



The effect of coral reef degradation on the trophic structure of reef fishes from Bahía Culebra, North Pacific coast of Costa Rica

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Abstract

Fishes play numerous key ecological roles that are critical for maintaining the structure and function of coral reefs. Natural and anthropogenic disturbances can produce structural changes in coral reef habitats, which consequently may affect the trophic structure and dynamics of reef fish assemblages. Therefore, changes in the coral cover of coral reefs, caused by disturbance events can impact the abundance of reef fishes. This study determined the effect of habitat degradation on the trophic structure of coral reef fishes from Bahía Culebra, a bay located in the north Pacific of Costa Rica. We examined whether spatial and temporal changes in live coral cover (LCC) and substrate type between two periods (1995–1996 and 2014–2016) influenced the trophic structure of coral reef fishes. While planktivorous fishes maintained similar abundances between periods, omnivorous fishes (mainly facultative corallivores) were less abundant in sites with low LCC. There was a decline in abundance of mesopredators (e.g. sharks, groupers, snappers), probably because of both shelter loss and overfishing. Macroalgae feeders, herbivores-detritivores and invertivores showed high abundance in disturbed coral reefs, which could be related to predator decline or to increased algal resource abundance. Despite high abundance of herbivorous fishes, high macroalgae coverage persisted during the 2014–2016 period. The results from this study suggest that degradation of coral reef habitats from Bahía Culebra have affected the trophic structure of reef fish assemblages, and potentially the functioning of this coastal ecosystem.

Keywords Anthropogenic disturbances · Overfishing · Phase shifts · Predators · Trophic ecology

Introduction

Coral reefs of the world are increasingly threatened by the direct and indirect impact of both natural and anthropogenic disturbances (Hughes et al. 2018). Natural events such as upwelling, storms, earthquakes and thermal oscillations (El Niño, La Niña) are responsible for shaping the structure and ecology of coral reefs (Glynn et al. 2017). However, during the last decades, human development has increased the disturbance levels on coral reefs, causing substantial changes in their structure and dynamics (Graham et al. 2017). Drastic reductions in live coral cover may induce changes in the trophic structure of fish assemblages, due to the decrease of shelter and the reduction or replacement of food resources (Graham and Nash 2013; Aburto-Oropeza et al. 2015).

Understanding the trophic structure and dynamics of reef fishes is crucial to evaluate the functionality and health of coral reef ecosystems (Roff et al. 2016). Defining functional groups within a reef, based on species morphology and diet, can provide information about how natural and anthropogenic threats affect the integrity of coral reefs (Sandin et al. 2008).

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Each fish trophic group plays a key role in maintaining a dynamic ecological equilibrium (Pratchett et al. 2014). For example, herbivores are a crucial link between primary and secondary productivity (Graham et al. 2017). Some herbivorous species regulate macroalgae populations, preventing phase shifts from coral to algal dominance (Cheal et al. 2010). Planktivorous fishes transport part of the biomass contained in the plankton to the higher trophic levels, connecting benthic and pelagic food webs (Wyatt et al. 2012). Predators exert a top-down control on their prey, thus regulating their population growth (Roff et al. 2016).

The degradation of coral reefs may lead to changes in abundance of fishes (Graham et al. 2007). Larger individuals are highly vulnerable to habitat loss, because they are easily preyed upon and overexploited (Rogers et al. 2014). A relaxed predatory pressure can cause the release of herbivores such as parrotfishes (Labridae, Scarinae) and sea urchins, which can result in higher bioerosion rates on coral reef structures (Bellwood et al. 2012). Subsequently, herbivorous fishes become the new target group for fisheries, due to the collapse of large-bodied predatory fish populations (Bellwood et al. 2012). The reduction of herbivores can favor the overgrowth of epilithic algae, leading the ecosystem towards a macroalgae-dominated environment, especially in coastal areas exposed to nutrient over-enrichment (Norström et al. 2009). Coral-macroalgal phase shifts have been frequently observed in the last decades, affecting not only coral reef ecosystems but also associated economical activities in the Great Barrier Reef, the Caribbean Sea and the Eastern Tropical Pacific (ETP) (McManus and Polsenberg 2004; Mouillot et al. 2013; Fong et al. 2017).

Bahía Culebra, in the north Pacific coast of Costa Rica, had a large cover of pocilloporid reefs during the 1990s. However, over the past two decades coral reefs experienced intense coral bleaching and mass coral mortalities caused by El Niño Southern-Oscillation (ENSO) and recurrent harmful phytoplankton blooms (Cortés and Jiménez 2003; Cortés and Reyes-Bonilla 2017). Massive coral bleaching events favored the recruitment and survival of macroalgae (Fernández-García et al. 2012). Macroalgae proliferation resulted in high densities of sea urchins, mainly *Diadema mexicanum* (Alvarado et al. 2012). High bioerosion rates caused the undermining of calcareous structures, generating severe damages on coral reef architecture (Alvarado et al. 2016). Previous work suggested that structural changes in coral reefs from Bahía Culebra have affected reef fish assemblages (Arias-Godínez et al. 2019). However, impacts on the trophic ecology of fishes have not yet been evaluated. Changes in the quality of coral reefs can affect the abundance and trophic structure of coral reef fishes, depending on the resources and microhabitats exploited by each (Alvarez-Filip et al. 2015). This study compared the trophic structure of coral reef fishes from Bahía Culebra before and after disturbances that occurred between

1995 and 1996 and 2014–2016 and that caused a substantial reduction in live coral cover, as described by Arias-Godínez et al. (2019). We tested whether spatial and temporal changes in live coral cover and substrate type influence the trophic structure of coral reef fishes.

Materials and methods

Study site

Surveys were conducted in Bahía Culebra, a bay located in the Gulf of Papagayo, at the north Pacific coast of Costa Rica (Fig. 1). This region has a strong seasonality, with a dry season from December to April, followed by two periods of precipitation from May to June and from August to October (rainy season). During the dry season, there is an increase in the intensity of the northeast Trade winds, resulting in the upwelling of nutrient-enriched cold waters (Alfaro and Cortés 2012). In the 1990s, coral reefs from Bahía Culebra were considered one of the most diverse along the Pacific coast of Costa Rica, with mean live coral coverages (LCC) up to 40% (Jiménez 2001a; Cortés and Jiménez 2003). However, in the last two decades there was a drastic loss of live coral cover (down to 5%; Alvarado et al. 2018), and the system is now dominated by macroalgae, turf and sandy bottoms (Fernández-García et al. 2012; Arias-Godínez et al. 2019).

Sampling design

For both periods (1995–1996 and 2014–2016), reef fish assemblages were surveyed using underwater visual censuses (UVC) at six sites within Bahía Culebra that harbored shallow (< 10 m depth) and nearshore coral reefs (see Arias-Godínez et al. 2019). During 1995–1996, UVC consisted of timed roving surveys and they were conducted only once at each site from November 1995 to May 1996. Average dive time was 40.78 ± 14.18 min (total dive time = 359 min; Min. = 25 min; Max. = 73 min). The number of individuals per species was recorded for each dive. The 2014–2016 surveys were conducted in July 2014, February and August 2015, and February and April 2016 at the same sites surveyed in 1995–1996 and each site was visited at least twice. Three to six 10×5 m belt transects (total $n = 98$), separated from each by 3 m, were deployed parallel to the coast at each site. Surveys lasted approximately 10 min per transect (total surveying time = 980 min). At each transect one diver counted the number of individuals per species. The benthic composition of coral reefs at each site, during each period, was obtained from Arias-Godínez et al. (2019), with the objective of explaining the reef fish trophic structure based on changes in live coral cover. Three LCC categories were defined: low (< 10%), medium (10–

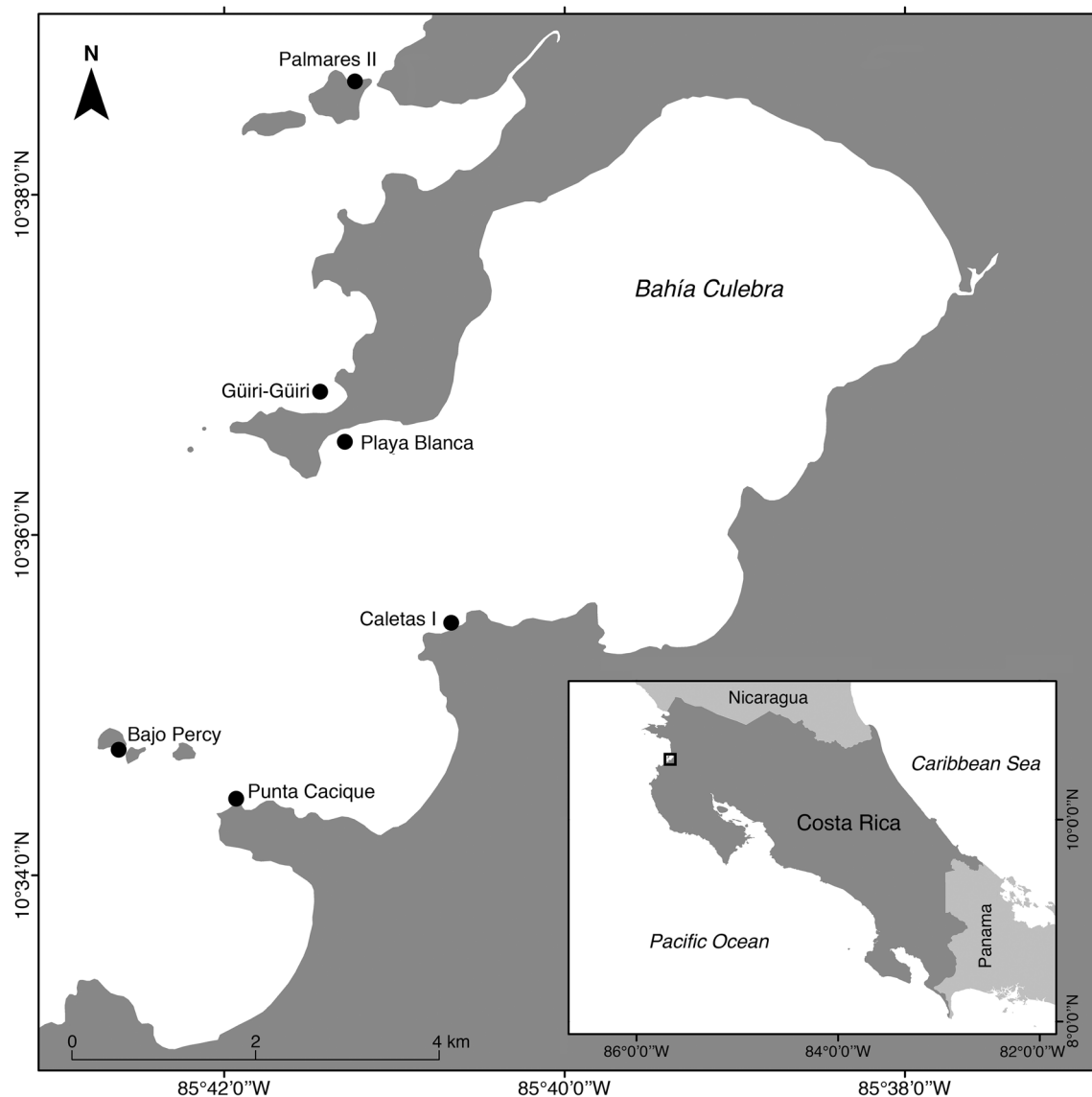


Fig. 1 Sites (black dots) sampled in Bahía Culebra, north Pacific coast of Costa Rica, during 1995–1996 and 2014–2016

30%) and high (> 30%), according to Glynn et al. (2014). Continuous LCC data were not used, because only average values were available for the 1995–1996 period.

Temporal changes in reef fish trophic structure and dynamics

To determine changes in the trophic structure of reef fish assemblages between 1995–1996 and 2014–2016, species were classified into six trophic groups following the criteria of Roff et al. (2016): (i) mesopredators, (ii) planktivores, (iii) invertivores, (iv) omnivores, (v) herbivores-detritivores and (vi) macroalgae feeders. Trophic groups were assigned using the information published on the website “*Shorefishes of the Tropical Eastern Pacific online information system*”, available at <http://biogeodb.stri.si.edu/sftep/es/pages> (Robertson

and Allen 2015). To compare changes in reef fish trophic structure between the 1995–1996 and 2014–2016 periods, the trophic groups abundance observed at each site was expressed as catch per unit effort (CPUE; ind min⁻¹). Differences in mean CPUE between periods (six sites as replicates per period) were tested using the bootstrapping t-test approach (1000 iterations). This analysis also considered the difference in dive time (min) for each sampling event, allowing a comparison of the abundances between periods. To standardize the diving time effort (min) from both study periods, a random sampling approach with replacement was used to select CPUE values of each trophic group from transects conducted in 2014–2016 completing a dive time equivalent to that obtained in 1995–1996. To add variability to the 1995–1996 period, a random sampling approach (with replacement) was conducted along the confidence interval

estimated from the CPUE values obtained across all sites. Analyses were done in R v.3.2.3 (R Development Core Team 2005).

To detect spatial and temporal changes in the trophic structure of reef fish assemblages between study periods, a non-metric Multidimensional Scaling Analysis (n-MDS) followed by Analysis of Similarities (ANOSIM) was performed (Clarke and Gorley 2015). ANOSIM generates an R value ranking between 0 (very similar assemblages) and 1 (highly dissimilar assemblages). *P*-values < 0.05 indicate significant differences between fish assemblages. In the ANOSIM, the study period (1995–1996 and 2014–2016) and LCC categories from each site were used as fixed factors. The data matrix consisted of reef fish CPUE by trophic group at each site. The CPUE data were transformed with the fourth root function, considering the predominance of rare species and the presence of outliers caused by the sighting of large fish schools (Clarke and Gorley 2015). A Bray-Curtis similarity matrix was created prior to the n-MDS analysis. The abundance of each trophic group at each site was shown using bubble plots within a multidimensional scaling plot (Clarke and Gorley 2015), both based on similarities between CPUE values. Analyses were performed using the software PRIMER v.7 (Clarke and Gorley 2015).

Results

Temporal changes in reef fish trophic structure and dynamics.

A total of 78 species, from 32 families and 12 orders were sighted during the 1995–1996 surveys. Mesopredators and invertivores were the most abundant and diverse trophic groups, with 28 and 27 species, respectively. Omnivores were represented by only two species, the Three-banded butterflyfish *Chaetodon humeralis* (Chaetodontidae) and the Leatherjacket *Aluterus scriptus* (Monacanthidae) (Table 1). In contrast, 56 species from 24 families and seven orders were recorded during the 2014–2016 surveys. Invertivores were the dominant trophic group (22 species), followed by mesopredators (15 species) and macroalgae feeders (10 species) (Table 1). Around 51% of the species observed during the 1995–1996 surveys were sighted in 2014–2016, including representatives of all trophic groups. Mesopredators was the trophic group most affected by loss of biodiversity, since 16 species (57%) recorded in 1995–1996 were not observed in 2014–2016, while only three mesopredatory species that had not been previously observed were recorded in 2014–2016. Nine invertivorous species (33%) and five planktivores (50%) were sighted in the 1990s but not in the 2010s. During this last period, three previously undetected species of invertivores and macroalgae feeders were observed. There were some herbivores-detritivores species not shared between

periods, and one omnivorous species restricted to the 1990s only (Table 1).

Planktivores were the dominant trophic group during both periods, and there were no differences in the CPUE of this trophic group between periods (Fig. 2). The CPUE of mesopredators was significantly lower in 2014–2016 relative to 1995–1996, when reefs exhibited high LCC (Fig. 2). Similar results were obtained for omnivorous fishes. However, unlike mesopredators, omnivores maintained low abundances compared with other trophic groups. The CPUE of invertivores, herbivores-detritivores and macroalgae feeders, was higher in 2014–2016 than in 1995–1996 (Fig. 2). Fish assemblages from disturbed (2014–2016) and healthy (1995–1996) coral reefs differed in terms of species composition and abundance (Fig. 3; ANOSIM: $R = 0.31$, $p < 0.05$). However, live coral cover did not explain those differences by itself (ANOSIM: $R = 0.27$, $p > 0.05$).

Discussion

This study suggests that disturbances on coral reefs can cause profound changes on trophic structure and dynamics of reef fish assemblages. In less than 20 years, coral reefs from Bahía Culebra experienced a substantial decline in coral cover, shifting to macroalgae-dominated environments (Sánchez-Noguera et al. 2018; Arias-Godínez et al. 2019). Although planktivores maintained similar abundances between study periods, other trophic groups were widely affected by coral reef degradation. Omnivores and mesopredators were more abundant in healthier reef habitats than in disturbed coral reefs. In contrast, macroalgae feeders, herbivores-detritivores and invertivores increased their abundance in macroalgae-dominated environments, probably as a response to predator decline and increased food resources such as epilithic algae and benthic invertebrates.

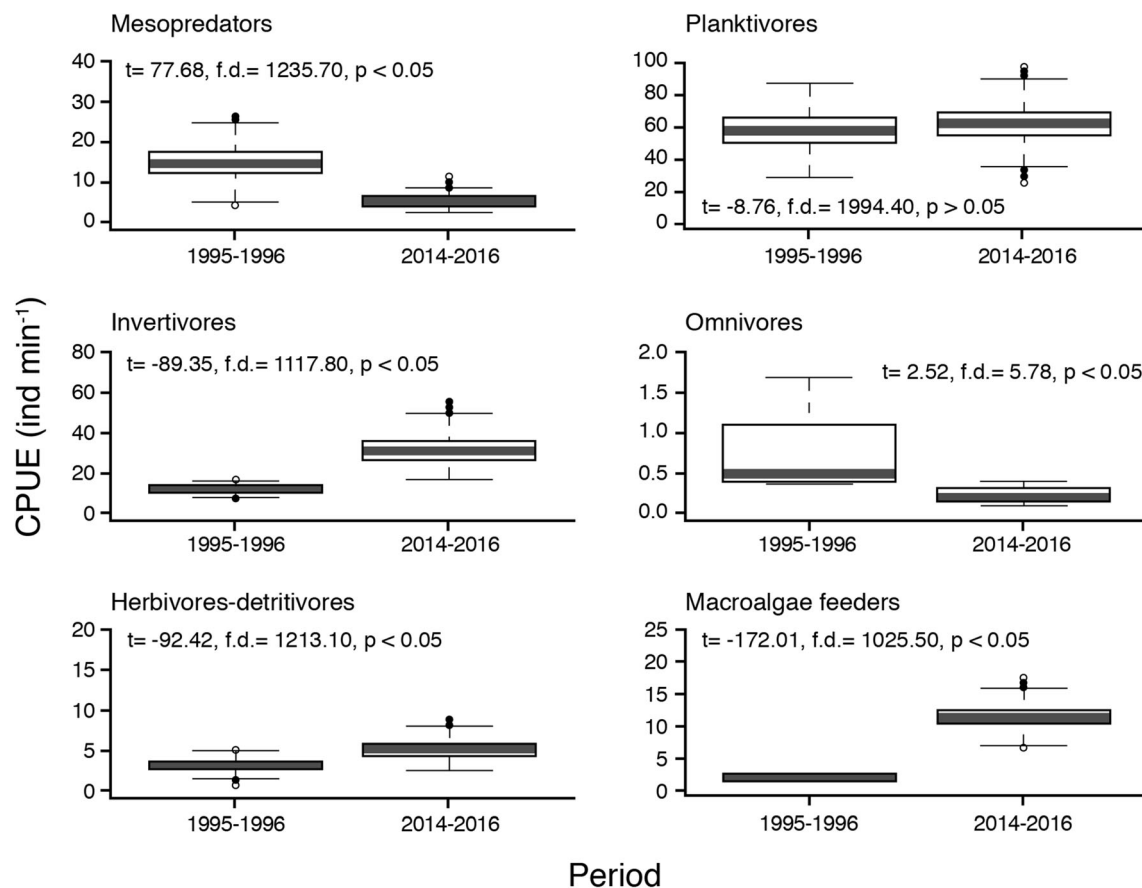
The high abundance of planktivorous fishes in both periods may be related to the ability of some species to expand their population size in upwelling areas (Cury et al. 2000). In Bahía Culebra, coastal upwelling enhances the nutrient concentration in surface waters during the dry season (Rixen et al. 2012). Moreover, artificial increases of phosphate (PO_4^{3-}) and nitrate (NO_3^-) have been detected during the non-upwelling period (Fernández-García et al. 2012). Some studies argued that the runoff of sediments, nutrients and contaminants from coastal areas could affect some reef-associated planktivorous fishes, even causing physiological stress during hypoxia periods (Breitburg 2002; Wenger et al. 2015). Nevertheless, certain small gregarious species can maintain high abundances near sewage plumes, as a result of increased plankton biomass (Guidetti et al. 2002). Some planktivorous species in Bahía Culebra may have been affected by harmful algal blooms, which frequently occurred in this disturbed area

Table 1 Number of fish species and total individuals by trophic group at coral reefs ($n = 6$) in Bahía Culebra (north Pacific of Costa Rica) during the 1995–1996 and 2014–2016 periods

| Period | Trophic group | Species number | Species (%) | Unique species per period | Individuals number | Individuals (%) |
|-----------|-------------------------|----------------|-------------|---------------------------|--------------------|-----------------|
| 1995–1996 | Mesopredators | 28 | 35.90 | 16 | 3568 | 15.18 |
| | Invertivores | 27 | 34.62 | 9 | 3602 | 15.32 |
| | Planktivores | 10 | 12.82 | 5 | 14,854 | 63.19 |
| | Macroalgae feeders | 8 | 10.26 | 1 | 431 | 1.83 |
| | Herbivores-detritivores | 3 | 3.84 | 1 | 919 | 3.91 |
| | Omnivores | 2 | 2.56 | 1 | 134 | 0.57 |
| | Total | 78 | 100 | 33 | 23,508 | 100 |
| 2014–2016 | Invertivores | 22 | 39.29 | 3 | 4793 | 47.26 |
| | Mesopredators | 15 | 26.78 | 3 | 629 | 6.20 |
| | Macroalgae feeders | 10 | 17.86 | 3 | 1188 | 11.72 |
| | Planktivores | 5 | 8.93 | 1 | 3128 | 30.85 |
| | Herbivores-detritivores | 3 | 5.36 | 1 | 393 | 3.88 |
| | Omnivores | 1 | 1.78 | 0 | 9 | 0.09 |
| | Total | 56 | 100 | 11 | 10,140 | 100 |

(Jiménez 2001b, 2007; Morales-Ramírez et al. 2001). High mortalities of corals, fishes and other marine taxa due to red tide events have occurred at other localities across the Pacific coast of Costa Rica, such as the Caño Island and Gulf of

Nicoya (Guzmán et al. 1990; Vargas-Montero and Freer 2004a, 2004b); however, direct impacts of eutrophication processes on reef fish assemblages in Bahía Culebra have not yet been evaluated.

**Fig. 2** Mean (\pm standard deviation) CPUE (ind min⁻¹) of six reef fish trophic groups observed at coral reefs ($n = 6$ sites) of Bahía Culebra (north Pacific of Costa Rica) during 1995–1996 and 2014–2016. Y-axis has different scales, according to the relative abundance of each trophic group

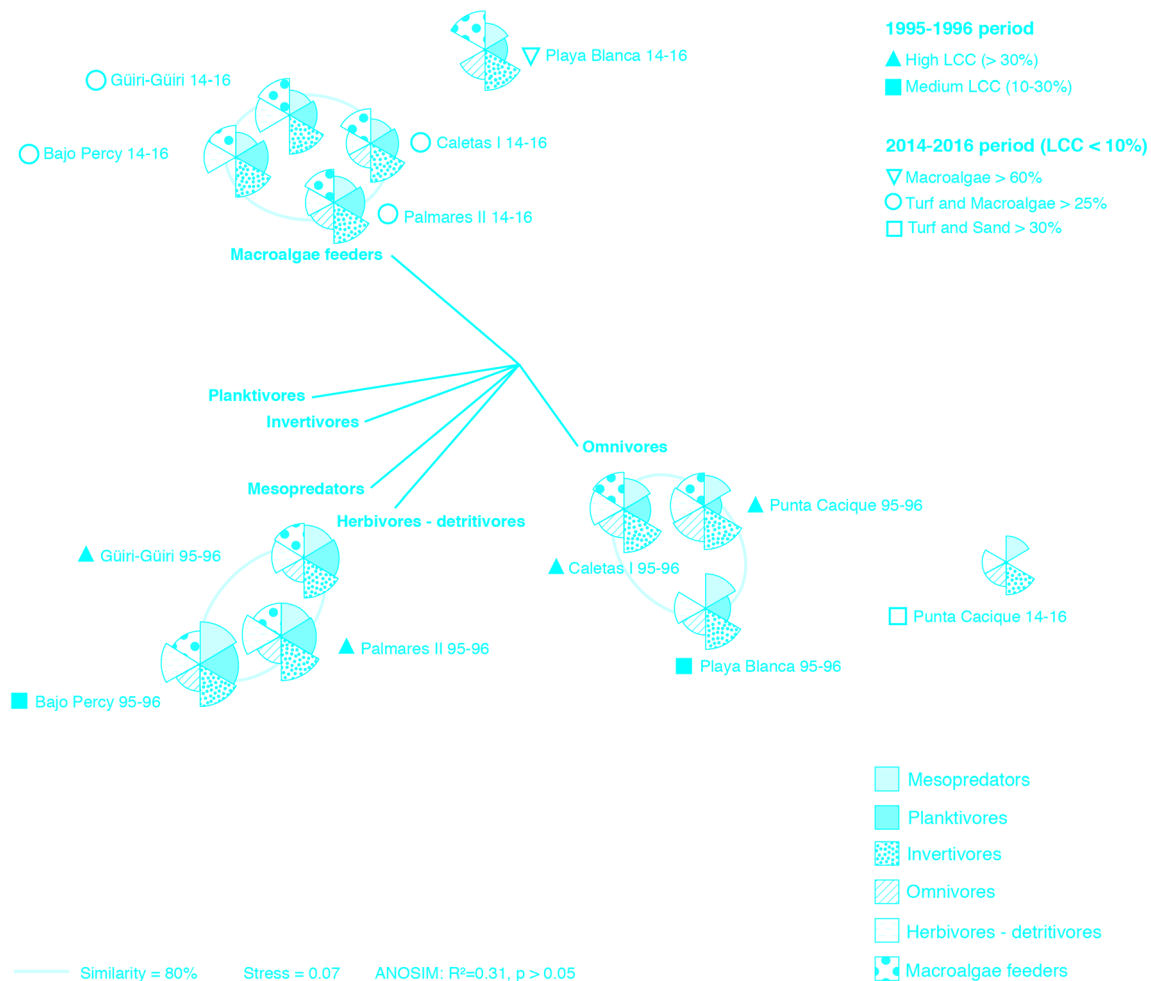


Fig. 3 Non-metric multidimensional scaling plot of fish trophic structure in Bahía Culebra (north Pacific of Costa Rica), based on a Bray-Curtis resemblance matrix constructed from the reef fish relative abundance

Omnivores (mainly represented by *C. humeralis*) were more abundant in coral reefs than in macroalgae-dominated environments. Obligatory and some facultative corallivorous fishes (such as butterflyfishes) are one of the first groups to be negatively affected by reductions in LCC, due to the decline of their food sources and substrates for larval settlement (Russ and Leahy 2017). In Uva Island (Pacific of Panama), Glynn et al. (2014) found increased abundance of facultative corallivorous species at high live coral covers and the opposite when the live coral cover decreased. Another study conducted in the Mexican Pacific found that *C. humeralis* is associated with complex substrates, including branching coral reefs (Galván-Villa 2015). Therefore, it is possible that the decrease in abundance of some facultative corallivorous species in Bahía Culebra was also related to reduction in LCC.

Mesopredators were another trophic group affected by structural changes in reef habitats from Bahía Culebra. The abundance of predatory species, particularly top predators, is often considered a reliable indicator of coral reef health (McCauley et al. 2012; Aburto-Oropeza et al. 2015). This is

(CPUE; ind min⁻¹). Pie plots compare the relative abundance between trophic groups (color code) at each site according to live coral cover (LCC) and period (1995–1996 and 2014–2016)

supported by studies conducted at healthy and relatively isolated reefs (e.g. Cocos Island), where predatory species dominate over other trophic groups (Friedlander et al. 2012). Although biomass-based (t ha⁻¹) comparisons were not possible in the present study, the CPUE of mesopredatory fishes was consistently higher when coral reefs in Bahía Culebra showed no signals of severe degradation. Large-bodied predators such as the Scalloped Hammerhead shark *Sphyrna lewini* and the Whitetip shark *Triaenodon obesus* were sighted in 1995–1996, but not during 2014–2016. Moreover, commercially important mesopredatory fishes such as *Alphistes multiguttatus*, *Cephalopholis panamensis*, *Haemulon scudder* and *Lutjanus guttatus* were detected only during the first period, when the reef structure remained intact (Arias-Godínez et al. 2019). Marine ecosystems in the north Pacific coast of Costa Rica have been exposed to intense fishing pressure in the last decades (Villalobos-Rojas et al. 2014; Beita-Jiménez et al. 2019). As a result, there was a decrease in catch rates of reef-associated mesopredators, such as groupers and snappers (Villalobos-Rojas et al. 2014).

Predator decline often causes the release of their prey, especially if large predatory fishes are removed from the system (Sandin and Zgliczynski 2015; Graham et al. 2017). The predominance of lower trophic level consumers over top-predatory and mesopredatory fishes often occurs on degraded and overfished marine ecosystems (Ruppert et al. 2013). This is of concern in Bahía Culebra, because the abundance of invertivores, macroalgae feeders and herbivores-detritivores was higher in macroalgal-dominated than in coral-dominated ecosystems. Increase in abundance of the Blue-barred parrotfish *Scarus ghobban* was reported in disturbed environments during the 2014–2016 period, relative to non-disturbed coral reefs surveyed in 1995–1996. Moreover, the Orangeside triggerfish *Sufflamen verres* and the Longspined porcupinefish *Diodon holocanthus* were common and abundant components of fish assemblages in macroalgae-dominated environments (Arias-Godínez et al. 2019). Both, herbivorous and benthic invertivorous fishes contribute positively to the balance of carbonates in coral reefs when their populations are under effective top-down controls (Mallela and Perry 2007; Bellwood et al. 2012), thus their presence on degraded reefs within Bahía Culebra may help reverse reef degradation over time. Macroalgae feeders favor the growth of corals and crustose calcareous algae (CCA) by removing epilithic macroalgae species (O’Leary and McClanahan 2010). In contrast, benthic invertivores feed on bioeroding organisms such as bivalves and sea urchins, thus preventing high bioerosion rates (Tuya et al. 2004). However, there is still a concern because under relaxed predation pressure, species such as parrotfishes, pufferfishes and triggerfishes may cause damages on reef calcareous structures, as a result of their scraping and excavatory feeding behaviors (O’Leary and McClanahan 2010; Burkepile 2012; Palacios et al. 2014; Adam et al. 2015).

The invasion of the opportunistic green macroalgae *Caulerpa sertularioides* in the early 2000s favored the population growth of sea urchins in Bahía Culebra (Alvarado et al. 2012; Fernández-García et al. 2012). The high density of the sea urchin *D. mexicanum* caused severe damages on calcareous structures, thus reducing the structural complexity of coral reefs (Alvarado et al. 2012, 2016). It has been proposed that *Diadema* populations were favored not only by the increase in algal cover, but also by the decrease of predators (Alvarado et al. 2012). This hypothesis agrees with studies from other sites in the Pacific, where depletion of predator populations resulted in high densities of bioeroders (Sonnenholzner et al. 2009; Vermeij et al. 2010).

Despite the increased abundance of macroalgae feeder fishes in Bahía Culebra, high macroalgae coverage dominated over corals in 2014–2016. The evidence provided by another study suggests that macroalgae-dominated environments within the bay are maintained by high growth rates of *C. sertularioides*, which are enhanced

by nutrient over-enrichment (Fernández-García et al. 2012). In addition, *Caulerpa* species produce toxins as defense against herbivores, which may have a negative impact on grazing rates by herbivorous fishes (Davis et al. 2005).

Differences in LCC between sites were not a conclusive factor to explain trophic changes at the community level in coral reefs of Bahía Culebra; however, comparisons between periods revealed shifts in the trophic structure and dynamics of fish assemblages. Disruptions in top-down trophic cascades have been underlined as one of the most important causes of coral reef degradation (Roff et al. 2016). However, bottom-up processes (e.g. loss of structural complexity and failures in recruitment) can also impact the resilience of coral reefs (Ruppert et al. 2016). The results obtained by the present study suggest that both, top-down and bottom-up mechanisms have favored the persistence of macroalgae-dominated environments in sites previously occupied by complex coral reefs. Terrestrial and marine ecosystems in Bahía Culebra have been exposed to multiple natural and anthropogenic stressors over time (Sánchez-Noguera 2012). Some natural disturbances, for example algal blooms and red tides, have been enhanced by human impacts such as water eutrophication and sedimentation (Jiménez 2001a, 2007; Fernández-García et al. 2012). Thus, the multiple and synergistic influence of disturbances makes it difficult to pinpoint the main cause of coral reef degradation.

This study was not able to assess the influence of the upwelling events on the reef fish assemblages, due to data limitations at spatial and temporal scales, especially for the 1995–1996 period. This issue, did not allow to answer how much the trophic shifts, attributed in first instance to changes in benthic composition, were influenced by seasonal patterns. In this regard, the present work offers an overview of the trophic changes in the fish community, based on the comparison of two clearly identified reef states (degraded and healthy). However, evidence gathered by a previous study conducted in Bahía Culebra from March to October 1997, support the strong influence of variables such as substrate type and structural complexity on the fish assemblages in that area. The researchers found that fishes could be consistently clustered in four main groups based on the physical characteristics of their habitat, including not only substrate type but depth. They argued, their findings suggested that spatial patterns could be stronger than the temporal ones to explain the way in which the fish community was structured (Dominici-Arosemena et al. 2005). Future studies, addressing additional influencing variables (e.g. sea surface temperature, season and depth) could clarify the relative contribution of the forces in charge of shaping the structure and functioning of reef fish communities in upwelling areas.

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Compliance with ethical standards

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

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