since Williams et al. [44] and Araya-Vargas and Nova-Bustos [43]. Among all 24 sites surveyed, this report is also the most spatially representative coral reef assessment ever recorded for the region, as it includes many reefs whose status has never been reported in the literature. The 14% average coral cover estimated for the surveyed reefs falls in a similar range to the 15.9% regional average reported for the Great Caribbean in 2019 [53]. However, the 77% total algae cover, including all algae functional groups, appears to be at the higher end of the values reported for coral reefs of the Great Caribbean, which averaged 52% in 2019 [53]. Compared to the Mesoamerican region, the average 31% fleshy macroalgae cover estimated for Costa Rican reefs is similar to that reported for Guatemalan reefs in 2022 (30%) and higher than that reported for Mexico (24%), Belize (18%), and Honduras (25%) [54].

The high fleshy macroalgae and low coral cover found on the coral reefs of the Caribbean coast of Costa Rica may indicate that these ecosystems have undergone a phase shift from hard coral to macroalgae domination. For the reefs around Puerto Viejo, coral cover was around 23% in 1988 and 14% in 1993 [33], which are lower than the average coral cover of 5.6 to 12% recorded for the reefs surveyed in the area in 2021 (site codes: pv7 and sb8). In contrast, total algae cover appears to have increased from 38% in 1993 to about 85% in 2021 [33]. For reefs around Puerto Vargas in Cahuita National Park (site codes: pv15 and bi16), we estimated coral covers between 12 and 25%, which are much lower than the 40% cover recorded in the early 1980s [36]. Also, the increasing trends in algae cover previously reported between 2003 (37%) and 2008 (61%) [41] seem to have continued until now, as we recorded total algae covers of about 70 to 73% for the Puerto Vargas area. When making these comparisons, it is important to consider that the specific site and methodologies used to quantify the coral and algae covers differ between studies. Thus, although the impression that macroalgae cover has increased substantially on the reefs of the Caribbean coast of Costa Rica seems like a fair assumption, the lack of monitoring records and the spatial and methodological disparity between existing assessments make it difficult to state this as a fact.

Nutrient enrichment of coastal waters due to coastal development may be one of the main factors driving the high abundance of fleshy macroalgae, as has been reported for reefs in other regions of the Caribbean [3,55–58]. In Cahuita, average nitrite concentrations were higher in 2017–2018 than in 2005–2004 and 1997, reflecting an increased nitrogen loading [59–61]. Water quality assessments around Cahuita and Isla Uvita [59,62] also found nitrite and nitrate concentrations which were much higher that the reported values for reefs in Panama and Florida [3,63,64]. Thus, excess nutrients may have led to increased algal growth on Costa Rican Caribbean reefs. However, there are only a few available water quality assessments that report nutrient concentration levels for sites along the Caribbean coast of Costa Rica, which makes it difficult to determine if nutrient enrichment is the main factor driving the spatial variability in the abundance of macroalgae in the reefs of the region.

Increased sediment loading may also be a factor driving the dominance of fleshy algae. Sediment loading can alter the reef benthos through light attenuation and smothering, as well as deter herbivores from grazing and even displace them entirely [65–67]. Cahuita's reefs experienced a significant increase in sediment loading from the 1950s to the 1980s, thought to be associated with extensive logging and the establishment of banana plantations in the area [27]. The increased sediment loading was correlated with a reduction in the growth rates of the coral colonies [27]. Since the 1980s, suspended sediment concentrations in Cahuita appear to have increased even more and continue to be a major stress factor for its marine habitats [41,59]. Beach erosion is also a factor contributing to the increased sediment loading, as many sandy beaches of the Costa Rican Caribbean coast have been identified as hotspots of erosion in the past 20 years [68,69]. The Limón earthquake of 1991, which uplifted the coastal zone between Moín and Panama, also caused a substantial increase in sediment loads, which affected the reef organisms [37].

The low abundance of sea urchins recorded in the surveyed reefs may also be related to the overall dominance of fleshy algae. Multiple studies identify the 1983–1984 massive die-off of the herbivorous urchin *Diadema antillarum* as an important cause of the proliferation of macroalgae in Caribbean reefs [4,8]. Before 1983, *D. antillarum* was common on coral reefs of the Caribbean Coast of Costa Rica, with estimated densities of 3.6–8.8 ind. m^{-2} for reefs in Cahuita [70]. After the massive die-off in 1983, *Diadema* densities reduced to 0.2–2 ind. m^{-2} [40]. In 1992, very low densities (0.01 ind. m^{-2}) were observed, and between 1999 and 2003, densities ranged between 0.3 and 0.7 ind. m^{-2} [36,71]. Almost 40 years later, we found that *Diadema* densities for the whole region are very low (0.05 ind. m^{-2}), and the population does not seem to have recovered. The lack of recovery of this keystone herbivore may be one of the factors driving the high fleshy algae cover found in Costa Rican's Caribbean reefs, which concurs with the significantly higher urchin densities found on reefs with low fleshy macroalgae covers. Further evidence is that macroalgae cover declined and coral recruitment increased on Caribbean reefs where *D. antillarum* densities recovered [72–75]. Also, *D. antillarum* seem to have an affinity for brown macroalgae of the genus *Dictyota*, which may also be evidence that their low abundance is driving the algae dominance found on the reefs, because *Dictyota*/*Dictyopteris* spp. were the algae species that contributed the most to the reported fleshy macroalgae covers [76].

The estimated values of most of the ecosystem metrics considered were in the lower range of the values reported for other regions of the Caribbean, especially those related to the fish community—fish species richness, biomass, herbivore biomass, large fish density (>20 cm), and fishery value [6,18,77]. There was also a surprising lack of variability in fish community metrics between sites and regions, despite the presence of Marine Protected Areas (MPAs). This is because one would expect that metrics such as fish biomass and fishery value would be higher in reefs within well-enforced MPAs, but this was not reflected in our results. This may indicate that the current management efforts are not sufficient to protect the region's coral reefs and associated organisms from the local stressors they face, such as water pollution and sediment loading. To assess the water quality problem, future studies should quantify and monitor the water quality along the Caribbean coast of Costa Rica and explore its relationship with spatial and temporal changes in the reef communities.

In terms of the relationships between coral and fleshy macroalgae with the other ecosystem metrics, we found that reefs with lower fleshy macroalgae cover were associated with higher substrate rugosity, urchin density, fish richness, fish biomass, large fish density and fishery values. Our results are consistent with the prevailing paradigm that phase shifts from coral- to macroalgae-dominated reefs could reduce the ecosystem services provided by coral reefs [14–16]. In contrast, most ecosystem metrics did not vary significantly with coral cover. These results conflict with past studies that found stronger linkages between coral cover and ecosystem services, and align with Lester et al. [18], who reported weak correlations between coral cover and numerous non-coral ecosystem metrics for Caribbean reefs. As discussed by Lester et al. [18], these results may suggest that, following the dramatic losses of coral cover in the 1980s and the subsequent changes in the coral species composition [8,11], some of the ecological relationships that once existed for Caribbean reefs may no longer hold. In the past, branching *Acropora* species were the dominant corals on many Caribbean reefs and may have played a crucial role in supporting the fish community [13,78]. Currently, the dominant coral species in the Caribbean tend to be smaller and less structurally complex [11]. Thus, the relationships between coral cover and fish community metrics in the Caribbean may depend more on the cover of specific species, such as corals of the *Acropora* genus, than on the general coral cover [18]. This is reflected in our results, as the reef with the highest cover of *A. palmata* had also the highest mean fish richness, fish biomass, herbivore fish biomass, and large fish density among all survey sites.

Lester et al. [18] found numerous coral reefs in the Caribbean where metrics relating to reef functions and services were high despite having low coral covers (<10%). However, among the reefs surveyed in the Caribbean coast of Costa Rica, none had high ecosystem metrics despite their low coral covers. Lester et al. [18] suggested that the high variability in the ecosystem metrics for reefs with low coral cover was related to the existing range of distinct low-coral community types in the Caribbean, including those typified by sponges, gorgonians, macroalgae, or CCA [21,79,80]. Thus, the low variability in the ecosystem metrics quantified for reefs with low coral cover in this study may be because most of these reefs were dominated by turf and/or fleshy macroalgae. This is because, based on what is known about the functionality of low-coral communities, it is likely that reef communities with a greater abundance of CCA, soft corals, or sponges will be able to support a greater variety of the ecosystem services provided by coral reefs than communities dominated by turf and/or macroalgae [16,81,82]. Also, none of the reefs with low coral cover appeared to be structurally complex, with mean rugosity values of around 0.18, which may explain the overall low fish community metrics [22]. It is important to consider that the reefs surveyed were mostly small fringing and patch reefs, and that the capacity of non-coral-dominated reefs to support ecosystem functions and services may be very different in other coral reef systems [18,83].

In conclusion, fleshy macroalgae exceed coral cover in most coral reefs of the Caribbean coast of Costa Rica. Based upon the existing literature, the high macroalgae cover may be driven by water pollution from coastal development. Lower fleshy macroalgae covers were associated with higher substrate rugosity, urchin density, fish richness, total fish biomass, large fish density, and the potential fishery value of the reef. The overall high fleshy macroalgae covers and the low average variability of the fish community metrics despite the presence of marine protected areas (MPA) suggest that the current management actions are not sufficient to protect the region's coral reefs. In the future, management actions to reduce water pollution may prove useful to reduce the fleshy macroalgae cover and increase the resilience of the coral reefs. It is crucial to continue monitoring the status of the reef communities in order to evaluate the effectiveness of existing and future management actions.

Supplementary Materials: The following supporting information can be downloaded at: https://www.mdpi.com/article/10.3390/oceans4030022/s1, Table S1: Survey site coordinates and mean depth; Table S2: Coral species registered in the survey sites of the Caribbean coast of Costa Rica; Table S3: Similarity Percentages (SIMPER) analysis showing the benthic taxa that contributed the most to the overall dissimilarity between regions; Table S4: Density, biomass, and fishery value of fish species registered in the survey sites of the Caribbean coast of Costa Rica.

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