ORIGINAL ARTICLE

WILEY *marine ecology*

Spatial and temporal changes in reef fish assemblages on disturbed coral reefs, north Pacific coast of Costa Rica

Gustavo Arias-Godínez[1,2] 🅘 | Carlos Jiménez[3] | Carlos Gamboa[4] | Jorge Cortés[2,5] | Mario Espinoza[2,5] | Juan José Alvarado[2,5]

[1]Sistema de Estudios de Posgrado, Universidad de Costa Rica, San Pedro, Costa Rica

[2]Centro de Investigación en Ciencias del Mar y Limnología (CIMAR), Universidad de Costa Rica, San Pedro, Costa Rica

[3]Enalia Physis Environmental Research Centre, Nicosia, Cyprus

[4]Independent consultant, San José, Costa Rica

[5]Escuela de Biología, Universidad de Costa Rica, San Pedro, Costa Rica

Correspondence
Gustavo Arias-Godínez, Sistema de Estudios de Posgrado, Universidad de Costa Rica, San Pedro, Costa Rica.
Email: gustavoarg7@gmail.com

Abstract

Benthic structure of coral reefs determines the availability of refuges and food sources. Therefore, structural changes caused by natural and anthropogenic disturbances can have negative impacts on reef-associated communities. During the 1990s, coral reefs from Bahía Culebra were considered among the most diverse ecosystems along the Pacific coast of Costa Rica; however, recently they have undergone severe deterioration as consequence of chronic stressors such as El Niño-Southern Oscillation and harmful algal blooms. Reef fish populations in this area have also been intensely exploited. This study compared reef fish assemblages during two periods (1995–1996 and 2014–2016), to determine whether they have experienced changes as a result of natural and anthropogenic disturbances. For both periods, benthic composition and reef fish abundance were recorded using underwater visual censuses. Live coral cover (LCC) decreased from 43.09 ± 18.65% in 1995–1996 to 1.25 ± 2.42% in 2014–2016 ($U = 36$, $p < 0.05$). Macroalgal cover (%) in 2014–2016 was sixfold higher than mean values reported for the Eastern Tropical Pacific region. Mean ($±SD$) fish species richness in 1995–1996 (36.67 ± 14.20) was higher than in 2014–2016 (23.00 ± 9.14; $U = 20$, $p < 0.05$). Over 40% of reef fish orders observed in 1995–1996 were not detected in the 2014–2016 surveys, including large-bodied predators. Reduction in abundance of fish predators such as sharks, grunts, and snappers is likely attributed to changes in habitat structure. Herbivorous such as parrotfishes and pufferfishes increased their abundance at sites with low LCC, probably in response to predators decline and increased algal cover. These findings revealed significant degradation and drastic loss of structural complexity in coral reefs from Bahía Culebra, which now are dominated by macroalgae. The large reduction in structural complexity of coral reefs has resulted in the loss of diversity and key ecological roles (e.g., predation and herbivory), thus potentially reducing the resilience of the entire ecosystem.

KEYWORDS
bioerosion, diversity loss, eutrophication, habitat deterioration, resilience

1 | INTRODUCTION

Coral reefs are one of the most diverse and complex ecosystems on the planet, yet they are also one of the most threatened (Bellwood, Hughes, Folke, & Nyström, 2004; Spalding & Brown, 2015). Natural (e.g., earthquakes, storms, and hurricanes) and anthropogenic disturbances (e.g., fishing, habitat degradation, pollution, release of exotic species) are severely impacting the structural complexity and functioning of coral reefs (Gardner et al., 2005; Glynn et al., 2017; Graham, Chong-Seng, Huchery, Januchowski-Hartley, & Nash, 2014; Jackson et al., 2001). Even more concerning is the fact that climate-driven changes are threatening the health of coral reefs at a global-scale, which consequently may speed up biodiversity loss (Hughes et al., 2018).

Reef fishes are highly susceptible to disturbances that affect the structure and health of coral reefs (Gratwicke & Speight, 2005). Changes in topographic complexity (Aburto-Oropeza et al., 2015; Almany, 2004), Substrate composition (Dominici-Arosemena & Wolff, 2006), and live coral cover (LCC) (Gratwicke & Speight, 2005; Lamy, Galzin, Kulbicki, Lison de Loma, & Claudet, 2016) are arguably the most important factors influencing the distribution and abundance of reef fishes. Drastic reductions in LCC can directly affect species that feed or recruit in coral reefs (Russ & Leahy, 2017). Loss

of structural complexity is known to influence reef fish assemblages by reducing shelter and food sources, exposing fishes to threats such as predation and fishing (Rogers, Blanchard, & Mumby, 2014). Predator decline and high cover of epilithic algae can favor the release of lower trophic level consumers, thus changing the dynamics of reef fish assemblages (Bellwood, Hoey, & Hughes, 2012; Edwards et al., 2014). In some cases, species replacement may occur after significant declines in LCC, maintaining species richness, but affecting critical ecological roles (Wilson et al., 2009). However, reef fish diversity may be severely affected in degraded environments exposed to multiple and chronic natural and anthropogenic disturbances (Mouillot, Graham, Villéger, Manson, & Bellwood, 2013).

Coral reefs in Bahía Culebra (BC) were among the most diverse environments in the Pacific coast of Costa Rica (Cortés & Jiménez, 2003); however, over the past two decades, these reefs have experienced severe degradation, as a result of coral bleaching during intense El Niño-Southern Oscillation (ENSO) events and harmful algal blooms (Alvarado, Cortés, Guzman, & Reyes-Bonilla, 2016; Fernández-García, Cortés, Alvarado, & Nivia-Ruiz, 2012; Jiménez, 2001a; Jiménez, Cortés, León, & Ruíz, 2001). Moreover, marine ecosystems in BC have been historically exposed to an intense fishing pressure (Villalobos-Rojas, Herrera-Correal, Garita-Alvarado, Clarke, & Beita-Jiménez, 2014). In the early 2000s, a substantial reduction of LCC followed by the invasion
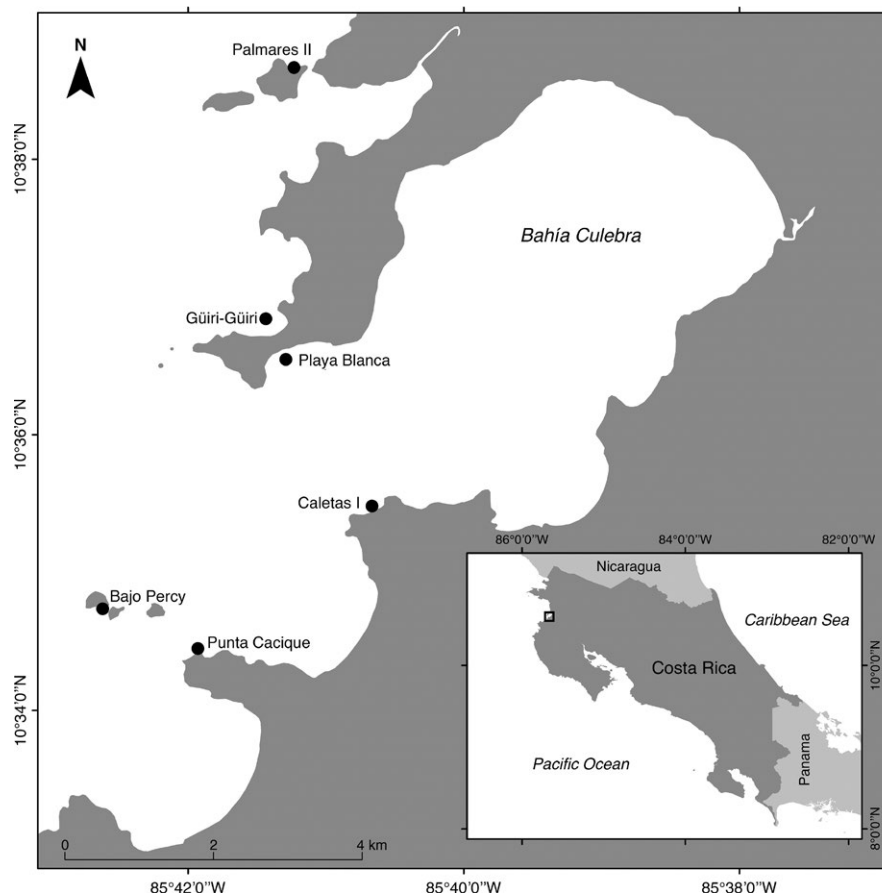

FIGURE 1 Sampling sites (black dots) in Bahía Culebra, Gulf of Papagayo, north Pacific coast of Costa Rica, during 1995–1996 and 2014–2016

of the green algae *Caulerpa sertularioides* was reported (Fernández-García et al., 2012). Macroalgae and turf algae proliferation caused an increase in the density of the sea urchin *Diadema mexicanum*, thus triggering the deterioration of calcareous structures (Alvarado et al., 2016; Alvarado, Cortés, & Reyes-Bonilla, 2012). Consequently, coral reefs of BC became less complex environments dominated by fleshy macroalgae (Alvarado et al., 2012; Fernández-García et al., 2012). However, it is unknown how changes in the benthic composition and structure of coral reefs have influenced reef fish assemblages.

Given that changes in the benthic structure of coral reefs could influence reef fish assemblages, we expected that coral reefs dominated by macroalgae (in this case *C. sertularioides*) have a lower fish species richness and abundance than reefs dominated by corals. This study compared reef fish assemblages in BC during two periods (1995–1996 and 2014–2016), based on ecological and environmental factors obtained through underwater visual censuses (UVC). We quantified the composition and abundance of reef fish assemblages during both periods and investigated spatial and temporal changes in reef fish assemblages in relation to substrate type and LCC.

2 | MATERIALS AND METHODS

2.1 | Study site

Surveys were carried out in BC (10°36′N, 85°39′W), located in the Gulf of Papagayo, north Pacific coast of Costa Rica (Figure 1). This region has a strong seasonality, with a dry season from December to April, followed by two periods of maximum precipitation from May to June and from August to October (rainy season). The increase in the intensity of the northeast Trade winds during the dry season results in the upwelling of enriched cold waters (Alfaro & Cortés, 2012; Jiménez, 2001b). During the 1990s, coral reefs in BC were mainly composed by branching coral species of the genus *Pocillopora*, with mean coverages up to 40% (Jiménez, 2001a). However, since the early 2000s, macroalgae have dominated the benthic structure of coral reefs (Alvarado et al., 2016, 2012; Fernández-García et al., 2012). A detailed description of the studied sites can be found in Jiménez (2001a).

2.2 | Temporal changes in coral reef benthic structure

The benthic structure of coral reefs in 1995–1996 was obtained from an existing dataset (Jiménez, 2001a). The LCC and the substrate types were estimated at six sites within BC in November 1995 and March and May 1996, using four belt transects per site (total *n* = 24). Transects were defined by a 10 m long chain (1.1 cm long links) placed in a straight line, perpendicular to the depth gradient and following the substrate irregularities (Jiménez, 2001a). At each transect, one diver counted the number of chain links on each substrate category. Then, count data for each substrate were transformed in percent coverages, considering the total number (*n* = 91) of chain links in each transect (Jiménez, 2001a). However, only mean LCC values and dominant substrate categories were available from the existing dataset.

The 2014–2016 surveys were carried out in July 2014, February and August 2015, and February and April 2016, at the same sites sampled in 1995–1996 (Figure 1). Three to six belt transects (*n* = 129) separated by 3 m were deployed parallel to the coast at each site. To determine the benthic composition, a 1 m² quadrant divided into 0.01 m² cells was placed every meter along each transect line (Alvarado et al., 2015). One diver counted the number of cells occupied by live coral, bleached coral, macroalgae, turf, encrusting algae, crustose calcareous algae (CCA), rubble, and sand. Count data for each substrate were transformed in percent coverages, considering the total number of cells (*n* = 100) within each quadrant.

To examine the benthic composition of coral reefs, a principal component analysis (PCA) was performed. The PCA approach was based on a correlation matrix constructed from mean cover percentages obtained for each substrate category at each site during 2014–2016. Differences in mean cover values between substrate categories were tested using a multivariate analysis of variance (MANOVA). A $\log_{10}(x + 1)$ transformation of the data was applied to satisfy the assumptions of normality and homoscedasticity. Differences in the benthic composition between study periods were showed in a canonical centroid plot. Mean LCC percentages for each period were calculated from average values obtained at each site. Differences in mean LCC percentages between periods were tested using the Mann–Whitney–Wilcoxon U (significance level =0.05).

2.3 | Temporal changes in fish diversity, composition, and abundance

Underwater visual censuses were conducted in both periods using SCUBA. During 1995–1996, UVC consisted of timed roving surveys at six sites, most of which were visited only once. Average dive time was 40.78 ± 14.18 min (total surveying time: 359 min; range: 25–73 min). Date, site, and species abundance were recorded for each dive. During 2014–2016, UVC were conducted at the same sites sampled in 1995–1996 and each site was visited at least twice. Reef fish composition and abundance were recorded using between three and six belt transects (10 × 5 m; *n* = 98) deployed parallel to the coast, separated from each other by 3 m. Surveys at each transect lasted approximately 10 min (total surveying time = 980 min). UVC in both periods included benthic, mesopelagic, and cryptic species.

To compare the reef fish diversity between 1995–1996 and 2014–2016, mean number of species (*S*) and Shannon–Wiener diversity index (*H*′, $\log_{10}$) were calculated from values obtained at each site, and differences were tested using the Mann–Whitney–Wilcoxon U. Catch per unit effort (CPUE; individuals/min) data from each fish species in each period was calculated as an indicator of abundance. Differences in mean CPUE values between study periods were tested using a bootstrapping *t* test approach (1,000 iterations). This analysis considered differences in dive time for each sampling event, equating the sampling effort between periods, and thus making abundances comparable. To standardize the diving time effort (min) from both study periods, a random sampling approach with replacement was used to select CPUE values
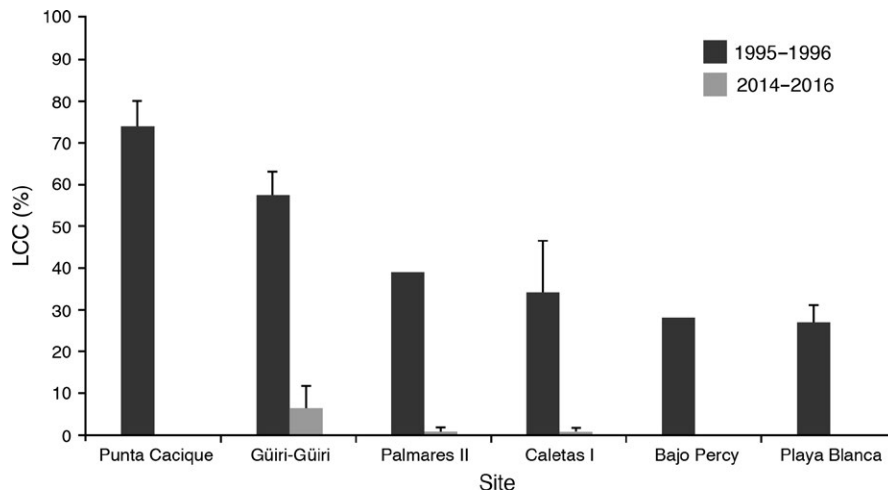
FIGURE 2 Percent mean (±*SE*) live coral cover (LCC) at six sites within Bahía Culebra in 1995–1996 and 2014–2016

from transects conducted during 2014–2016. During this process, CPUE values from reef fish species were summed to have a similar diving effort at the same sites for each period. To add variability to the 1995–1996 period, the random sampling approach (with re-placement) was conducted along the confidence interval estimated from the CPUE values obtained across all sites. Analyses were per-formed in R v.3.2.3 (R Development Core Team, 2005).

To detect spatial and temporal changes in reef fish community structure between study periods, a non-metric multidimensional scaling analysis (n-MDS, 100 restarts), followed by an analysis of similarities (ANOSIM), was performed (Clarke & Gorley, 2015). Three LCC categories (low, medium, and high) and the period (1995–1996 and 2014–2016) were defined as fixed factors a priori. The LCC categories were assigned based on Glynn, Enochs, Afflerbach, Brandtneris, and Serafy (2014): low LCC (<10%), medium LCC (10%–30%), and high LCC (>30%). According to Glynn et al. (2014), the maximum fish species richness was found at 20% LCC, while it de-clined when LCC was higher than 35%. The data matrix used to con-duct the n-MDS approach consisted of CPUE by species at each site. The CPUE data were transformed using the fourth root function, due to the predominance of rare species and the presence of outli-ers caused by the sighting of large fish schools. A Bray–Curtis sim-ilarity matrix was created from transformed CPUE values, prior to conducting the n-MDS analysis. To identify species with the greatest contribution to the dissimilarity between periods, a similarity per-centage analysis (SIMPER) was conducted (Clarke & Warwick, 2001). Species-specific differences between periods were examined using boxplots. Multivariate statistical analyses were performed with the software PRIMER 7 (Clarke & Gorley, 2015).

3 | RESULTS

3.1 | Temporal changes in coral reef benthic structure

Live coral cover recorded at six coral reefs decreased from 43.1 ± 18.6% in 1995–1996 to 1.25 ± 2.42% in 2014–2016 (Figure 2;

TABLE 1 Eigenvectors for two principal components (PC1 and PC2) from a PCA analysis based on mean cover values (%) of 11 substrate categories at six sites in Bahía Culebra during 2014–2016

Substrate category	PC1	PC2
Coral	−0.011	0.089
Bleach coral	−0.002	0.013
Crustose calcareous algae	0.000	0.063
Encrusting algae	0.000	0.000
Rhodoliths	−0.001	0.012
Sponge	−0.006	−0.015
Turf	0.361	**0.717**
Macroalgae	**−0.804**	−0.068
Rubble	0.115	−0.049
Sand	0.456	**−0.680**
Other	−0.039	−0.063

Note. Values in bold correspond to the main substrate categories that explained the variance of principal components.

U = 36, $p < 0.05$). The benthic structure of coral reefs in 2014–2016 was dominated by macroalgae, turf, and sand (Table 1; 95% of the var-iance explained); however, these three main substrates were hetero-geneously distributed among sampled sites (Figure 3; $F_{20,450}$ = 9.75, $p < 0.05$). Macroalgae (mainly *C. sertularioides*) covered more than 50% of the total sampled area in 2016, whereas reef-building corals and CCA maintained coverages lower than 5% along the 2014–2016 period (Figure 4).

3.2 | Temporal changes in fish diversity, composition, and abundance

A total of 78 species and 32 families were recorded in 1995–1996. In contrast, the 2014–2016 surveys reported 56 species and 24 families (Table 2). The mean species richness (*S*) in 1995–1996 (36.67 ± 14.20) was higher than in 2014–2016 (23.00 ± 9.14; U = 20, $p < 0.05$). Labridae (including the subfamily Scarinae) was the most
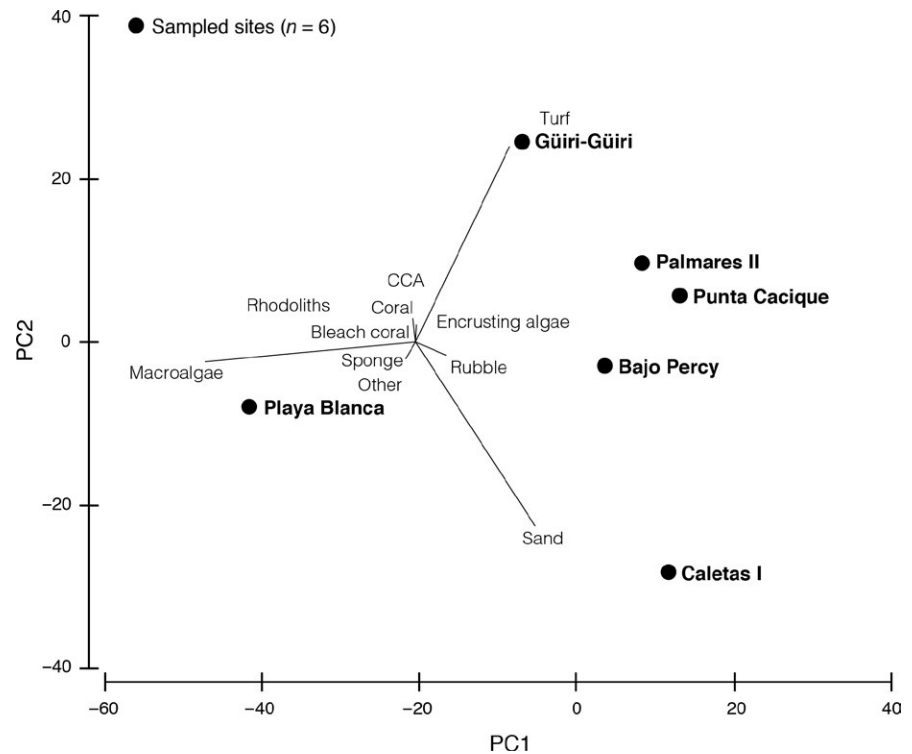
FIGURE 3 Principal component analysis (PCA) based on mean cover values (%) of 11 substrate categories observed at six sites in Bahía Culebra during 2014–2016. CCA, crustose calcareous algae
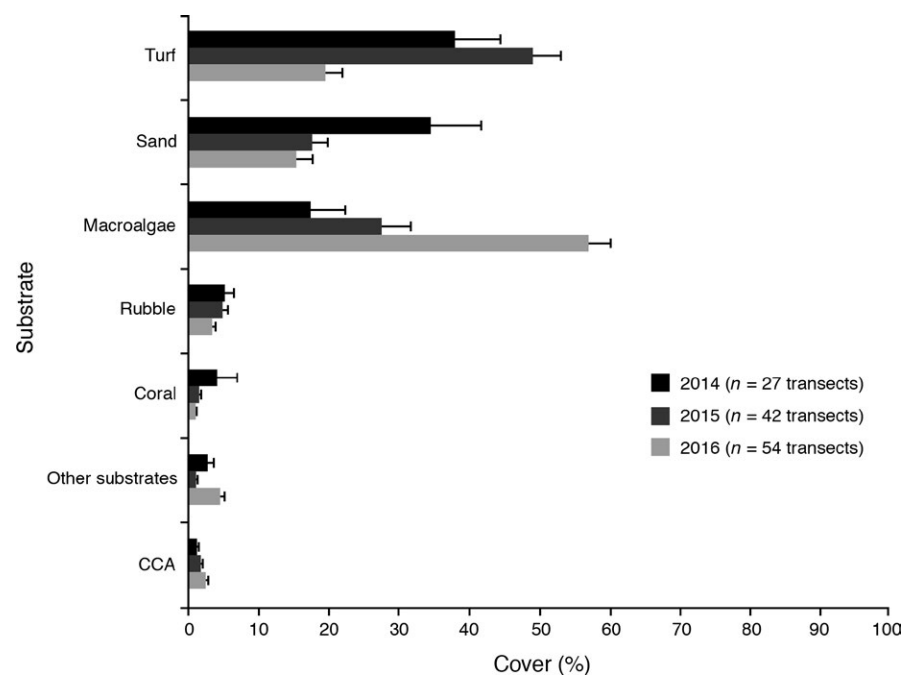

FIGURE 4 Mean (±SE) coverage (%) of seven substrate categories estimated from six sites in Bahía Culebra during 2014–2016. CCA, crustose calcareous algae

diverse family in both 1995–1996 and 2014–2016, with 10 and eight species, respectively. Pomacentridae, Serranidae, Haemulidae, and Lutjanidae (four to six species each) were some of the most diverse families in the 1990s; however, their contribution to the total species richness decreased in the 2010s, whereas the number of acanthurids (Acanthuridae) and Tetraodontiformes increased (Table 3). Reef fish diversity changes were also reflected in the mean H', which was higher in 1995–1996 (3.05 ± 0.39) than in 2014–2016 (2.32 ± 0.44; $U = 32$, $p < 0.05$). About 42% of the reef fish orders observed in coral reefs during the 1990s were absent during the 2014–2016 surveys (Table 3).

Fish abundance observed in BC was significantly greater in 1995–1996 (Mean ± SD; 80.0 ± 13.6 ind/min) than in 2014–2016 (69.4 ± 11.4 ind/min; $t = 18.02$, df = 1925.50, $p < 0.05$). *Chromis atrilobata* was the most abundant species in 1995–1996, representing around 30% of total CPUE, whereas the wrasse *Thalassoma lucasanum* was the dominant species (~38% of total fish abundance) in 2014–2016. Fish assemblages were spatially and temporally

TABLE 2 Summary of reef fish diversity at six sites sampled in Bahía Culebra during the 1995–1996 and 2014–2016 periods

Site	1995–1996				2014–2016				% of shared taxa between periods			
	Species	Genera	Families	Orders	Species	Genera	Families	Orders	Species	Genera	Families	Orders
Palmares II	52	42	26	8	26	23	13	2	37	41	44	25
Bajo Percy	51	40	23	9	27	22	16	4	37	47	70	44
Güiri-Güiri	45	34	23	6	35	29	20	6	45	54	59	71
Punta Cacique	27	23	18	6	9	9	8	2	24	33	37	33
Caletas I	24	21	15	6	25	25	16	5	29	35	48	57
Playa Blanca	21	19	14	4	16	15	12	3	37	48	73	75
Total taxa per period	78 (33)	61 (22)	33 (10)	12 (5)	56 (11)	46 (7)	25 (2)	7 (0)	51%	57%	66%	58%

Notes. Values in parentheses indicate the number of unique taxa of each period within each taxonomic category.

separated according to the CPUE obtained at each site (Figure 5; ANOSIM: $R = 0.60$, $p < 0.05$). Sites sampled in 1995–1996 were divided into two main groups, both dominated by small mesopredators, including jacks, grunts, and snappers (Figure 5). In contrast, most of the sites sampled in 2014–2016 were relatively homogeneous (60% of similarity) in terms of fish composition and abundance. Macroalgal and sandy bottoms were mainly dominated by parrotfishes (Labridae: Scarinae), Tetraodontiformes (specifically *Diodon holocanthus* and *Sufflamen verres*), and small wrasses (Labridae; Figure 5). Chaetodontids (mainly *Chaetodon humeralis*) were less abundant in degraded environments. The LCC was an important factor explaining differences between fish assemblages (Figure 5; ANOSIM: $R = 0.52$, $p < 0.05$). Pairwise ANOSIM comparisons showed differences between sites with high and low LCC ($p < 0.05$). The abundances of the main reef fish species that contributed to the dissimilarity between periods are shown in Figure 6.

4 | DISCUSSION

This study demonstrated that reef fish assemblages in BC (north Pacific, Costa Rica) were affected by structural changes in the coral reefs. In two decades (1990s–2010s), coral reefs within the bay experienced severe degradation and loss of structural complexity. Furthermore, there was strong evidence suggesting a shift from a coral to a macroalgae-dominated ecosystem, which resulted in the reduction of reef fish diversity and abundance. It is quite possible that shelter loss, decrease in water quality, and overfishing have caused the reduction in abundance of small and large mesopredators, including sharks, rays, jacks, grunts, groupers, and snappers. Predator decline resulted in the release of lower trophic level consumers such as parrotfishes, pufferfishes, and triggerfishes that increased their richness and abundance in disturbed habitats with low LCC. Natural and anthropogenic disturbances have completely changed the structure and functioning of coral reefs in BC, thus reducing their resilience and affecting the local economy.

4.1 | Temporal changes in coral reef benthic structure

Mean LCC recorded in BC during 1995–1996 (~40%) was similar to LCC from other fringing pocilloporid coral reef on a pre-disturbed state (20%–50%; Alvarez-Filip & Reyes-Bonilla, 2006; Glynn et al., 2014). During 2014–2016, LCC was below 5% in the majority of studied sites and they never exceeded 10%. Likewise, the cover of CCA (0%–1.5%) in 2014–2016 was lower than the reported (~5%) for the same reefs in the 1990s (Jiménez, 2001a). In both study periods, the CCA cover was lower than the estimated within the bay in 2010 (~60%) and the mean coverages reported for the Eastern Tropical Pacific (ETP) region (~15%; Alvarado et al., 2016; Fong, Smith, & Muthukrishnan, 2017). Macroalgae, turf, and sandy bottoms became the dominant substrates in all studied sites. According to Fong et al. (2017), turf algae typically occupy about half of benthic composition

TABLE 3 Number of fish species per family and order sighted in coral reefs of Bahía Culebra during 1995–1996 and 2014–2016

Order	Family	Species 1995–1996	Species 2014–2016
Anguilliformes	Muraenidae	3	1
Aulopiformes	Synodontidae	1	0
Beryciformes	Holocentridae	3	1
Carcharhiniformes	Sphyrnidae	2	0
	Carcharhinidae	1	0
Elopiformes	Elopidae	1	0
Myliobatiformes	Urotrygonidae	2	0
Orectolobiformes	Ginglymostomatidae	1	1
Perciformes	Labridae	10	8
	Pomacentridae	6	5
	Serranidae	6	2
	Haemulidae	5	3
	Lutjanidae	5	3
	Carangidae	3	3
	Apogonidae	2	1
	Blenniidae	2	2
	Chaetodontidae	2	2
	Cirrhitidae	2	2
	Gobiidae	2	0
	Kyphosidae	2	3
	Pomacanthidae	2	2
	Sciaenidae	2	1
	Labrisomidae	1	0
	Malacanthidae	1	1
	Sparidae	1	0
	Acanthuridae	0	2
Rajiformes	Rhinobatidae	1	0
Scorpaeniformes	Scorpaenidae	1	1
Syngnathiformes	Aulostomidae	0	1
	Fistulariidae	1	1
Tetraodontiformes	Balistidae	3	4
	Diodontidae	2	3
	Monacanthidae	1	0
	Tetraodontidae	1	3
Total		78	56

Notes. Orders in bold were only observed in 1995–1996.

in the ETP coral reefs, whereas fleshy macroalgae usually represent <10%. Although turf coverage (20%–50%) in BC during 2014–2016 was close to mean values reported for the ETP, mean macroalgae coverage was two to six times higher.

A coral-dominated state results from a dynamic equilibrium between constructive (bioaccretion) and destructive processes (mainly bioerosion and fragmentation) (Mallela & Perry, 2007). High coverages of macroalgae and turf were reported for the first time in BC in the early 2000s (Fernández-García et al., 2012). In response to increased turf algae cover, there was an increase in the density of sea urchins, which caused the deterioration of calcareous structures, including coral skeletons and CCA (Alvarado et al., 2016). In healthy coral reefs, CCA provide substrate for coral larval settlement and attachment of asexual coral recruits, contributing in this way with reef bioaccretion (Manzello, Eakin, & Glynn, 2017). However, severe damage to calcareous structures, as occurred in BC, can drastically affect the recruitment of corals, thus hindering recovery of LCC.
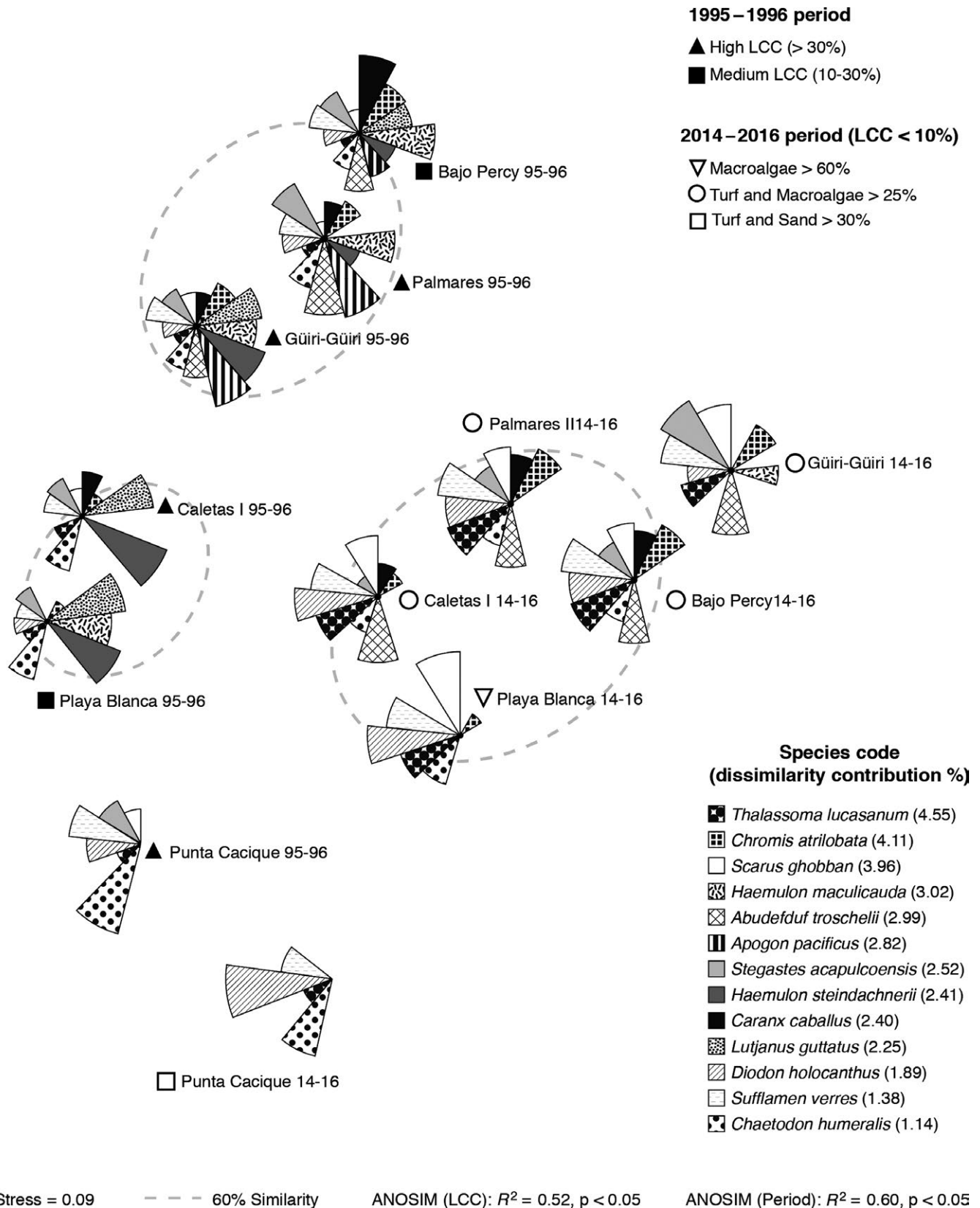
1995–1996 period
▲ High LCC (> 30%)
■ Medium LCC (10-30%)

2014–2016 period (LCC < 10%)
▽ Macroalgae > 60%
○ Turf and Macroalgae > 25%
□ Turf and Sand > 30%

**Species code
(dissimilarity contribution %)**

▧ *Thalassoma lucasanum* (4.55)
▦ *Chromis atrilobata* (4.11)
□ *Scarus ghobban* (3.96)
▨ *Haemulon maculicauda* (3.02)
⊠ *Abudefduf troschelii* (2.99)
▯▯ *Apogon pacificus* (2.82)
▨ *Stegastes acapulcoensis* (2.52)
▓ *Haemulon steindachnerii* (2.41)
■ *Caranx caballus* (2.40)
▒ *Lutjanus guttatus* (2.25)
▨ *Diodon holocanthus* (1.89)
▫ *Sufflamen verres* (1.38)
▨ *Chaetodon humeralis* (1.14)

Stress = 0.09   – – – 60% Similarity   ANOSIM (LCC): $R^2 = 0.52$, p < 0.05   ANOSIM (Period): $R^2 = 0.60$, p < 0.05

FIGURE 5 Non-metric multidimensional scaling plot of fish assemblage structure in Bahía Culebra, based on a Bray–Curtis resemblance matrix from fish relative abundance (Catch per unit effort; ind/min), according to live coral cover (LCC) and substrate categories estimated at six sites during 1995–1996 and 2014–2016. Pie plots compare the relative abundance between species that contributed most to the dissimilarity between periods, according to similarity percentage analysis

4.2 | Temporal changes in fish diversity, composition, and abundance

Species richness estimated in BC during 1995–1996 was closer to the number of species estimated for other coastal ETP coral reefs (Cortés et al., 2017). In addition, the species richness found by this study was similar to previously reported data for four coral reefs from BC in 1997, despite differences in sampling methods (roving vs. point count surveys) (Dominici-Arosemena, Brugnoli-Oliveira, Cortés-Núñez, Molina-Ureña, & Quesada-Alpizar, 2005). However, both species richness (S and H') and abundance (CPUE) found in 2014–2016 were lower than those estimated during the 1990s, revealing a shift in the fish assemblages. Reduction in fish diversity and abundance in BC could be related to structural changes in coral reefs. In the 1990s, coral reefs from BC were dominated by pocilloporid corals, which formed relatively flat and homogeneous carpets interspersed with rocky reefs and sandy bottoms (Jiménez, 2001a). Therefore, although it is possible that decline in LCC did not imply a drastic reduction in structural complexity, many fish species may have been affected by the loss of microhabitats after the invasion of a single macroalgae species. In this regard, there is evidence supporting that, in general, healthy coral reefs provide numerous microhabitats to fishes, favoring the coexistence of more species, whereas disturbed reefs exhibit fewer microhabitats and are less diverse (Kerry & Bellwood, 2011; Ledlie et al., 2007; Munday, Jones, & Caley, 2001).

There is evidence that higher taxa decrease in degraded ecosystems (Brown, Clarke, & Warwick, 2002). Therefore, upper taxonomic levels could be used as a tool to evaluate coral reef health (Saldivar-Lucio & Reyes-Bonilla, 2011). Five of 12 (42%) reef fish orders sighted in 1995–1996 were not observed in 2014–2016, including large-bodied mesopredators (*Triaenodon obesus* and *Rhinobatos productus*) and top predators (*Sphyrna lewini*). Although most of the orders absent in 2014–2016 were rare during 1995–1996, their decline may lead to the deterioration of key ecological roles, mainly of upper trophic level consumers (McCauley et al., 2012; Roff et al., 2016). This is concerning given that high abundance of large predatory species such as sharks and groupers has been identified as an important indicator of coral reef health (Aburto-Oropeza et al., 2015).

The planktivorous damselfish *C. atrilobata* and the Cortez rainbow wrasse *T. lucasanum* were the most abundant species in 1995–1996 and 2014–2016, respectively. Both species have been identified as two of the most important components of fish assemblages across the ETP, contributing with more than 60% of the total fish biomass in coastal sites (Dominici-Arosemena & Wolff, 2006; Salas, Sánchez-Godínez, & Montero-Cordero, 2015; Saldivar-Lucio & Reyes-Bonilla, 2011). Small planktivores within BC showed higher abundances in sites located in the outer side of the bay (Bajo Percy, Palmares II, and Güiri-Güiri) than in protected embayments (Caletas I and Playa Blanca). Other studies have found that planktivorous species are strongly associated with reef zones exposed to intense water movements and interconnected with pelagic food webs, including reef edges and rocky platforms (Dominici-Arosemena & Wolff, 2006; Friedlander & Parrish, 1998). However, habitat structural

changes in BC possibly affected species such as *Apogon pacificus* and *Cephalopholis colonus*, which were absent from disturbed coral reefs.

The butterflyfish *Chaetodon humeralis* was one of the species that contributed most to the dissimilarity between periods, showing a higher abundance in 1995–1996 than in 2014–2016. Butterflyfishes are highly associated with live coral reefs, as the latter provide food for both, obligate and facultative corallivorous species (Pratchett et al., 2015). Some studies have demonstrated that coral-dependent species are affected early by habitat loss, as many of them migrate or die during and after events that cause reductions in LCC (Russ & Leahy, 2017; Spalding & Jarvis, 2002). For this reason, the reduction of chaetodontids in response to LCC decline has been highlighted as one of the first symptoms of coral reef degradation (Flower et al., 2017).

Small mesopredatory fishes such as *Caranx caballus*, *Haemulon maculicauda*, and *Haemulon steindachneri* were more abundant in coral reefs with high and medium LCC than in disturbed habitats. Other commercially important species, such as the grunts *Haemulon scudderi*, *Microlepidotus brevipinnis*, the groupers *Alphestes multi-guttatus* and *Cephalopholis panamensis*, and the snappers *Lutjanus guttatus* and *Lutjanus inermis*, were only observed in 1995–1996. Mesopredatory species are often associated with complex habitats, which provide ambush sites and protection against larger predators (Kerry & Bellwood, 2011). Degradation of coral reefs in BC probably caused the reduction of microhabitats and food sources, thus exposing predatory species to intense fishing pressure. In this regard, it is important to note that grunts, snappers, and jacks are considered three of the main target groups for local fisheries (longline, gillnet, spearfishing, and sportfishing) (Villalobos-Rojas et al., 2014). Potential failures in recruitment due to habitat fragmentation in conjunction with overfishing could accelerate the decline of fish stocks, impacting not only ecosystems, but also fisheries and the local economy (Erisman et al., 2010; Graham et al., 2017).

Based on this study, herbivorous (*Scarus ghobban* and *Stegastes acapulcoensis*) and invertivorous fishes (*D. holocanthus* and *S. verres*) were more abundant in degraded than healthy coral reefs. Increase in abundance of lower trophic level consumers can be associated with predator decline and the increasing availability of turf, macroalgae, and benthic invertebrates that are left unprotected due to the decline of refuges (Glynn, 2008; Graham et al., 2017; Sandin et al., 2008). Triggerfishes and pufferfishes control the populations of sea urchins through predation, which favors the grazing on algae without damaging the reef structure (O'Leary & McClanahan, 2010). In addition, diodontids and tetraodontids can contribute to the asexual coral reproduction, through the fragmentation of colonies during their feeding activities (Palacios, Muñoz, & Zapata, 2014). However, released parrotfish and pufferfish populations can have negative effects on disturbed and overfished reefs, causing the detachment of fragile porous calcareous structures and incipient live coral colonies (Palacios et al., 2014).

Parrotfishes and sea urchins play a key role in the resilience of coral reefs, because they control macroalgae growth (Cheal et al., 2010; Idjadi, Haring, & Precht, 2010). Despite the increased
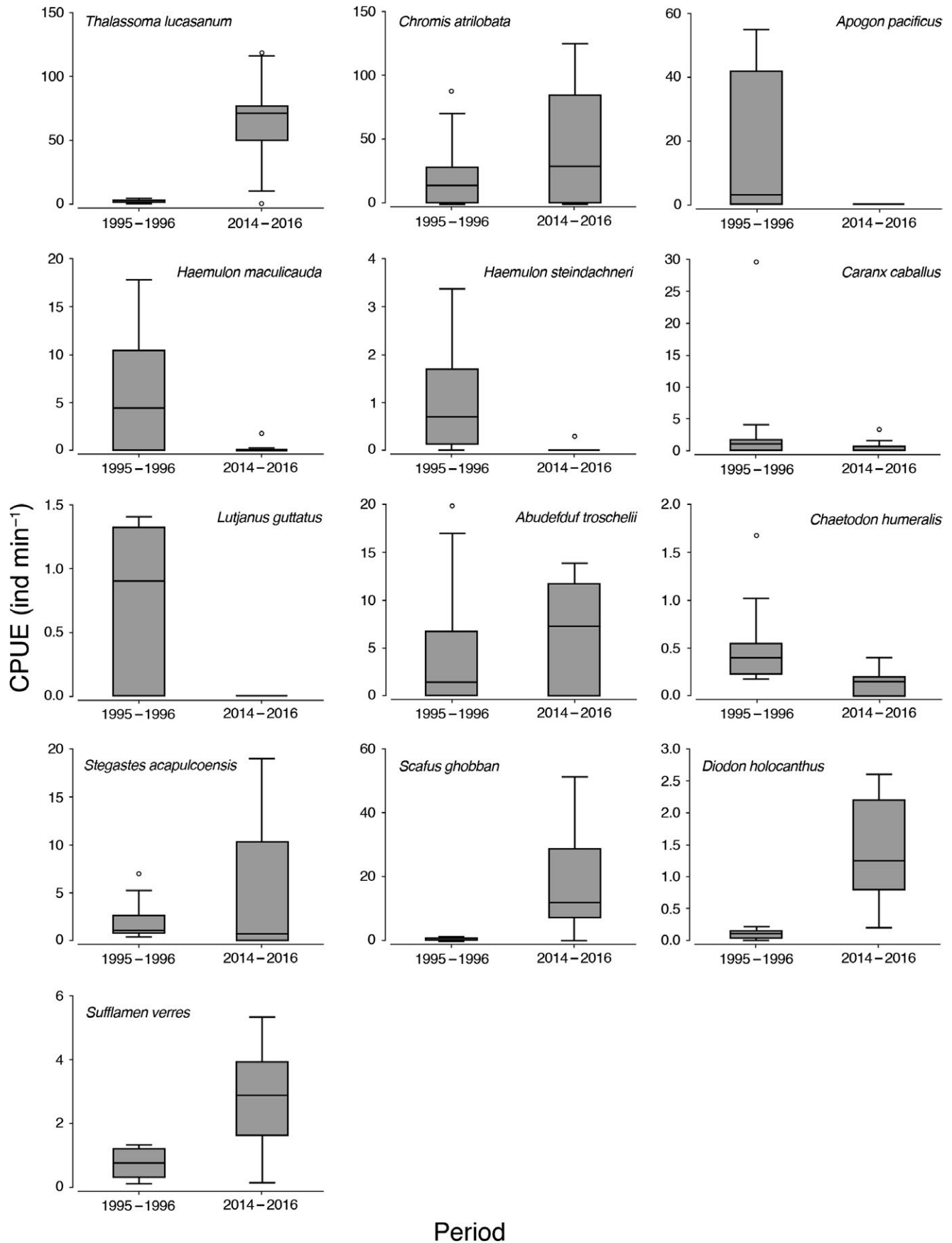
FIGURE 6 Relative abundance (CPUE; ind/min) of the main species that explain the dissimilarity between the 1995–1996 and 2014–2016 fish assemblages in Bahía Culebra, according to the similarity percentage analysis. °Empty points represent outliers

abundance of some herbivorous fishes, high coverages of fleshy macroalgae persisted in BC in 2014–2016. The proliferation of *C. sertularioides* within the bay has been attributed to the run-off of nutrients (mainly phosphate and nitrate) from coastal areas (Fernández-García et al., 2012). In addition, *Caulerpa* species present an extraordinary phenotypic and physiological plasticity, clonal reproduction, high growth rates, and toxins that give them resistance to herbivores (Erickson, Paul, Van Alstyne, & Kwiatkowski, 2006; Fernández-García et al., 2012).

4.3 | Ecological and management implications

Coral–macroalgae phase shifts may occur in coral reefs with or without human influence; however, coral reefs exposed to multiple natural and anthropogenic chronic stressors are more prone to fall into resilient macroalgae states (Fung, Seymour, & Johnson, 2011). Water eutrophication caused by non-natural nutrient supply and low herbivory on macroalgae have been underlined as the two main factors that contribute with macroalgal resilience (Dell, Longo, & Hay, 2016; Fong et al., 2017). Coral reefs in BC present many symptoms of severe degradation, including a drastic decline in LCC, high macroalgal coverages, diversity loss, a decline of corallivorous and predatory species, and high abundance of some few opportunistic fish species. Structural changes in fish assemblages of BC suggest the reduction of functional redundancy, since some ecological roles were favored (e.g., bioerosion) to the detriment of others (e.g., predation).

As in BC, pocilloporid coral reefs in Uva Island (Panama) experienced mass coral mortalities after intense ENSO events followed by a high density of bioeroders, which resulted in the decline of LCC to mean values close to 0% (Glynn et al., 2014). The recovery of LCC (~35%) took around 30 years; however, unlike BC, Uva Island did not experience the direct consequences of unregulated coastal human development (Jiménez, 2001a, 2001a, 2007; Sánchez-Noguera, 2012). Anthropogenic influence has increased the frequency and magnitude of disturbances on coral reefs, resulting in less complex and increasingly less productive environments dominated by macroalgae. If disturbances persist, the ecosystems could reach a point of no return, becoming alternative stable states unable to support the ecosystem services provided by coral reefs (Fong et al., 2017).

Reversing the damage caused to coral reefs and preventing the loss of biodiversity and ecosystem function requires of integrated coastal management approaches. The design and effective implementation of regulatory policies for the management of sewage in BC is a crucial step in the short-term. Only then, it will be possible to reduce nutrient over-enrichment and prevent current ecosystem phase shifts. Moreover, fisheries must be managed on the basis of technical and scientific criteria that assess the status of the local and regional resources. Facing these and other challenges needs a greater degree of commitment and cooperation at the inter-institutional level, including the participation of government institutions, academy, non-governmental organizations, private enterprise, and local and regional communities.

CONFLICT OF INTEREST

On behalf of all authors, the corresponding author states that there is no conflict of interest.

ORCID

Gustavo Arias-Godínez https://orcid.org/0000-0001-9807-1322

REFERENCES

Aburto-Oropeza, O., Ezcurra, E., Moxley, J., Sánchez-Rodríguez, A., Mascareñas-Osorio, I., Sánchez-Ortiz, C., … Ricketts, T. (2015). A framework to assess the health of rocky reefs linking geomorphology, community assemblage, and fish biomass. *Ecological Indicators*, *52*, 353–361. https://doi.org/10.1016/j.ecolind.2014.12.006

Alfaro, E. J., & Cortés, J. (2012). Atmospheric forcing of cool subsurface water events in Bahía Culebra, Gulf of Papagayo, Costa Rica. *Revista De Biología Tropical*, *60*(Suppl. 2), 173–186. https://doi.org/10.15517/rbt.v60i2.20001

Almany, G. R. (2004). Does increased habitat complexity reduce predation and competition in coral reef fish assemblages? *Oikos*, *106*, 275–284. https://doi.org/10.1111/j.0030-1299.2004.13193.x

Alvarado, J. J., Beita-Jiménez, A., Mena, S., Cortés, J., Fernández-García, C., & Guzmán-Mora, A. G. (2015). Ecosistemas coralinos del Área de Conservación Marina Isla del Coco, Costa Rica: análisis estructural y temporal. *Revista De Biología Tropical*, *63*(Suppl. 1), 219–259. https://doi.org/10.15517/rbt.v64i1.23423

Alvarado, J. J., Cortés, J., Guzman, H., & Reyes-Bonilla, H. (2016). Bioerosion by the sea urchin *Diadema mexicanum* along Eastern Tropical Pacific coral reefs. *Marine Ecology*, *37*, 1088–1102.

Alvarado, J. J., Cortés, J., & Reyes-Bonilla, H. (2012). Reconstruction of *Diadema mexicanum* bioerosion impact on three Costa Rican Pacific coral reefs. *Revista De Biología Tropical*, *60*(Suppl. 2), 121–132. https://doi.org/10.15517/rbt.v60i2.19975

Alvarez-Filip, L., & Reyes-Bonilla, H. (2006). Comparison of community structure and functional diversity of fishes at Cabo Pulmo coral reef, western Mexico between 1987 and 2003. *Proceedings of the 10th International Coral Reef Symposium*, *225*, 216–225.

Bellwood, D. R., Hoey, A. S., & Hughes, T. P. (2012). Human activity selectively impacts the ecosystem roles of parrotfishes on coral reefs. *Proceedings of the Royal Society B-Biological Sciences*, *279*, 1621–1629. https://doi.org/10.1098/rspb.2011.1906

Bellwood, D. R., Hughes, T. P., Folke, C., & Nyström, M. (2004). Confronting the coral reef crisis. *Nature*, *429*, 827–833. https://doi.org/10.1038/nature02691

Brown, B. E., Clarke, K. R., & Warwick, R. M. (2002). Serial patterns of biodiversity change in corals across shallow reef flats in KO Phuket,

Thailand, due to the effects of local (sedimentation) and regional (climatic) perturbations. *Marine Biology*, *141*, 21–29. https://doi.org/10.1007/s00227-002-0810-0

Cheal, A. J., McNeil, M. A., Cripps, E., Emslie, M. J., Jonker, M., Schaffelke, B., & Sweatman, H. (2010). Coral – macroalgal phase shifts or reef resilience: Links with diversity and functional roles of herbivorous fishes on the Great Barrier Reef. *Coral Reefs*, *29*, 1005–1015. https://doi.org/10.1007/s00338-010-0661-y

Clarke, K. R., & Gorley, R. N. (2015). *PRIMER v7: User manual/tutorial* (p. 300). Plymouth, UK: PRIMER-E Ltd.

Clarke, K. R., & Warwick, R. M. (2001). *An approach to statistical analysis and interpretation*, 2nd ed. (p. 203). Plymouth, UK: PRIMER-E Ltd.

Cortés, J., & Jiménez, C. (2003). Corals and coral reefs of the Pacific of Costa Rica: History, research and status. In J. Cortés (Ed.), *Latin American coral reefs* (pp. 361–385). Amsterdam, the Netherlands: Elsevier.

Cortés, J., Sibaja-Cordero, J., Hernández, J., Alvarado, J. J., Breedy, O., Cruz-Barraza, J. A., ... Zapata, F. A. (2017). Marine biodiversity of the Eastern Tropical Pacific coral reefs. In P. W. Glynn, D. Manzello & I. Enochs (Eds.), *Coral reefs of the Eastern Pacific: Persistence and loss in a dynamic environment* (pp. 203–250). Dordrecht, the Netherlands: Springer Science+Business Media.

Dell, C. L. A., Longo, G. O., & Hay, M. E. (2016). Positive feedbacks enhance macroalgal resilience on degraded coral reefs. *PLoS ONE*, *11*, e0155049. https://doi.org/10.1371/journal.pone.0155049

Dominici-Arosemena, A., Brugnoli-Oliveira, E., Cortés-Núñez, J., Molina-Ureña, H., & Quesada-Alpizar, M. (2005). Community structure of Eastern Pacific reef fishes (Gulf of Papagayo, Costa Rica). *Tecnociencia*, *7*, 19–41.

Dominici-Arosemena, A., & Wolff, M. (2006). Reef fish community structure in the Tropical Eastern Pacific (Panamá): Living on a relatively stable rocky reef environment. *Helgoland Marine Research*, *60*, 287–305. https://doi.org/10.1007/s10152-006-0045-4

Edwards, C. B., Friedlander, A. M., Green, A. G., Hardt, M. J., Sala, E., Sweatman, H. P., ... Smith, J. E. (2014). Global assessment of the status of coral reef herbivorous fishes: Evidence for fishing effects. *Proceedings of the Royal Society B-Biological Sciences*, *281*, 20131835. https://doi.org/10.1098/rspb.2013.1835

Erickson, A. A., Paul, V. J., Van Alstyne, K. L., & Kwiatkowski, L. M. (2006). Palatability of macroalgae that use different types of chemical defenses. *Journal of Chemical Ecology*, *32*, 1883–1895. https://doi.org/10.1007/s10886-006-9116-x

Erisman, B., Mascarenas, I., Paredes, G., Sadovy de Mitcheson, Y., Aburto-Oropeza, O., & Hastings, P. (2010). Seasonal, annual, and long-term trends in commercial fisheries for aggregating reef fishes in the Gulf of California, Mexico. *Fisheries Research*, *106*, 279–288. https://doi.org/10.1016/j.fishres.2010.08.007

Fernández-García, C., Cortés, J., Alvarado, J. J., & Nivia-Ruiz, J. (2012). Physical factors contributing to the benthic dominance of the alga *Caulerpa sertularioides* (Caulerpaceae, Chlorophyta) in the upwelling Bahía Culebra, north Pacific of Costa Rica. *Revista De Biología Tropical*, *60*(Suppl. 2), 93–107. https://doi.org/10.15517/rbt.v60i2.19970

Flower, J., Ortiz, J. C., Chollett, I., Abdullah, S., Castro-Sanguino, C., Hock, K., ... Mumby, P. J. (2017). Interpreting coral reef monitoring data: A guide for improved management decisions. *Ecological Indicators*, *72*, 848–869. https://doi.org/10.1016/j.ecolind.2016.09.003

Fong, P., Smith, T. B., & Muthukrishnan, R. (2017). Algal dynamic: Alternative stable states of reefs in the Eastern Tropical Pacific. In P. W. Glynn, D. Manzello & I. Enochs (Eds.), *Coral reefs of the Eastern Pacific: Persistence and loss in a dynamic environment* (pp. 339–367). Dordrecht, the Netherlands: Springer Science+Business Media.

Friedlander, A. M., & Parrish, J. D. (1998). Habitat characteristics affecting fish assemblages on a Hawaiian coral reef. *Journal of Experimental Marine Biology and Ecology*, *224*, 1–30. https://doi.org/10.1016/S0022-0981(97)00164-0

Fung, T., Seymour, R. M., & Johnson, C. R. (2011). Alternative stable states and phase shifts in coral reefs under anthropogenic stress. *Ecology*, *92*, 967–982. https://doi.org/10.1890/10-0378.1

Gardner, T. A., Côté, I. M., Gill, J. A., Grant, A., Watkinson, A. R., & Jan, N. (2005). Hurricanes and Caribbean coral reefs: Impacts, recovery patterns, and role in long-term decline. *Ecology*, *86*, 174–184. https://doi.org/10.1890/04-0141

Glynn, P. W. (2008). Food-web structure and dynamics of Eastern Tropical Pacific coral reefs: Panamá and Galápagos Islands. In T. McClanahan & G. M. Branch (Eds.), *Food webs and the dynamics of marine reefs* (pp. 185–208). New York, NY: Oxford University Press.

Glynn, P. W., Enochs, I. C., Afflerbach, J. A., Brandtneris, V. W., & Serafy, J. E. (2014). Eastern Pacific reef fish responses to coral recovery following El Niño disturbances. *Marine Ecology Progress Series*, *495*, 233–247. https://doi.org/10.3354/meps10594

Glynn, P. W., Alvarado, J. J., Banks, J. J., Cortés, J., Feingold, J. S., Jiménez, C., ... Zapata, F. A. (2017). Eastern Pacific coral reef provinces, coral community structure and composition: An overview. In P. W. Glynn, D. Manzello & I. Enochs (Eds.), *Coral reefs of the Eastern Pacific: Persistence and loss in a dynamic environment* (pp. 107–176). Dordrecht, the Netherlands: Springer Science+Business Media.

Graham, N. A. J., Chong-Seng, K. M., Huchery, C., Januchowski-Hartley, F. A., & Nash, K. L. (2014). Coral reef community composition in the context of disturbance history on the Great Barrier Reef. *Australia. Plos One*, *9*, e101204. https://doi.org/10.1371/journal.pone.0101204

Graham, N. A. J., McClanahan, T. R., MacNeil, M. A., Wilson, S. K., Cinner, J. E., Huchery, C., & Holmes, T. H. (2017). Human disruption of coral reef trophic structure. *Current Biology*, *27*, 231–236. https://doi.org/10.1016/j.cub.2016.10.062

Gratwicke, B., & Speight, M. R. (2005). The relationship between fish species richness, abundance and habitat complexity in a range of shallow tropical marine habitats. *Journal of Fish Biology*, *66*, 650–667. https://doi.org/10.1111/j.0022-1112.2005.00629.x

Hughes, T. P., Anderson, K. D., Connolly, S. R., Heron, S. F., Kerry, J. T., Lough, J. M., ... Wilson, S. K. (2018). Spatial and temporal patterns of mass bleaching of corals in the Anthropocene. *Science*, *359*, 80–83. https://doi.org/10.1126/science.aan8048

Idjadi, J. A., Haring, R. N., & Precht, W. F. (2010). Recovery of the sea urchin *Diadema antillarum* promotes scleractinian coral growth and survivorship on shallow Jamaican reefs. *Marine Ecology Progress Series*, *403*, 91–100. https://doi.org/10.3354/meps08463

Jackson, J. B. C., Kirby, M. X., Berger, W. H., Bjorndal, K. A., Botsford, L. W., Bourque, B. J., ... Warner, R. R. (2001). Historical overfishing and the recent collapse of coastal ecosystems. *Science*, *293*, 629–637. https://doi.org/10.1126/science.1059199

Jiménez, C. (2001a). Arrecifes y ambientes coralinos de Bahía Culebra, Pacífico de Costa Rica: Aspectos biológicos, económico-recreativos y de manejo. *Revista De Biología Tropical*, *49*(Suppl. 2), 215–231.

Jiménez, C. (2001b). Seawater temperature measured at the surface and at two depths (7 and 12 m) in one coral reef at Culebra Bay, Gulf of Papagayo. *Costa Rica. Revista De Biología Tropical*, *49*(Suppl. 2), 153–161.

Jiménez, C. (2007). Arrecifes coralinos ¿víctimas de los cambios? *Ambientico*, *171*, 5–7.

Jiménez, C., Cortés, J., León, A., & Ruíz, E. (2001). Coral bleaching and mortality associated with the 1997–98 El Niño in an upwelling environment in the Eastern Pacific (Gulf of Papagayo, Costa Rica). *Bulletin of Marine Science*, *69*, 151–169.

Kerry, J. T., & Bellwood, D. R. (2011). The effect of coral morphology on shelter selection by coral reef fishes. *Coral Reefs*, *31*, 415–424. https://doi.org/10.1007/s00338-011-0859-7

Lamy, T., Galzin, R., Kulbicki, M., Lison de Loma, T., & Claudet, J. (2016). Three decades of recurrent declines and recoveries in corals belie ongoing change in fish assemblages. *Coral Reefs*, *35*, 293–302. https://doi.org/10.1007/s00338-015-1371-2

Ledlie, M. H., Graham, N. A. J., Bythell, J. C., Wilson, S. K., Jennings, S., Polunin, N. V. C., & Hardcastle, J. (2007). Phase shifts and the role of herbivory in the resilience of coral reefs. *Coral Reefs*, *26*, 641–653. https://doi.org/10.1007/s00338-007-0230-1

Mallela, J., & Perry, C. T. (2007). Calcium carbonate budgets for two coral reefs affected by different terrestrial runoff regimes, Rio Bueno, Jamaica. *Coral Reefs*, *26*, 129–145. https://doi.org/10.1007/s00338-006-0169-7

Manzello, D. P., Eakin, C. M., & Glynn, P. W. (2017). Effects of global warming and ocean acidification on carbonate budgets of Eastern Pacific coral reefs. In P. W. Glynn, D. Manzello & I. Enochs (Eds.), *Coral reefs of the Eastern Pacific: Persistence and loss in a dynamic environment* (pp. 517–533). Dordrecht, the Netherlands: Springer Science+Business Media.

McCauley, D. J., Young, H. S., Dunbar, R. B., Estes, J. A., Semmens, B. X., & Micheli, F. (2012). Assessing the effects of large mobile predators on ecosystem connectivity. *Ecological Applications*, *22*, 1711–1717. https://doi.org/10.1890/11-1653.1

Mouillot, D., Graham, N. A. J., Villéger, S., Manson, N. W. H., & Bellwood, D. R. (2013). A functional approach reveals community responses to disturbances. *Trends in Ecology and Evolution*, *28*, 167–177. https://doi.org/10.1016/j.tree.2012.10.004

Munday, P. L., Jones, G. P., & Caley, M. J. (2001). Interspecific competition and coexistence in a guild of coral-dwelling fishes. *Ecology*, *82*, 2177–2189. https://doi.org/10.1890/0012-9658(2001)082[2177:ICACIA]2.0.CO;2

O'Leary, J. K., & McClanahan, T. R. (2010). Trophic cascades result in large-scale coralline algae loss through differential grazer effects. *Ecology*, *91*, 3584–3597. https://doi.org/10.1890/09-2059.1

Palacios, M. M., Muñoz, C. G., & Zapata, F. A. (2014). Fish coralli-vory on a pocilloporid reef and experimental coral responses to predation. *Coral Reefs*, *33*, 625–636. https://doi.org/10.1007/s00338-014-1173-y

Pratchett, M. S., Blowes, S. A., Coker, D., Kubacki, E., Nowicki, J., & Hoey, A. S. (2015). Indirect benefits of high coral cover for non-corallivorous butterflyfishes. *Coral Reefs*, *34*, 665–672. https://doi.org/10.1007/s00338-014-1254-y

R Development Core Team (2005). *R: A language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing. Retrieved from http://www.r-project.org/

Roff, G., Doropoulos, C., Rogers, A., Bozec, Y. M., Krueck, N. C., Aurellado, E., ... Mumby, P. J. (2016). The ecological role of sharks on coral reefs. *Trends in Ecology and Evolution*, *31*, 395–407. https://doi.org/10.1016/j.tree.2016.02.014

Rogers, A., Blanchard, J. L., & Mumby, P. J. (2014). Vulnerability of coral reef fisheries to a loss of structural complexity. *Current Biology*, *24*, 1000–1005. https://doi.org/10.1016/j.cub.2014.03.026

Russ, G. R., & Leahy, S. M. (2017). Rapid decline and decadal-scale recovery of corals and *Chaetodon* butterflyfish on Philippine coral reefs. *Marine Biology*, *164*, 29. https://doi.org/10.1007/s00227-016-3056-y

Salas, E., Sánchez-Godínez, C., & Montero-Cordero, A. (2015). Peces marinos de la Reserva Biológica Isla del Caño: Estructura de las comunidades de peces de arrecife y lista taxonómica actualizada de los peces costeros. *Revista De Biología Tropical*, *63*(Suppl. 1), 97–116.

Saldivar-Lucio, R., & Reyes-Bonilla, H. (2011). Monitoreo de la ictiofauna usando grupos taxonómicos superiores en el Parque Nacional Cabo Pulmo, México. *Revista De Biología Tropical*, *59*, 871–885. https://doi.org/10.15517/rbt.v0i0.3146

Sánchez-Noguera, C. (2012). Entre historias y culebras: más que una bahía (Bahía Culebra, Guanacaste, Costa Rica). *Revista De Biología Tropical*, *60*(Suppl. 2), 1–17. https://doi.org/10.15517/rbt.v60i2.19960

Sandin, S. A., Smith, J. E., DeMartini, E. E., Dinsdale, E. A., Donner, S. D., Friedlander, A., ... Sala, E. (2008). Baselines and degradation of coral reefs in the Northern Line Islands. *PLoS ONE*, *3*, e1548. https://doi.org/10.1371/journal.pone.0001548

Spalding, M. D., & Brown, B. E. (2015). Warm-water coral reefs and climate change. *Science*, *350*, 769–771. https://doi.org/10.1126/science.aad0349

Spalding, M. D., & Jarvis, G. E. (2002). The impact of the 1998 coral mortality on reef fish communities in the Seychelles. *Marine Pollution Bulletin*, *44*, 309–321. https://doi.org/10.1016/S0025-326X(01)00281-8

Villalobos-Rojas, F., Herrera-Correal, J., Garita-Alvarado, C. A., Clarke, T., & Beita-Jiménez, A. (2014). Actividades pesqueras dependientes de la ictiofauna en el Pacífico Norte de Costa Rica. *Revista De Biología Tropical*, *62*(Suppl. 4), 119–138. https://doi.org/10.15517/rbt.v62i4.20038

Wilson, S. K., Dolman, A. M., Cheal, A. J., Emslie, M. J., Pratchett, M. S., & Sweatman, H. P. A. (2009). Maintenance of fish diversity on disturbed coral reefs. *Coral Reefs*, *28*, 3–14. https://doi.org/10.1007/s00338-008-0431-2