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Drivers of reef fish assemblages in an upwelling region from the Eastern Tropical Pacific Ocean

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Abstract

Reef fish assemblages are exposed to a wide range of anthropogenic threats as well as chronic natural disturbances. In upwelling regions, for example, there is a seasonal influx of cool nutrient-rich waters that may shape the structure and composition of reef fish assemblages. Given that climate change may disrupt the natural oceanographic processes by altering the frequency and strength of natural disturbances, understanding how fish assemblages respond to upwelling events is essential to effectively manage reef ecosystems under changing ocean conditions. This study used the baited remote underwater video stations (BRUVS) and the traditional underwater visual census (UVC) to investigate the spatiotemporal patterns of reef fish assemblages in an upwelling region in the North Pacific of Costa Rica. A total of 183 reef fish species from 60 families were recorded, of which 166 species were detected using BRUVS and 122 using UVC. Only 66% of all species were detected using both methods. This study showed that the upwelling had an important role in shaping reef fish assemblages in this region, but there was also a significant interaction between upwelling and location. In addition, other drivers such as habitat complexity and habitat composition had an effect on reef fish abundances and species. To authors' knowledge, this is the first study in the Eastern Tropical Pacific that combines BRUVS and UVC to monitor reef fish assemblages in an upwelling region, which provides more detailed information to assess the state of reef ecosystems in response to multiple threats and changing ocean conditions.

KEYWORDS
biodiversity, conservation management, fish survey, overfishing, rocky reefs

1 | INTRODUCTION

Understanding processes that shape the distribution and abundance of fish assemblages is crucial given their role in reef ecosystem dynamics (Wilson *et al*., 2006). Reef fish assemblages are exposed to not just a wide range of anthropogenic threats (Kennedy *et al*., 2013; Worm *et al*., 2006) but also climate-driven changes, which are already impacting the functioning of reef fish assemblages at a global scale, speeding up the loss of biodiversity and reducing their resilience to multiple chronic stressors (Hughes *et al*., 2017; Munday *et al*., 2008; Pandolfi *et al*., 2011). Given that climate change may increase the frequency and strength of natural disturbances (Cai *et al*., 2015; Sydeman *et al*., 2014), understanding how reef fish assemblages respond to these types of events is essential to assess the potential impacts on coral reef ecosystems (Bestion and Cote, 2018; FAO, 2014; Worm *et al*., 2006).

Natural disturbances such as seasonal upwellings occur in many regions and are known to affect the distribution and composition of fishes (Guarderas Sevilla, 2019; Pérez-Matus *et al*., 2017; Sato *et al*., 2018). Seasonal upwellings typically bring cool nutrient-rich water from the bottom, enhancing coastal productivity and biodiversity (Stuhldreier *et al*., 2015). In some areas, for example, coastal upwellings can reduce water temperatures by as much as 10–15°C, which have important repercussions in fish physiology and reproduction (Parsons *et al*., 2016; Roth *et al*., 2015). Temperature changes can affect fish larval duration, growth and reproduction (Green and Fisher, 2004; Miller *et al*., 2015) but may also impact predator–prey behaviours by enhancing the predation success rate (Allan *et al*., 2015). Some species seem to adapt to these variable conditions by adjusting their reproductive strategies and taking advantage of seasonal food resources available for the offspring due to higher productivity during upwelling (Cubillos *et al*., 2001). Others have been observed to move away from upwelling areas to avoid colder waters (Sato *et al*., 2018). Nevertheless, there is still a limited understanding of how seasonal upwellings affect the distribution and composition of fish assemblages in tropical regions.

In the Eastern Tropical Pacific Ocean, there are three main upwelling regions: the Bowl of Tehuantepec in Mexico, the Bay of Panama and the Thermal Dome of Costa Rica (Lavín *et al*., 2006). The Thermal Dome is located in the North Pacific of Costa Rica, and this seasonal upwelling is known to modify the structure and dynamics of marine communities, speeding up coral growth rates, algae dominance and the settlement of sessile invertebrate (Fernández-García *et al*., 2012; Jiménez and Cortés, 2003; Roth *et al*., 2015). Recent studies in the North Pacific of Costa Rica have provided important information on how fish assemblages are influenced by the state of the reef (Arias-Godínez *et al*., 2019) and habitat protection (Beita-Jiménez *et al*., 2019). Nevertheless, it is still unclear whether seasonal upwelling events are also a major driver of reef fish assemblages in this region.

Numerous studies have shown that habitat composition, habitat complexity and depth are important drivers of the distribution and diversity of reef fishes (Cheal *et al*., 2017; Eggertsen *et al*., 2019; Ferrari *et al*., 2017). Structurally complex habitats tend to be more diverse and productive, mainly because they provide additional shelter and resources to a wide range of species (Ferrari *et al*., 2017). In addition, changes in reef fish species richness and abundance with depth have been attributed to changes in habitat composition, light and temperature (Garcia-Sais, 2010; Kane and Tissot, 2017). Nevertheless, information about the interaction of these drivers with seasonal upwelling events is scarce.

Reef fish assemblages have traditionally been studied using underwater visual census (UVC), an accessible technique, but dependent on diver experience and limited by time, depth, visibility and suitable weather conditions (Caldwell *et al*., 2016; Colton and Swearer, 2010). Divers can alter the behaviour of fish through noise generated by their diving gear, which may underestimate the presence of key species such as predatory fishes (Dickens *et al*., 2011; Lindfield *et al*., 2014). Baited remote underwater video stations (BRUVS) are becoming an alternative approach to UVC, providing a less-invasive method to quantify fish abundances and species richness in a wide range of habitats and depths (Espinoza *et al*., 2020; Lowry *et al*., 2012). The use of BRUVS reduces disturbances such as noise, visual distraction and fear-induced effects produced by divers (Dickens *et al*., 2011; Lindfield *et al*., 2014). Moreover, the use of bait increases the probability of encountering predators, which are a key ecological group that is commonly targeted by fisheries (Dorman *et al*., 2012).

This study provided the first detailed examination of reef fish assemblages using UVC and BRUVS in an upwelling region from the Eastern Tropical Pacific. In particular, it was determined how the seasonal upwelling and other key habitat and environmental drivers affect the abundance and diversity of reef fish in the North Pacific of Costa Rica. Seasonal upwelling is associated with changes in water temperature and productivity, which is expected to be a major driver shaping reef fish assemblages in this region (Pérez-Matus *et al*., 2017; Roth *et al*., 2015).

2 | MATERIALS AND METHODS

The care and use of experimental animals complied with SINAC-Costa Rica animal welfare laws, guidelines and policies as approved by R-SINAC-ACG-PI-029-2018/R-SINAC-ACG-PI-034-2019.

2.1 | Study site

This study was conducted from 2017 to 2019 in the Islas Murciélago Archipelago (10° 51′ 27.8″ N, 85° 54′ 39.9″ W) and the Gulf of Santa Elena (10° 57′ 41.0″ N, 85° 43′ 46.5″ W), North Pacific of Costa Rica (Figure 1). The Islas Murciélago Archipelago consists of 5 islands and 10 islets, ranging in size from a few square metres to *c*. 1 km^2 (Denyer *et al*., 2005). This location was declared a no-take marine-protected area (MPA) in 1987 and provides *c*. 460 km^2 of marine protection in the surrounding areas (Alvarado *et al*., 2012). Islas Murciélago are part of the Guanacaste Marine Conservation Area, a region known for its high biodiversity and productivity (Cortés, 1997). In the Gulf of Santa Elena, two locations were surveyed: Isla Loros and Bajo Rojo. These are two relatively small rocky reef formations (covering a total area of *c*. 15 km^2), which are currently not protected.

The North Pacific of Costa Rica is characterized by the presence of several species of corals, including *Pocillopora damicornis*, one of the most common species in shallow waters (<30 m), and *Psammocora stellata*, which tends to be more abundant in deeper waters. Other species such as *Pocillopora eydouxi* and *Pavona gigantea* corals are usually found in low densities in similar areas, typically forming small reef patches (Cortés, 1997). Coral distribution and composition in this region is quite unique and is partially explained by the seasonal upwelling event between December and April (Cortés, 1997; 2014) and a strong wave action (Alfaro *et al*., 2012). During the upwelling season, water temperature can drop to 15°C, whereas during the rest of the year, water temperatures fluctuate from 28 to 34°C (Alfaro and Cortés, 2012; Stuhldreier *et al*., 2015).

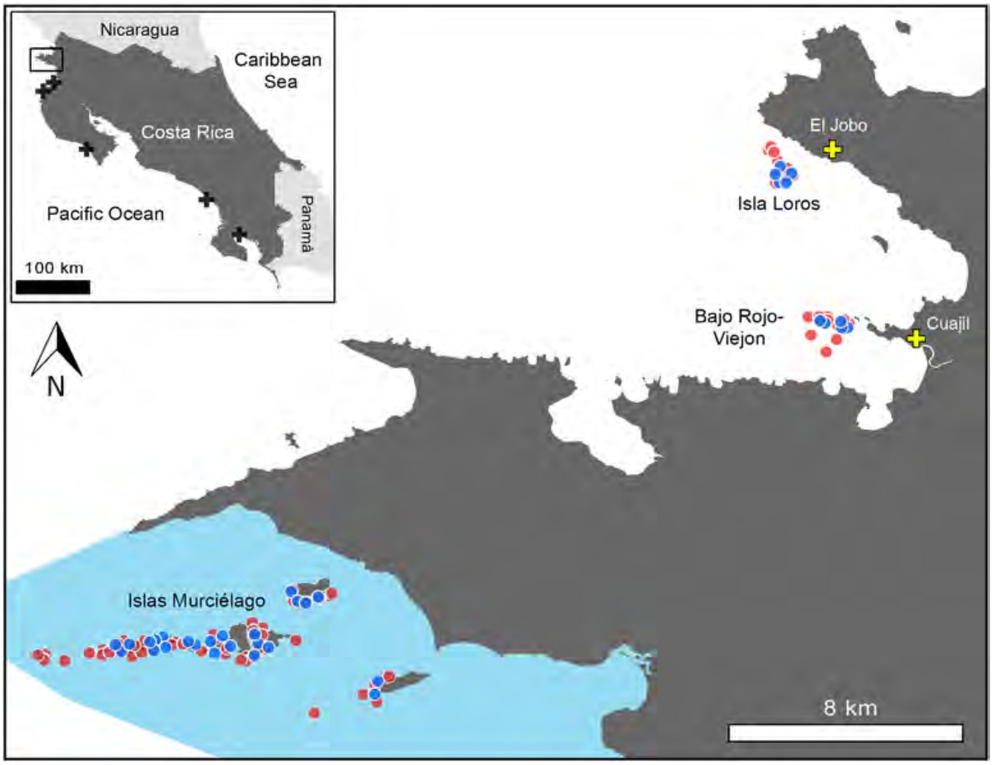

FIGURE 1 Map of the study region in the North Pacific of Costa Rica showing the location of baited remote underwater video stations (BRUVS, red dots) and underwater visual census (UVC, blue dots). The blue polygon represents the extent of the marine-protected area of the Santa Rosa National Park. El Jobo and Cuajiniquil (Cuajil) are the main fishing communities (represented by the crosses) in the surrounding areas

2.2 | BRUVS set-up

Two types of BRUVS were used to survey reef fishes in different environments: (a) benthic BRUVS – a pyramid-shape steel frame placed on the seabed (Cappo *et al*., 2007), and (b) semi-pelagic BRUVS – a triangle-shape steel frame anchored to the bottom with a small weight and suspended 1 m in the water column by an underwater buoy system (see Acuña-Marrero *et al*., 2018). Benthic BRUVS were used to record species associated with a relatively flat seafloor, whereas semi-pelagic BRUVS were used to record species in high topographic structures (*e.g*., underwater pinnacles) or irregular bottoms. Both camera set-up (GoPro Hero4; GoPro,San Mateo, CA; www.gopro.com) and bait arms were identical in benthic and semi-pelagic BRUVS. Each video was recorded at a resolution of 1080p at 60 frames per second with a sampling period greater than 90 min (101.4 ± 24.8 min). Detachable bait arms, consisting of a metal bar, and a plastic mesh cylinder containing 1 kg of crushed mackerel (*Scomber japonicus*) were used as bait. Polystyrene surface floats were attached by an 8 mm polypropylene rope to facilitate the retrieval of steel frames. BRUVS were deployed with a distance greater than 400 m from each other to reduce the probability of recounting the same individuals (Espinoza *et al*., 2014).

2.3 | Sampling design

BRUVS and UVC were used to quantify the distribution and abundance of reef fish across locations and seasons (upwelling and non-upwelling). A total of 142 BRUVS (125 benthic and 17 semi-pelagic) were deployed. Given that most of the deployments were benthic and there were no significant differences in species richness between BRUVS set-up, all deployments were analysed together, hereafter referred to as BRUVS. About half of the BRUVS were deployed in Islas Murciélago (n = 67), and the other half was equally distributed between Isla Loros (n = 38) and Bajo Rojo (n = 37) due to differences in the size (km^2) of each location (Figure 1). Seventy-three BRUVS were deployed during the upwelling season, and 69 were deployed during the non-upwelling season.

A temperature logger (ONSET Hobo Pendant UA; ONSET Computer Corporation, Bourne; www.onsetcomp.com) was attached to each BRUVS to record water temperature, which ranged from 20.2 to 34.2°C with a mean temperature of 27.4 ± 2.4°C. In addition, the date/time, location (latitude/longitude) and depth of each BRUVS were recorded. BRUVS were deployed at depths ranging from 3.5 to 32.4 m (mean ± s.d.: 10.9 ± 5.1 m). Video footage was analysed using the software EventMeasure (SeaGIS, Bacchus Marsh, Australia; www.seagis.com.au). From each video, the maximum number of individuals of each species observed in a single video frame (MaxN) was recorded (Santana-Garcon *et al*., 2014). To account for differences in soak times between stations, the relative abundance was calculated as the MaxN per hour (MaxN h^{-1}) from each fish species (Parker *et al*., 2016). All individuals were identified to the lowest taxonomic level using local fishing guides and expert criteria if needed (Robertson and Allen, 2015).

For UVC, 119 belt transects were conducted, covering an area of 30 × 5 m (150 m^2) using scuba. The depth of UVC ranged from 3 to 17 m (mean ± s.d.: 8.6 ± 2.8 m). The abundance and size frequency of each species within each transect were estimated, and the date/time, location (latitude/longitude), water temperature and depth were recorded. The temperature during UVC ranged from 18 to 31°C with a mean temperature of 27.1 ± 2.7°C. Many transects were also conducted in Islas Murciélago (n = 55) than in Isla Loros (n = 32) and Bajo Rojo (n = 32) (Figure 1). A total of 56 UVCs were conducted during the upwelling, and 63 were conducted during the non-upwelling season. To determine if sufficient BRUVS and UVC were conducted at each location, rarefaction curves were created (Supporting Information Figure S1). For more information on the sampling design of BRUVS and UVC surveys, see Supporting Information Table S1.

2.4 | Habitat structure and composition

Habitat composition was estimated by analysing still images from BRUVS and directly from UVC. For still images from BRUVS, a matrix of 20 × 20 (totally 400) evenly distributed red dots that were overlaid on the image to assign and count substrate types as a proxy of habitats available was used (Supporting Information Figure S2). Based on this information, the proportion of each habitat in relation to the total number of overlapping points on quantifiable habitats was estimated (see Espinoza *et al*., in review). Camera stations that did not contain any images with quantifiable bottom cover (9.6%) were not considered for the analysis. Classification and estimation of habitat cover were made by at least two independent observers and averaged across observers.

Habitat types were classified as reef-building coral, turf, macroalgae, rock, sand (including rubble) and others (*i.e*., anemones, barnacles, cyanobacteria, octocoral, sponges, soft coral and tunicates). The dominant habitat types recorded by BRUVS were sand/rubble (35.2%), turf (29.7%), rock (14.6%) and others (7%). The mean coral cover was 4.2% and ranged from 0% to 48.9%. In addition, images were classified as having low (1), medium (2) or high (3) visibility and topographic complexity. BRUVS with average values of visibility below 1.5 across observers were not included in the analysis.

For UVC, the topographic complexity was estimated using a 10 m long chain, which was placed next to the transect line, following the substrate rugosity (as an indicator of topographic complexity). The rugosity index (RI) was calculated by dividing the distance of the chain on the substrate with the distance of the extended chain, which was then subtracted from 1 (Friedlander and Parrish, 1998). For each transect, three values of RI were estimated. In addition, the chain was marked every metre to record the type of substrate present (hereafter referred to as "habitat").

Habitat was organized in the same categories as for BRUVS. The corals observed belonged to the genus *Pavona*, *Pocillopora*, *Porites* and *Psammocora* and were pooled together for analysis. The 30 values of habitat per transect were then summarized per habitat type. The sum of each habitat type per transect was converted into percentage. To calculate the mean of each habitat type per location, the absolute percentages per transect were used. The major habitat types recorded during UVC included turf (26.9%), rock (25.8%), rubble (15.9%) and coral (13.7%). Coral cover from individual transects ranged from 0% to 63.3%.

2.5 | Comparison between methods and locations

The mean fish species richness per location was compared using ANOVA. For fish abundance, the data did not have a normal distribution, so non-parametric Kruskal–Wallis tests were used. A presence–absence matrix was generated as a relative measure of the fish assemblage to compare species detection between methods (BRUVS *vs*. UVC). The abundance of each species was not considered because of the differences in sampling effort and detection probability (Lowry *et al*., 2012).

To determine if one method outperformed the other in the detection of specific trophic groups, the species richness of the groups detected by each method was compared. Fish species were assigned to the following trophic groups: small sized (including cryptobenthic and species <5 cm total length), planktivorous, herbivorous, omnivorous, small predators (species <50 cm total length) and large predators (species >50 cm total length), following discussions by Heupel *et al*. (2014) and Roff *et al*. (2016). Trophic groups were represented by fish silhouettes obtained from the R package fishualize (Schiettekatte *et al*., 2020).

Based on a species presence–absence matrix, clusters were generated using Jaccard dissimilarity index to compare the differences in fish assemblages between methods, locations and seasons (upwelling/non-upwelling). To determine the significant differences between clusters, pair-wise permutational multivariate analysis of variance (PERMANOVA) tests were used with the package vegan (Oksanen, *et al*., 2019). The PERMANOVA is based on a chosen dissimilarity measure and calculates a pseudo-F value, similar to the F statistic that would be produced with an ANOVA, but is unaffected by non-normal distributed data (Anderson, 2001). The cluster was visualized using Dendextend (Galili, 2015), and the P-values for pair-wise PERMANOVA tests were adjusted using the Bonferroni correction. For the PERMANOVA, the following fixed-effect model was used:

$$\text{Species matrix} \sim \text{sampling method} + \text{sites} + \text{season}$$

2.6 | Drivers of reef fish assemblages

The similarity between study sites and seasons was compared with a species abundance matrix using canonical analysis of principal (CAP) coordinates. The species abundance matrix included the species with at least 2.5% of the total abundance. For a normal distribution and a higher weight of rare species in the CAP, the abundance matrix was transformed using a fourth root transformation (Mueller *et al*. 2013). For the CAP, the function *capscale* was used with Bray–Curtis dissimilarity, which is also provided in the package vegan (Oksanen, *et al.*, 2019). Before the CAP, significant differences of potential predictors on fish assemblages were tested using a PERMANOVA. A total of 1000 permutations of residuals were used to test the statistical significance of variance components. For the CAP, the following model was used:

$$\text{Fish assemblages} \sim \text{location} \times \text{season}$$

The impact of fish species on the (dis)similarity of study sites was analysed with a similarity percentages (SIMPER) analysis, using the same abundance matrices as for the CAP. All species that accounted for up to 85% of the variance were extracted from the analysis. SIMPER was performed using the function *simper*, also provided in the package vegan (Oksanen, *et al*., 2019).

2.7 | Analysis of habitat

PCA was used to reduce the dimensions of habitat types explaining the variability of reef fishes recorded by each method. A matrix with the percentages of each habitat type was built, in which each row represents an individual UVC transect or BRUVS deployment and each column a certain habitat type. The PCA was calculated using the package FactoMineR 2.0 (Le *et al*., 2008). In both methods, PC1 and PC2 scores were extracted as they explained most of the habitat-related variance. For UVC, PC1 was defined by the presence of algal turf and the absence of rock, whereas PC2 was characterized by the presence of coral and the absence of algal turfs. Both PC1 and PC2 explained over 70% of the total variance among habitat types (Supporting Information Figure S3). For BRUVS, PC1 included the presence of algal turf and the absence of sand/rubble, which explained 43.4% of the variance, whereas PC2 included the presence of turf and the absence of rock, which explained 28.4% of the variance. The two principal components explained 71.8% of the total variance (Supporting Information Figure S3).

2.8 | Drivers of species richness and abundance

Generalized linear models (GLMs) were used to determine the influence of environmental factors on species richness and relative abundance with UVC and BRUVS.

For response variables, species richness and relative abundance from the two sampling methods were used. The response variables were species richness and relative abundance, per hour of video (individual h^{-1}) for BRUVS and per transect (individual 150 m^{-2}) for UVC. Predictors included location, season, habitat complexity, visibility, depth, habitat scores (PC1 and PC2) and water temperature, as well as the interactions between location and upwelling with all other predictors. The normal distribution of model residuals was tested with the normal scores of standardized residual deviances (Breslow, 1996). The variables were tested for collinearity through variance inflation factor. The model assumptions satisfied normal distribution and homoscedasticity (Altman and Bland, 1995; Schützenmeister *et al*., 2012). All possible combinations of environmental predictors were considered in the GLMs, and model selection was based on the AIC to select the most parsimonious of the competing models (Link and Barker, 2006). For model predictions and c.i. (95%) of the best-fitted models, the function *predict* from the package stats in R was used (R Development Core Team, 2019). Visualization of GLM predictions, CAP and boxplots were performed using the package ggplot2 (Wickham 2016).

3 | RESULTS

A total of 183 species from 60 families and 18 orders in the study region were detected (Table 1; Supporting Information Table S2). From these, 166 species were detected by BRUVS and 122 by UVC. Fifty-six per cent of the species were detected by both methods, with 62 species detected exclusively by BRUVS and 17 by UVC (Supporting Information Table S2).

Overall, more species were detected in Islas Murciélago (156 species) relative to Bajo Rojo (119 species) and Isla Loros (115 species). Nevertheless, there were no significant differences in mean species richness across locations for either method [Figure 2a; BRUVS: F = 0.99, df = (2, 134), P > 0.05; Figure 2b; UVC: F = 2.1, df = (2113), P > 0.05]. Nevertheless, BRUVS did reveal significant differences in fish relative abundance between Islas Murciélago and Isla Loros (Figure 2c; Kruskal–Wallis test, H = 8.7, df = 2, P < 0.05), whereas UVC showed no significant differences in the relative abundance of fish across locations (Figure 2d; Kruskal–Wallis test, H = 5.4, df = 2, P > 0.05). Most species detected by BRUVS were from the family Carangidae, followed by Labridae, Muraenidae, Haemulidae and Serranidae (Table 1; Supporting Information Table S2). The Spottail Grunt *Haemulon maculicauda* (Gill 1862) was the dominant species across locations, mainly due to their schooling behaviour (Supporting Information Tables S2 and S4). For UVC, Labridae was the most diverse family, followed by the families Serranidae, Pomacentridae, Haemulidae and Lutjanidae. The composition of trophic groups varied between methods, with BRUVS detecting more planktivorous, omnivorous and predatory fishes, whereas small-sized species were more commonly detected by UVC (Figure 3).

3.1 | Drivers of fish assemblages

Based on the Jaccard dissimilarity index, reef fish assemblages differed between methods (Figure 4; PERMANOVA: F = 79.5, df = 1, P < 0.05). Fish assemblages from Bajo Rojo and Isla Loros clustered together in both methods, whereas Islas Murciélago formed a unique cluster demonstrating differences between locations as well (Figure 4; Supporting Information Table S3; PERMANOVA: F = 18.549, df = 5, P < 0.001). Predatory fish detected by BRUVS such as the Green Jack *Caranx caballus* (Günther 1868) and the Mexican Barracuda *Sphyraena ensis* (Jordan & Gilbert 1882) has a large contribution to the species

TABLE 1 Reef fish species richness and relative abundance recorded from underwater visual census (UVC) and baited remote underwater video stations (BRUVS) in the North Pacific of Costa Rica

	UVC		BRUVS	
Family	Species	Mean count	Species	Mean CPUE
Acanthuridae	4	22.6 ± 5.3	4	27.1 ± 3
Apogonidae	2	14.8 ± 5.5	0	–
Aulostomidae	1	15 ± 0	1	1.7 ± 0.6
Balistidae	3	4.4 ± 0.8	5	5.3 ± 0.8
Belonidae	0	–	2	1 ± 0.3
Blenniidae	3	4 ± 0.7	2	4.2 ± 1.2
Bothidae	0	–	1	2 ± 0
Carangidae	4	14.2 ± 4.4	14	42.4 ± 10.1
Carcharhinidae	0	–	5	1.5 ± 0.2
Chaenopsidae	2	15.1 ± 5.8	0	–
Chaetodontidae	2	15.7 ± 1.7	2	10.9 ± 1.3
Chanidae	1	3.5 ± 2.5	1	2.4 ± 0.7
Cirrhitidae	3	2.5 ± 0.3	2	1.6 ± 0.3
Congridae	0	–	1	16.3 ± 1.5
Dasyatidae	0	–	1	1.6 ± 0.2
Diodontidae	3	3 ± 0.3	3	3.8 ± 0.7
Echeneidae	0	–	1	0.8 ± 0
Elopidae	0	–	1	27.2 ± 13.9
Engraulidae	0	–	1	0.9 ± 0
Ephippidae	0	–	2	21.6 ± 9.5
Fistulariidae	1	1.3 ± 0.1	2	10.4 ± 2.9
Ginglymostomatidae	1	1 ± 0	1	2 ± 0.5
Gobiidae	3	7.6 ± 1.4	1	1 ± 0
Haemulidae	7	62.5 ± 11.3	10	74.1 ± 12.2
Holocentridae	2	2.1 ± 0.3	1	1.2 ± 0.2
Kyphosidae	3	6.5 ± 2.2	3	9.3 ± 1.9
Labridae	13	82.2 ± 11.8	11	34.1 ± 4.2
Lutjanidae	7	12.5 ± 3.7	8	11.4 ± 1.8
Malacanthidae	2	2.7 ± 0.5	2	4.9 ± 1.7
Microdesmidae	1	37 ± 0	0	–
Mobulidae	0	–	2	1.3 ± 0.4
Monacanthidae	2	2.3 ± 1.3	3	3.1 ± 0.3
Mugilidae	0	–	1	7.9 ± 5.6
Mullidae	2	10.7 ± 3.7	2	11.7 ± 3
Muraenesocidae	0	–	1	1 ± 0
Muraenidae	6	2.4 ± 0.8	10	2.7 ± 0.2
Myliobatidae	1	1 ± 0	2	3.6 ± 1.7
Narcinidae	2	1 ± 0	2	1 ± 0
Nematistiidae	0	–	1	0.9 ± 0.1
Ophichthidae	2	2.7 ± 0.8	4	1.7 ± 0.2
Opistognathidae	1	3 ± 1	1	1.2 ± 0.2
Pomacanthidae	2	3.4 ± 0.5	2	3.4 ± 1
Pomacentridae	7	80.3 ± 9.2	8	49.6 ± 8.4
Priacanthidae	0	–	1	1.1 ± 0

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TABLE 1 (Continued)

	UVC		BRUVS	
Family	**Species**	**Mean count**	**Species**	**Mean CPUE**
Rhincodontidae	0	–	1	0.9 ± 0
Rhinobatidae	1	1 ± 0	2	1 ± 0.1
Scaridae	4	9.6 ± 1.7	4	7.5 ± 2
Sciaenidae	1	1 ± 0	3	133.8 ± 133
Scombridae	0	–	6	1.3 ± 0.3
Scorpaenidae	1	1 ± 0	1	1.6 ± 0.3
Serranidae	9	14.3 ± 2.1	10	16.4 ± 2
Sparidae	1	1.5 ± 0.2	1	3 ± 0.6
Sphyraenidae	0	–	1	70.5 ± 53
Syngnathidae	1	3 ± 0	0	–
Synodontidae	1	1.5 ± 0.3	0	–
Tetraodontidae	5	3.2 ± 0.3	6	2.8 ± 0.2
Tripterygiidae	2	2.6 ± 0.9	1	1.4 ± 0
Urotrygonidae	2	2 ± 0.3	2	2 ± 0.2
Zanclidae	1	1.2 ± 0.2	1	1.7 ± 0.2

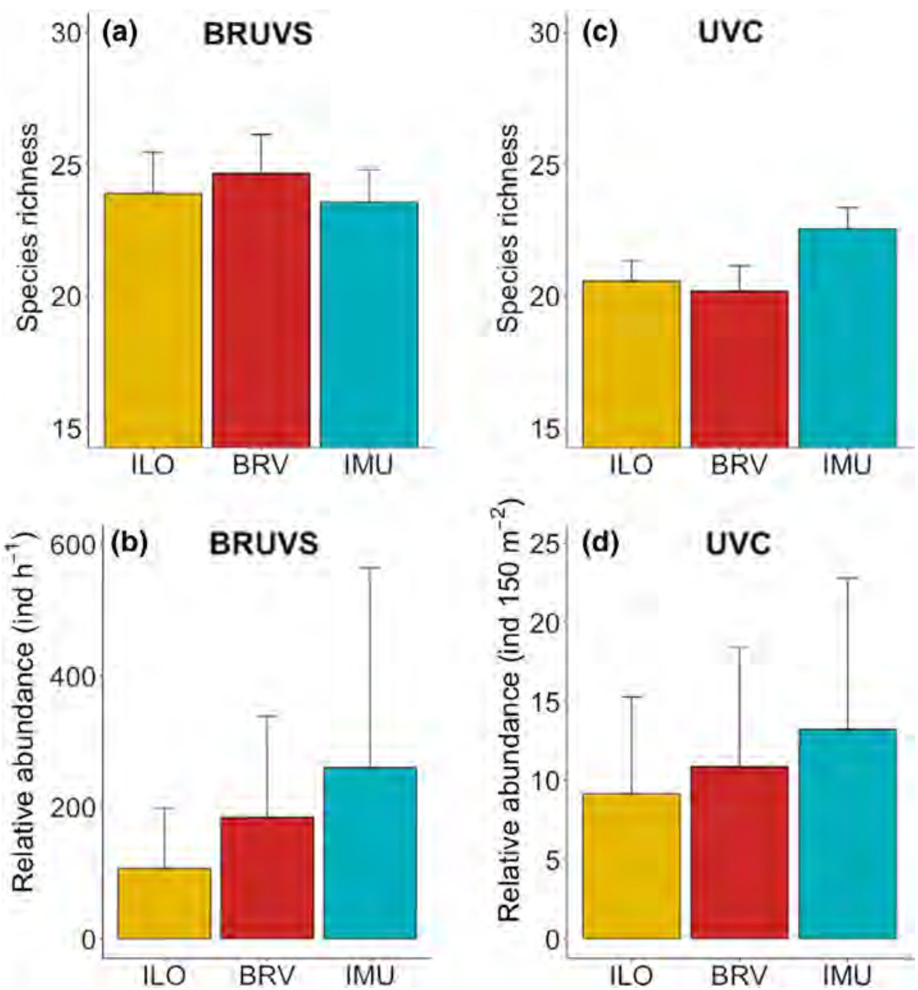

FIGURE 2 Species richness (mean ± S.E.) and relative abundance (mean ± S.D.) estimated from (a, b) baited remote underwater video stations (BRUVS) and (c, d) underwater visual census (UVC) in the North Pacific of Costa Rica. Sites: ILO: Isla Loros; BRV: Bajo Rojo-Viejón; IMU: Islas Murciélago

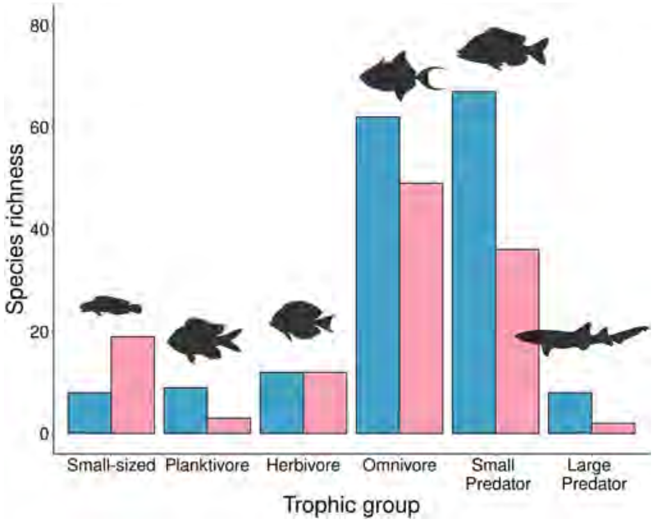

FIGURE 3 Functional groups recorded by baited remote underwater video stations (BRUVS) and underwater visual census (UVC) in the North Pacific of Costa Rica (■) BRUVS, and (■) UVC

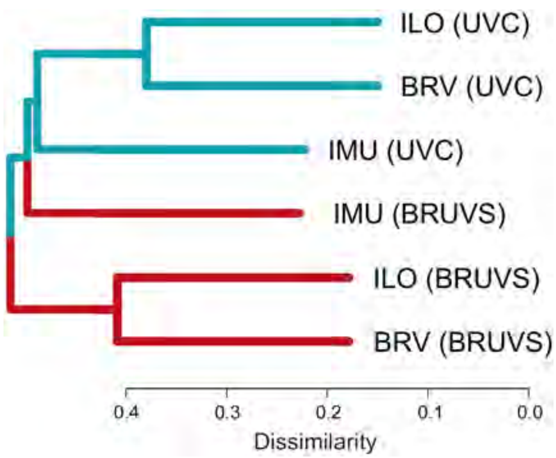

FIGURE 4 Jaccard dissimilarity clusters of reef fish assemblages recorded using baited remote underwater video stations (BRUVS) and underwater visual census (UVC) in North Pacific of Costa Rica. A presence–absence matrix for each method was used to examine reef fish assemblages by site. Sites: ILO: Isla Loros; BRV: Bajo Rojo-Viejón; IMU: Islas Murciélago

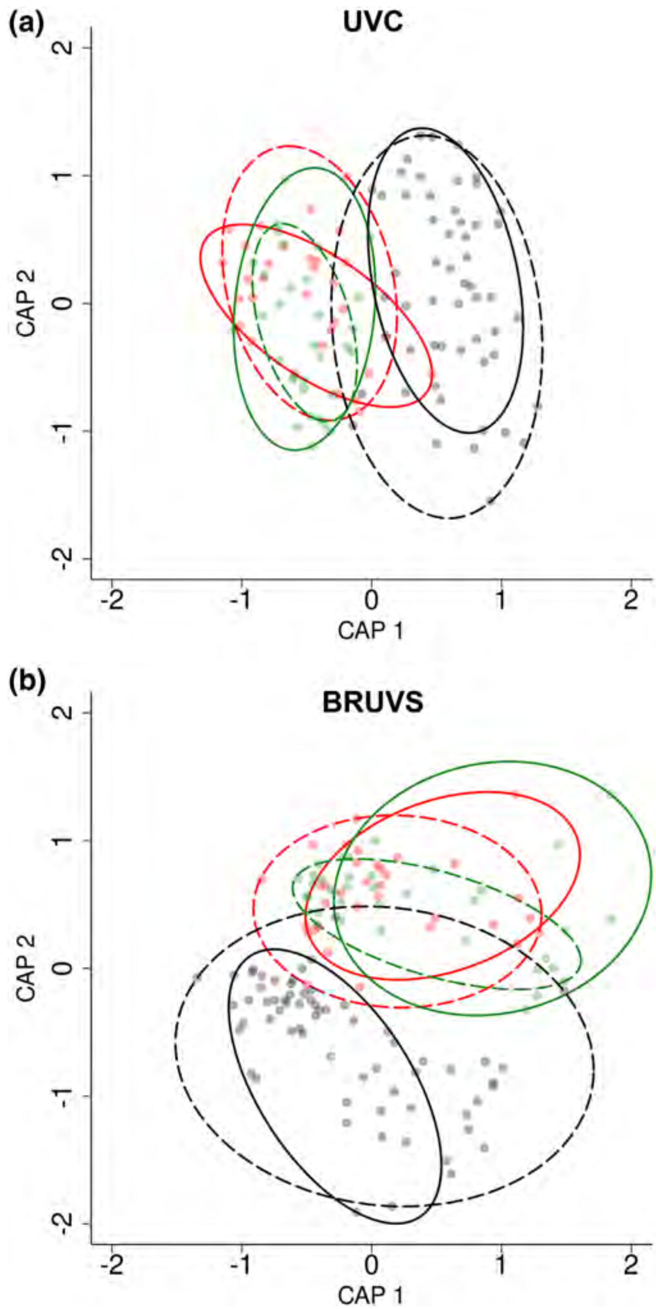

FIGURE 5 Canonical analysis of principal (CAP) coordinates, based on species abundance of the study sites of (a) underwater visual census (UVC) (——) Bajo Rojo, (——) Isla Loros and (——) Islas Murciélago and (b) baited remote underwater video stations (BRUVS) (——) Bajo Rojo, (——) Isla Loros and (——) Islas Murciélago. Species abundance was estimated using (a) total counts of individuals per species and (b) MaxN per species and camera station. The different locations are illustrated by colour and the season by the line type of the ellipses (upwelling: solid, non-upwelling: dashed)

dissimilarity across locations (Supporting Information Table S4). Bajo Rojo and Islas Murciélago showed a dissimilarity of 87.8%, whereas Isla Loros and Islas Murciélago showed a dissimilarity of 88.7%. The SIMPER analysis suggested that the species that contributed the most to the dissimilarity across locations in UVC were generally smaller fish, like the Cortez Rainbow Wrasse *Thalassoma lucasanum* (Gill 1862) (Supporting Information Table S4). Bajo Rojo and Islas Murciélago had 81% species dissimilarity, whereas Isla Loros and Islas Murciélago had 82% species dissimilarity.

Similarly, the results of the CAP also indicate a separation of Islas Murciélago from Isla Loros and Bajo Rojo. Fish assemblages in both Isla Loros and Bajo Rojo had a high degree of overlap, whereas Islas Murciélago showed more separation (Figure 5). Significant differences in reef fish assemblages between locations were found for UVC (Figure 5a, PERMANOVA: F = 14.9, df = 2, P < 0.001) and BRUVS (Figure 5b, PERMANOVA: F = 9.8, df = 2, P < 0.001). Seasonal upwelling also had a significant effect on the reef fish assemblages in UVC

(Figure 5a; PERMANOVA: F = 3.0, df = 1, P = 0.02) and BRUVS (Figure 5b; PERMANOVA: F = 2.8, df = 1, P = 0.02). Interestingly, the relationship between season and location explained more of the variance than season alone. The largest effect on fish abundance, nevertheless, can be attributed to spatial differences (Supporting Information Table S5).

3.2 | Drivers of species richness and abundance

Model selection based on AIC and maximum likelihood ratio tests revealed that the best-fitted GLM for species richness from BRUVS data included season, habitat complexity, water temperature and location (Figure 6; Table 2). The effect of water temperature and season on species richness varied between locations. Based on the selected model, predicted species richness increased with increasing habitat complexity and water temperature and decreased during the upwelling season. All variables in the model had a significant effect on species richness, except for water temperature (Table 2; Supporting Information Table S6). Species richness was significantly higher in warmer waters in Bajo Rojo (Figure 6d).

In contrast, species richness decreased with higher water temperature in Isla Loros and Isla Murciélago, but its effects were not statistically significant. Similarly, the best-fitted model that explained differences in relative abundance (MaxN h^{-1}) for BRUVS data included habitat complexity, upwelling and location (Figure 7; Table 2). Overall, the relative abundance of reef fishes increased in more-complex habitats, during the upwelling season, and was significantly higher in Islas Murciélago than in the other locations (Figure 7; Supporting Information Table S6). The effect size indicates that complexity explained most of the variance for species richness and abundance (Table 2). Upwelling had a stronger effect on both species richness and abundance than location (Table 2).

The selected model for species richness based on UVC data included water temperature, PC1 (rock) and PC2 (coral and algal turf cover) (Table 3; Supporting Information Table S6). Species richness increased in sites with higher water temperatures and with a higher proportion of rock (PC1), whereas more coral and less turf (PC2) were associated with a lower number of species (Figure 8a–c; Table 3). The best-fitted model explaining the relative abundance of reef fishes from UVC data included water temperature and coral/algal turf cover (PC2). Overall, the relative abundance of reef fishes increased with warmer water temperatures and with lower coral/higher turf cover (PC2) (Figure 8d,e; Table 3). In contrast to the effect sizes estimated from BRUVS models, temperature had the largest effect on species richness and abundance detected by UVC (Table 3).

4 | DISCUSSION

This study demonstrated that reef fish assemblages in the North Pacific of Costa Rica are influenced not just by the seasonal upwelling event but also by the interplay with other environmental and anthropogenic drivers. Differences in fish species richness and relative abundance in this region were most likely attributed to changes in water temperature and nutrient concentrations as a result of the seasonal upwelling (Stuhldreier

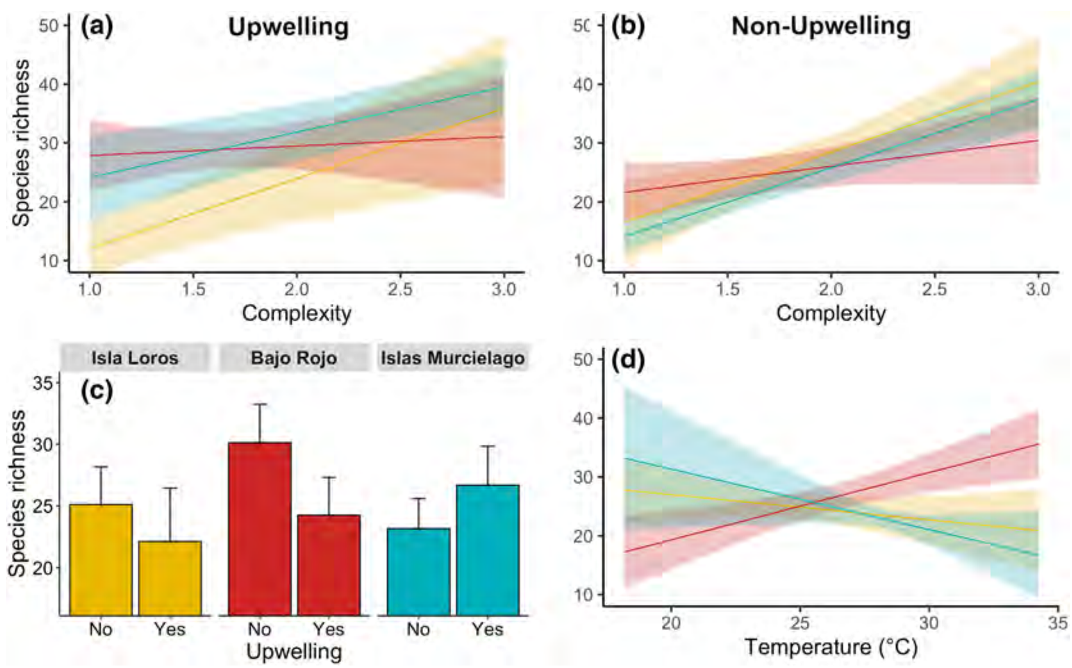

FIGURE 6 (a, b) Predicted effect of complexity (——) Isla Loros, (——) Bajo Rojo and (——) Islas Murciélago; (——) Isla Loros, (——) Bajo Rojo and (——) Islas Murciélago, (c) site and (d) temperature (——) Isla Loros, (——) Bajo Rojo and (——) Islas Murciélago on fish species richness recorded by baited remote underwater video stations deployed in the North Pacific of Costa Rica during upwelling (UW) and non-upwelling (NUW) seasons

TABLE 2 Summary of the generalized linear model used to assess the effect of habitat and environmental drivers on reef fish species richness and abundance (MaxN h^{-1}) from baited remote underwater video stations

Species richness	*df*	Deviance	Residual deviance	*F*	*P*-value	Effect size
Full model			12,321.5			
Location	2	180.0	12,141.5	2.3	NS	0.015
Upwelling	1	428.9	11,712.6	11.1	0.001	0.037
Complexity	1	5738.2	5974.4	148.5	<0.001	0.960
Temperature	1	32.3	5942.1	0.8	NS	0.005
Site × temperature	2	337.6	5604.5	4.4	0.01	0.060
Site × complexity	2	536.3	5068.2	6.9	0.001	0.106
Site × upwelling	2	238.0	4830.2	3.1	NS	0.049
Relative abundance	***df***	**Deviance**	**Residual deviance**	***F***	***P*-value**	**Effect size**
Full model			185.5			
Location	2	10.8	174.7	6.5	0.002	0.062
Upwelling	1	13.1	161.6	15.7	<0.001	0.081
Complexity	1	51.6	110	61.9	<0.001	0.469

Note: NS, not significant.

et al., 2015) but were also associated with habitat complexity, which creates additional refuges for reef fishes (Ferrari *et al*., 2017). To authors' knowledge, this is the first study in the Eastern Tropical Pacific that combined BRUVS and UVC to monitor reef fish assemblages in a seasonal upwelling region, further demonstrating that BRUVS are capable of providing fast and reliable data on the distribution, abundance and diversity of fishes over large spatial and temporal scales.

4.1 | Fish diversity

Based on the findings of the present study, BRUVS and UVC detected 183 reef fish species from 60 families, which is considerably higher than those by previous studies in the North Pacific of Costa Rica. For example, using UVC across a larger geographic area, Beita-Jiménez *et al*. (2019) reported 94 species from 37 families, whereas Arias-Godínez *et al*. (2019) found 56 species from 24 families in the Gulf of Papagayo (North Pacific of Costa Rica). UVC from the present study alone detected more species (122 species from 42 families) than these two studies; nevertheless, this number was likely because of differences in sampling effort, temporal variability and severe habitat degradation reported in some areas (Arias-Godínez *et al*., 2019; Beita-Jiménez *et al*., 2019).

The study by Arias-Godínez *et al*. (2019) compared reef fish assemblages during two periods (1995–1996 and 2014–2016), in which they showed approximately 40% decline in live coral cover and a drastic loss of reef structural complexity. Although Beita-Jiménez *et al*. (2019) sampled over a larger geographic area (31 sites) compared to the present study, they conducted less belt transects per site (*N* = 6–12). In other areas of Costa Rica like the Caño Island Biological Reserve (South Pacific of Costa Rica), a study using stationary fish counts reported 79 species (Salas *et al*., 2015). Caño Island is one of the most diverse and biologically important areas of Costa Rica, with relatively low habitat degradation compared to the North Pacific region (Alvarado *et al*., 2018; Arias-Godínez *et al*., 2019; Guzman & Cortés, 1989), but showed a considerably lower fish species richness compared to the present study.

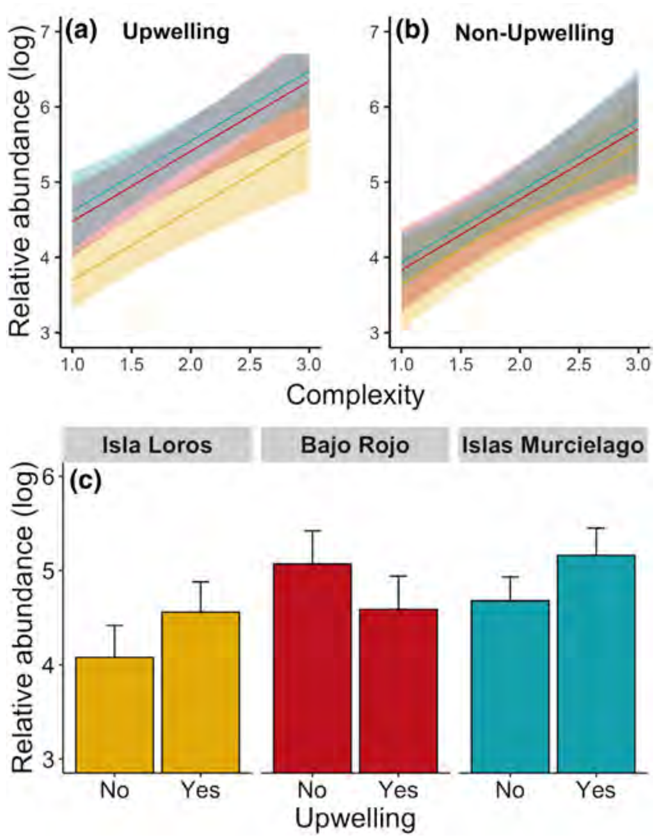

FIGURE 7 Predicted effect of (a, b) complexity (——) Isla Loros, (——) Bajo Rojo and (——) Islas Murciélago; (——) Isla Loros, (——) Bajo Rojo and (——) Islas Murciélago and (c) site on fish abundance (individual h^{-1}) recorded by baited remote underwater video stations in the North Pacific of Costa Rica during upwelling and non-upwelling seasons

TABLE 3 Summary of the generalized linear model used to assess the effect of habitat and environmental drivers on reef fish species richness and abundance (fish 150 m^{-2}) from underwater visual census

Species richness	*df*	Deviance	Residual deviance	*F*	*P*-value	Effect size
Full model			3576.9			
PC1	1	200.9	3375.9	7.9	0.006	0.06
PC2	1	226.7	3149.3	8.9	0.003	0.072
Temperature	1	310.4	2838.9	12.3	<0.001	0.109
Relative abundance	***df***	**Deviance**	**Residual deviance**	***F***	***P*-value**	**Effect size**
Full model			12.3			
PC2	1	1.5	10.8	18.2	<0.001	0.139
Temperature	1	1.6	9.3	18.9	<0.001	0.172

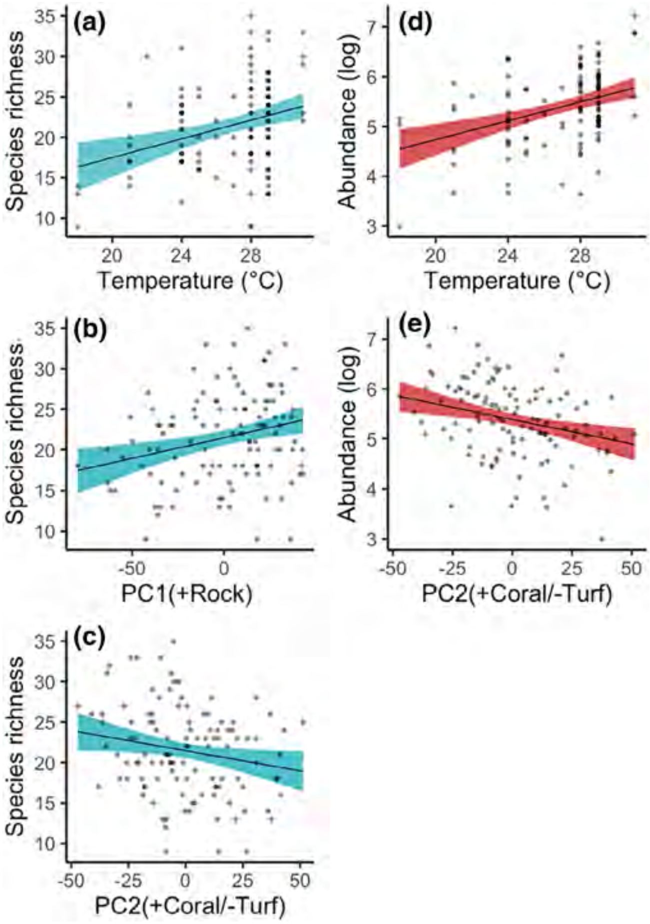

FIGURE 8 Drivers that influenced (a–c) fish species richness and (d, e) relative abundance (individual 150 m^{-2}) from underwater visual census conducted in the North Pacific of Costa Rica

At a regional scale, a study in Gorgona Island, located 35 km off the Pacific coast of Colombia, reported 70 species of coral reef fishes in 50 UVC (Palacios and Zapata, 2014). Their study, nevertheless, used smaller transects (30 × 2 m) than those in the present study and therefore had lower sampling effort. Dominici-Arosemena and Wolff (2006) documented reef fish community structures in a region of Panama (tropical eastern pacific), which is also affected by the seasonal upwelling. They conducted 288 UVC and reported 126 species in total. Even though the sampling effort with UVC in their study was much higher, the total number of species reported was almost identical to the UVC in the present study. This might be due to the higher sampling frequency and shorter sampling period (of only half a year). Increasing the sampling frequency can increase the detectability of fish species. Nevertheless, this does not affect all species uniformly – introducing biases in species diversity calculations (Zhao *et al*., 2017). In addition, fish distribution can change over time, in which case a short sampling period may provide only a snapshot of fish assemblages (Zhao *et al*., 2017). By using BRUVS and traditional survey techniques like UVC simultaneously in the same sites and across years, the present study provided a more detailed characterization of the reef fish assemblage in the North Pacific of Costa Rica. BRUVS also increased the probability of detecting small and large predatory fishes that are attracted to the bait, an important trophic group of marine food webs that is often underrepresented from UVC (Colton and Swearer, 2010; Dorman *et al*., 2012). In contrast, small species (including cryptic ones) were almost exclusively detected by UVC. Interestingly, BRUVS also recorded more omnivorous and planktivorous species than UVC, possibly due to opportunistic sampling of species in the field of view, species-specific schooling behaviours, diver avoidance behaviours and differences in sampling effort (Lowry *et al*., 2012).

Given that compressor-based diving is commonly used by artisanal fishers in the North Pacific of Costa Rica (Villalobos-Rojas *et al*., 2014), reef fishes may be even more sensitive to human disturbances, such as bubbles and noise from divers (Lindfield *et al*., 2014). The absence of human activities near the BRUVS deployments in the present study makes it a less-invasive sampling method, favouring the detection of elusive species that could be startled by divers (Colton and Swearer, 2010; Mallet and Pelletier, 2014). Sampling depth may also explain the differences in fish species richness between methods, as most BRUVS were deployed at greater depths, providing access to habitats that could not be easily sampled during UVC (Colton and Swearer, 2010; Kane and Tissot, 2017). On the contrary, higher species richness could simply be due to longer deployments, given that the average soak time by BRUVS was 1.5 h, whereas UVC transects rarely lasted more than 30 min (Mallet and Pelletier, 2014).

The limitations of both sampling methods may also explain the differences in species richness. For example, BRUVS detected a greater number of predators, including midwater and pelagic species, than UVC, possibly because the bait plume can trigger bait-search behaviours in nearby species (Westerberg & Westerberg, 2011; Dorman *et al*., 2012). The dispersion of bait plumes is largely unknown, which limits the calculation of the relative sampling area for BRUVS. In addition, the bait can trigger complex fish behavioural responses, which greatly influence the recording of fish species (Harvey *et al*., 2012). Moreover, the success of BRUVS and UVC deployments depends on visibility, which can also introduce biases (Chan and Hodgson, 2019; Espinoza *et al*., 2020; Harvey *et al*., 2012). BRUVS also underestimated small-sized species such as gobies and blennies. This is mostly because the inconspicuous colourations and sizes of these species are hard to observe with the fisheye lens of GoPro cameras (Lowry *et al*., 2012). Given that small-sized fishes (including cryptobenthic) are among the most abundant and productive reef fishes (Brandl *et al*., 2019; Stobart *et al*., 2007), combining BRUVS with more traditional approaches capable of detecting these small species is crucial for conducting more detailed sampling of all components of reef fish assemblages. The limitations of both sampling methods have been well documented; nevertheless, using non-destructive and non-lethal approaches to survey reef fish assemblages inside MPAs can provide fast and reliable estimates of the distribution, abundance and species richness, which more often outweigh the limitations.

4.2 | Comparison between locations

The changes in the structure and composition of reef fish assemblages between locations may be attributed to differences in reef size (km^2), human accessibility and protection status (Cinner *et al*., 2018). Isla Loros and Bajo Rojo are two small reef sites that share a similar fish assemblage due to their close proximity and accessibility by fishers. In contrast, Islas Murciélago has a larger size, is located in a more remote area relatively far from human population centres and has been protected since 1987 (Alvarado *et al*., 2012). The protection status of reefs and the degree of exposure to fishing pressure are known to impact reef fish assemblages (Cinner *et al*., 2018; Mora *et al*., 2011), which was recently shown by Beita-Jiménez *et al*. (2019) in this region. For example, large predators and commercially important species such as the yellowfin tuna *Thunnus albacares* (Bonnaterre 1788), bull shark *Carcharhinus leucas* (Valenciennes 1839), tiger shark *Galeocerdo cuvier* (Péron & Lesueur 1822), *S. ensis* and the bluestreak drum *Elattarchus archidium* (Jordan & Gilbert 1882) were commonly detected in Islas Murciélago. Nevertheless, in Bajo Rojo and Isla Loros, neither BRUVS nor UVC detected these species, possibly due to overfishing and habitat degradation. Moreover, in these locations, species like *H. maculicauda* and *C. caballus* showed a three-fold increase in abundance relative to Islas Murciélago, which may be an indicator that the absence of larger predators has resulted in competitive exclusion (Ashworth and Ormond, 2005) and/or mesopredator release (Boaden and Kingsford, 2015; Bolton *et al*., 2019). Nevertheless, more evidence is needed to clarify the effects of fishing in the trophic structure and dynamics of reef fishes in the region.

Although Islas Murciélago has been protected for over three decades, there is also evidence of illegal fishing due to the limited capacity for surveillance and enforcement (Alvarado *et al*., 2012). Illegal fishing can compromise the effectiveness and conservation benefits that reef fishes may gain from current spatial management approaches (Arias *et al*., 2014; Espinoza *et al*., 2020; Speed *et al*., 2019). The present study showed significant differences in fish abundances across locations but not on species richness, which could be attributed to the limited enforcement of illegal fishing activities. Therefore, it is critical to quantify changes in the composition and biomass of different target species and trophic groups across locations and seasons, which may increase the understanding of how fishing may be impacting reef fish assemblages in this region (Robinson *et al*., 2017). Such information could even help assess whether MPAs like Isla Murciélago are effective at maintaining the structure and functioning of reef ecosystems (Boaden and Kingsford, 2015; Robinson *et al*., 2017).

4.3 | Habitat composition and topographic complexity

As expected, habitat composition and topographic complexity had a strong effect on reef fish species richness and abundance. With BRUVS, it was possible to observe high species richness and abundance in structurally complex reef habitats that provide more shelter and resources available for fishes (Alvarado *et al*., 2018; Ferrari *et al*., 2017). The present study showed that fish species richness and abundance increased with rock cover but not necessarily coral cover, which contradicts the general pattern reported in the literature (Cheal *et al*., 2010; Wilson *et al*., 2006). This is expected given that rocky reefs in the North Pacific of Costa Rica are structured by large and complex rock foundations upon which relatively small and isolated coral colonies grow, instead of being structured by the calcareous deposition of centuries of coral growth (Cortés, 1997). Therefore, low coral cover in this region is not necessarily detrimental to fish assemblage biodiversity because rocky reef structure can also provide refuge and abundant resources for fishes (Bassey-Fallas, 2010; Beita-Jiménez *et al*., 2019; Espinoza and Salas, 2005). In addition, the effects of algal turf cover on fish assemblages could be linked to the presence of rock over which the algal turf is growing (Fong *et al*., 2017). A large number of fish species depend on algal turfs as a food source due to the high nutritional content (Wilson *et al*., 2003). These increases in food availability associated with algal turf cover could explain a high diversity and abundance among algal turfs (Tootell and Steele, 2016; Wilson *et al*., 2003). Other studies in the Eastern Tropical Pacific have also reported the absence of positive relations between coral cover and species richness (Glynn *et al*., 2014). These studies conclude that coral cover provides shelter and food mainly to particular species, whereas other species with different feeding strategies require other types of benthic cover to suit their needs (Dominici-Arosemena and Wolff, 2006; Glynn *et al*., 2014).

4.4 | Effects of seasonal upwelling

Seasonal differences in the distribution and abundance of reef fishes were likely due to the associated changes in temperature and productivity (López-López *et al*., 2017; Sato *et al*., 2018). The physiological range of temperature tolerance of fishes can vary considerably between species, with some staying and others leaving an area during upwelling events (Peck *et al*., 2013; Pérez-Matus *et al*., 2017; Sato *et al*., 2018). Several fish species have been observed to move towards warmer waters in offshore areas during upwelling (Sato *et al*., 2018). The changes in fish composition and the reduction in species richness observed during upwelling in the present study could be related to species-specific movement behaviours triggered by changes in water temperature (Espinoza *et al*., 2011; Mull *et al*., 2010; Sato *et al*., 2018).

The upwelling in Costa Rica is known to have peaks of higher intensity rather than constant conditions throughout the season (Jiménez, 2001); therefore, rapid temperature variations, which did not accurately reflect the upwelling state at the moment, may result in noisy data. Changes in the timing and intensity of seasonal upwelling have been observed in recent years (M. Lara, pers. comm.) and may have affected the interpretation of results. Moreover, due to severe weather conditions, sampling at remote areas like Islas Murciélago during the upwelling was restricted to periods of fair-weather conditions.

Contrary to UVC, BRUVS showed that fish abundance increased during the upwelling (with the exception of Bajo Rojo). The biomass of planktivorous fishes has been previously observed to increase during upwellings due to the enhanced productivity (Pérez-Matus *et al*., 2017). Because BRUVS favoured the detection of planktivorous species in the present study, the higher abundances are probably the result of large schools of these fishes opportunistically sampled by the camera's field of view (Dorman *et al*., 2012). The abundance of planktivorous species like *Halichoeres dispilus* (Labridae), *Chromis atrilobata* (Pomacentridae), *Kyphosus elegans* (Kyphosidae) and *Paranthias colonus* (Serranidae) had a two- to three-fold increase during upwelling months, possibly as a result of increased productivity (Pérez-Matus *et al*., 2017).

On the contrary, BRUVS also favoured the detection of small and large predatory fishes, which tend to be more mobile and wide-ranging (Colton and Swearer, 2010). It is possible that the higher fish abundances recorded by BRUVS were a result of the arrival of predators during upwelling that were not detected by UVC (Lowry *et al*., 2012). In contrast, lower fish abundances observed by UVC could be the result of fear-based effects on the rest of the fish assemblage created by the increased presence of predators undetected by this method (Shea *et al*., 2020). Future studies of trophic structure variations are needed to identify drivers of reef fish assemblages associated with the upwelling.

4.5 | Future research and recommendations

Reefs in the North Pacific of Costa Rica are exposed to multiple chronic threats such as overfishing, habitat degradation, coastal development and climate change (Alvarado *et al*., 2018; Arias-Godínez *et al*., 2019). The present study shed some light on the influence that natural oceanographic processes such as the seasonal upwelling may have on reef fish assemblages in the region; nevertheless, further research is needed to elucidate the action of multiple synergetic effects on these reefs. The interaction between reef fishes and their environment is essential for maintaining the ecosystem functioning of rocky reefs in the North Pacific of Costa Rica, a region that has experienced severe habitat degradation from rapid coastal development and poor management (Arias-Godínez *et al*., 2019). Both algae and corals have been observed to have increased the growth rates due to the increased availability of nutrients (Roth *et al*., 2015; Stuhldreier *et al*., 2015).

Despite the historically low coral cover in the region, various reefs have sparse patches of high coral cover that have experienced considerable declines over the past two decades, from about 40% live coral coverage to about 5% in some areas (Alvarado *et al*., 2018; Arias-Godínez *et al*., 2019). Under these escalating anthropogenic stressors and uncertainty due to climate change, ecosystem parameters like the amount of herbivorous fishes that frequent the reef could assist coral growth and resilience by curbing the competitive advantages of algae over coral (Cai *et al*., 2018; Hughes *et al*., 2007; Roth *et al*., 2015; Wilson *et al*., 2006). Therefore, the integration of trophic group–targeted conservation plans could be a first step towards a more effective management of reef fisheries in areas where full protection is not possible. Fishing on overexploited groups, such as herbivorous fishes in the North Pacific of Costa Rica, could be restricted to prevent further shift towards algae-dominated habitats, which ultimately benefits the entire reef fish assemblage.

Variation in the intensity of upwelling events as a result of changing ocean conditions is evident throughout the world (Sydeman *et al*., 2014) and may also have an important effect on the North Pacific of Costa Rica. Furthermore, the El Niño Southern Oscillation (ENSO) phenomenon, which now occurs more often and more intensely as a result of global warming, can alter upwelling events, affecting reef fish assemblage composition and ecosystem function (Cai *et al*., 2015; Glynn *et al*., 2014; Sydeman *et al*., 2014). To further understand the effects of the seasonal upwelling on reef fish assemblages and other aspects of the ecosystem, long-term studies are needed to consider phenomena such as ENSO and the changing patterns of upwelling events (Peck *et al*., 2013; Santora *et al*., 2017).

The highly diverse North Pacific of Costa Rica provides important ecosystem services to the surrounding communities through recreational diving, ecotourism, sports and commercial fishing (Beita-Jiménez *et al*., 2019). Now that patterns of upwelling seem to be shifting in the face of climate change, and reefs are subjected to increasing anthropogenic pressures, these benefits are at risk (Arias-Godínez *et al*., 2019). The resilience of these ecosystems and the benefits they provide can be ensured in the long term only with a comprehensive understanding of the environmental dynamics of the region and proper management and conservation programmes (Cai *et al*., 2015; Sydeman *et al*., 2014).

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AUTHOR CONTRIBUTIONS

Conception or design of the work: M.E.

Acquiring of funds: M.E.

Data generation: M.H.E., M.E.

Data analysis: M.H.E., S.M.-M., M.E.

Manuscript preparation: M.H.E., S.M.-M., M.E.

Review and edition of manuscript: M.H.E., S.M.-M., M.E.

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