Fish assemblage structure related to habitat heterogeneity in rocky reefs in the Mexican Pacific coast

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One of the major paradigms in ecology is the understanding of processes and patterns related to the structure of biological communities. Reef ecosystems, with their high productivity, habitat heterogeneity, and fish diversity provide a model for studying these processes. We sampled four sites three times during the season associated with the California Current and two times associated with the North Equatorial Current using video-transects on the coast of Zihuatanejo, Guerrero, Mexico to determine the relationship between the habitat characteristics and the structure of the fish assemblage. We recorded a total of 26 families and 54 species and estimated fish richness and abundance. In addition to measuring local water variables such as temperature (°C), salinity (PPT), pH and dissolved oxygen (O_2%), we determined habitat heterogeneity by processing photographs of the substrate and calculated rugosity using the tape chain. Oxygen and temperature were the variables associated to sea water conditions that differentiated the sampled sites. The fish community structure presented high correlations with temperature, salinity, and dissolved oxygen, followed by the heterogeneity components such as rugosity and substrate diversity. Our results showed that seasonal changes in water conditions and physical components in the coast of Zihuatanejo promotes changes in the fish community.

Keywords: California current, Ixtapa-Zihuatanejo bay, North equatorial current, Physical complexity, Seasonal changes.

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Uno de los principales paradigmas en ecología es el entendimiento de procesos y patrones relacionados con la estructura de las comunidades biológicas. Los ecosistemas de arrecifes, con su alta productividad, heterogeneidad de hábitat y diversidad de peces, proporcionan un modelo para estudiar estos procesos. Muestreamos cuatro sitios tres veces durante la temporada asociada a la Corriente de California y dos veces asociada a la Corriente Ecuatorial Norte utilizando video-transectos en la costa de Zihuatanejo, Guerrero, México para determinar la relación entre las características del hábitat y la estructura de la comunidad de peces. Registramos un total de 26 familias y 54 especies, y estimamos la riqueza y abundancia de peces. Además de medir variables locales del agua como temperatura (°C), salinidad (PPT), pH y oxígeno disuelto (O_2%), determinamos la heterogeneidad del hábitat procesando fotografías del sustrato y calculamos la rugosidad usando una cadena. El oxígeno y la temperatura fueron las variables asociadas a las condiciones del agua de mar que diferenciaron los sitios muestreados. La estructura de la comunidad de peces presentó altas correlaciones con la temperatura, salinidad y oxígeno disuelto, seguido por los componentes de la heterogeneidad como rugosidad y diversidad del sustrato. Nuestros resultados mostraron que los cambios estacionales en las condiciones del agua y los componentes físicos en la costa de Zihuatanejo promueven cambios en la estructura de la comunidad de peces.

Palabras clave: Bahía de Ixtapa-Zihuatanejo, Cambios estacionales, Complejidad física, Corriente de California, Corriente Ecuatorial del Norte.

INTRODUCTION

In the last decades, understanding the effects of heterogeneous habitats loss on living organisms has been a key goal of conservation management to maintain ecological processes and diversity at different scales (*e.g.*, Levey, 1988; Finch, 1989; Greenberg *et al.*, 1995; Willig *et al.*, 2003). Heterogeneity, defined as the relative abundance of different structural components of the habitat (*e.g.*, different kinds and sizes of rocks, vegetation, and sedimentation) is related with species richness and abundance in biological communities, and facilitates species coexistence (MacArthur, Wilson, 1967; McCoy, Bell, 1991).

Marine ecosystems harbor high diversity and different levels of heterogeneity related with high ecological dynamics at different temporal and spatial scales (Bowen *et al.*, 2013). Temporal variation is related to seasonal changes influenced by storms, hurricanes, dry-rain cycles, etc., which in turns modify sea water conditions (Androulidakis *et al.*, 2015). Moreover, in marine ecosystems, reefs are defined as heterogeneous and complex structures providing different types of substrates for the establishment of algae and animals enhancing biological diversity related to productivity and energy flux (Thomson *et al.*, 1979; Chiappa-Carrara *et al.*, 2019). Reefs cover ~284,300 km^2 worldwide (1.2% of the continental plateau and 0.09% of the oceanic area; Spalding *et al.*, 2001; Spalding, Brown, 2015) and harbor ~25% of the total marine fauna including one third of the fish species that present specific biotic interactions (Paulay, 1997; García-Charton, Pérez-Ruzafa, 2001). Even though these habitats cover a small area, the ecological functions they provide are also related to maintaining the diversity of hot spots and processes that occur on the mainland (*e.g.*, protection to the coastlines). Furthermore, reef areas are used to promote touristic activities and sustain local fisheries (Moberg, Folke, 1999; Calderón-Aguilera *et al*., 2017).

In the last two decades, reefs have undergone an increase in the rate of degradation related to overfishing, pollution, habitat modification, introduction of non-native species, and global warming, resulting directly and indirectly in the loss of coral cover and heterogeneity of these habitats (Jackson *et al*., 2001; Hughes *et al*., 2017). One important component in the reef functioning are fishes, which in most cases have a high relation and specific biological interactions within these habitats in at least one stage along their life history (Thomson *et al*., 1979; Arreola-Robles, Elorduy-Garay, 2002). Therefore, many factors are related to the abundance, richness, and structure of the fish assemblages in these marine habitats, such as: temporal variation, habitat heterogeneity, seasonal changes related to ocean currents, shelter availability, feeding resources, foraging areas (Allen, Robertson, 1994; Dominici-Arosemena, Wolff, 2006). Fish assemblage structure and reefs heterogeneity are highly correlated, therefore, the loss of heterogeneity results in low refuge availability and reduction of areas for foraging and reproduction, which in turns increases susceptibility to predation and fisheries (Rogers *et al*., 2014; Arias-Godínez *et al*., 2019; Lowe *et al*., 2019).

In the Mexican Pacific coast, fish diversity is mainly related to the habitat heterogeneity associated with the topography and historical geology of this coastline (Glynn, Morales, 1997; López-Pérez *et al*., 2012). This coast is the region with the highest rate of endemism per unit area worldwide with 71% of endemic fish species (Robertson, Allen, 2015). Furthermore, the differences in the reef heterogeneity and seasonal dynamics due to the influence of currents in this area provide an excellent study model to understand and evaluate hypotheses related to habitat heterogeneity that sustains and promotes high biodiversity.

One of the paradigms in ecology postulates that habitat heterogeneity presents a positive relation with species richness and biodiversity, which in turn triggers temporal and spatial changes in the assemblage structure, allowing coexistence through niche differentiation, and mediating competition and predation pressure by seasonal and daily dynamics (MacArthur, Levins, 1967; MacArthur, Wilson, 1967; Stubbs, Wilson, 2004; Mason *et al*., 2008; Morin, 2011). In this study, we investigated how the substrate diversity and rugosity as components of habitat heterogeneity, and seasonal changes of the seawater conditions due to marine currents (water temperature, salinity, dissolved oxygen) influence the structure (abundance, richness, and species composition) of the reef fish assemblages in the bays of Ixtapa and Zihuatanejo. We hypothesized that sites with greater habitat heterogeneity and higher seasonal changes in water conditions would harbor a more diverse assemblage in terms of species richness and fish abundance.

MATERIAL AND METHODS

Location and site characteristics. The bays of Ixtapa and Zihuatanejo are located at 300 m asl in the coast of the state of Guerrero in the southwest of the Mexican Tropical Pacific coast (Carranza *et al*., 1975). The shores in these bays present high variation in depth and are constituted of igneous, metamorphic, volcanic and limestones. The constant influence of tropical storms and upwellings causes reef to form mainly on rocks and boulders rather than on coral structures in contrast to the Caribbean reefs (Centeno-García *et al*., 2008). We sampled four rocky sites: Playa las Gatas (LG; 17°37'24.0"N 101°33'13.3"W) is located south of the bays of Ixtapa and Zihuatanejo, and regarding the short distance to human settlements, presents high impact by direct sewage discharge and tourism activities since 1990. This site presents 6–7 m in depth and reef range 1–2 m high (from the bottom); Zacatoso (ZC; 17°39'16.1"N 101°37'18.4"W) is 1 km east of the shore of the bay of Ixtapa, the reef at this site is found at 5–10 m depth with heights of 4–7 m. This reef presents low degree of deterioration or anthropogenic impact even when is near to touristic resorts and a marine harbor; Caleta de Chon (CH; 17°36'55.1"N 101°33'17.8"W) is located 1.5 km south-east of the Zihuatanejo shore, the reef in this area presents heights of 2–3 m, and is composed mainly by *Pocillopora* spp. found at 7–8 m depth. This site presents high rates of sedimentation related to coastal erosion since 2010 and; Playa Manzanillo (MZ; 17°37'07.1"N 101°31'21.4"W) is a relatively well-conserved ~40 ha rocky reef covered of corals (1–5 m high) at 2–7 m depth, located 4 km from the bay of Zihuatanejo (Nava, Ramírez-Herrera, 2012; Nava *et al*., 2014; 2021) (Fig. 1).

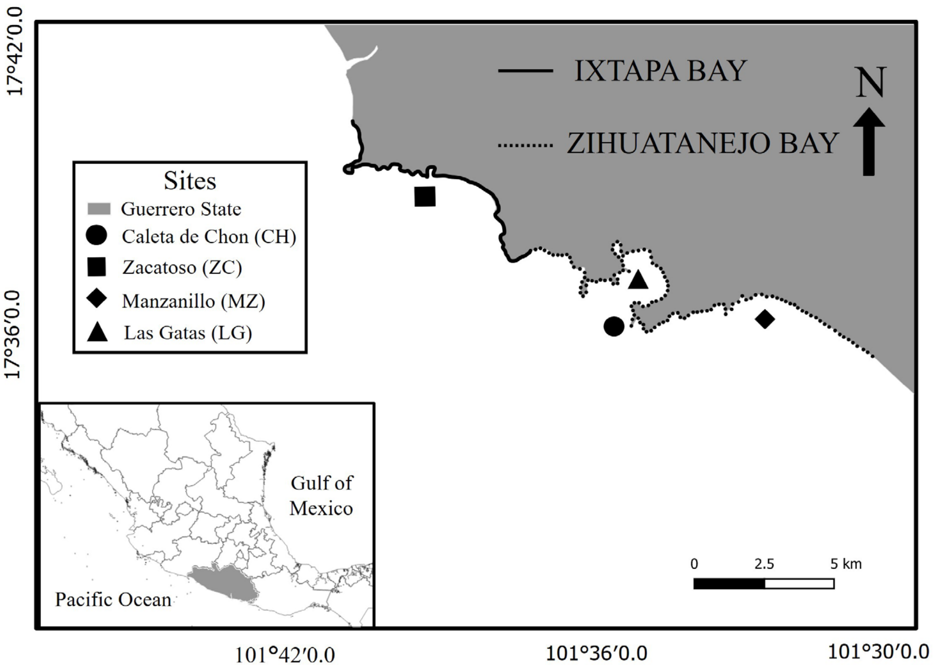

FIGURE 1 | Geographic location of the Ixtapa and Zihuatanejo bays in the Pacific Coast of Mexico and sampling sites.

The coast of the State of Guerrero belongs to the Eastern Pacific Warm Pool (EPWP), with a continuous flow of warm water from June–December related to the North Equatorial Current (hereafter NEC). The water temperature in this period ranges from 27–30°C and decreases to 19–26°C in January-May due to the presence of the California Current (hereafter CC), which is mainly constituted of cold-water masses from north to south along the Pacific Ocean (Wang, Enfield, 2001; Fiedler, Talley, 2006; Kessler, 2006; Kamikuri *et al*., 2009). Based on the above mentioned, we performed the field trips to record temporal variations in fish and site characteristics. Two field trips were performed in March and April 2019, and one in February 2020, which corresponded to CC; and two field trips were performed in June and December 2019, which corresponded to NEC.

During each field trip we recorded data on fish assemblages and habitat variables using SCUBA diving techniques. In each field trip, three underwater transects (with three replications) of 30 m length each (3 m wide) were performed in each site perpendicularly to the coastline using a metric rope and an underwater compass. We performed a total of 27 transects in each site under the influence of CC (3 field trips x 3 transects x 3 replications) and 18 for each site under the influence of NEC (2 field trips x 3 transects x 3 replications). All sites had up to 7–10 m in depth, and physicochemical variables of the sea water were recorded along each transect every 10 m, and at three different depths between ~0.5–9 m using a multiparametric sonde (YSI EXO2; YSI Inc., Yellow Springs, OH, U.S.A). The variables were temperature (°C), salinity (PPT), pH and dissolved oxygen (O_2%).

Rugosity of the reef bottom at each site was determined by the tape-chain method considering each 30 m transect, following Saleh (1993) and Friedman *et al*. (2012), where surface rugosity (SR) is the ratio obtained once the chain is placed over the undulating substrate (D_{chain}) and the total length of the chain (L_{chain}). The bottom substrate of each site was classified based on the percentage of rock, coral, sand, and rubble (pebbles and dead coral), using a 1 m^2 PVC quadrant with an underwater digital camera (GoPro Hero 8 black; aspect ratio of 4:3) fixed in the center facing downward. Photographs of the substrate were taken from 1.5 m at two meters intervals, on each lateral of the 30 m transect (15 photographs on the right side and 15 on the left side). As the photographs presented a concave distortion inherent to the camera lens, image correction was performed using the software Adobe Photoshop CC 2020 (v. 21.0.3 for windows) with the distort tool, using the PVC quadrant as reference; in each image, the four squares were fixed and "distorted" until a straight squared was obtained. Once the images were corrected, we used the software ImageJ (v. 1.52a) to obtain the percentage of substrate type by 1 m^2.

We recorded fish abundance and richness for each 30 m transects using the underwater video-transect technique with an underwater digital camera (GoPro Hero 8 black at 1080 p resolution). To standardize the sampling effort and enhance transect homogeneity while recording, the technic proposed by Ramos *et al*. (2010) and Safuan (2015) was followed. Based on preliminary dives, the recording velocity along the transect was set to ~6 m/min and the wide of the image captured ~3 m. The camera was set to a rig and an underwater compass was attached and used as spirit level to maintain a horizontal line while filming. To maintain the distance between the camera and the bottom (~1.5 m), a rope with a 0.1 kg lead weight was attached to the rig.

Video recordings were reviewed five times using the software Adobe Premier Pro 2020, the mean abundance obtained from the five revisions was used in the analyses, and taxonomic and trophic guild identification was following Robertson, Allen (2015).

Data analyses. We performed Principal Component Analysis (PCA) based on correlation matrices to determine environmental gradients and similarities among sites regarding habitat variables. Prior to these analyses multiple correlations were used to identify redundant variables and avoid collinearity. This analysis simplifies multidimensional spaces avoiding loss of information related to the different variables (McCune *et al*., 2002). The Shannon-Wiener index (H') was used as measure of substrate diversity ($H'=\sum p_i \log_2 p_i$; p_i = proportion of each substrate type; García-Charton, Pérez-Ruzafa, 2001). Seasonal differences among abiotic variables related to the marine currents (CC *vs.* NEC) and among sites (CH, LG, ZC and MZ), were tested using one-way analysis of variance (ANOVA). Prior to ANOVA, data represented by proportions were arcsine transformed, continuous variables were Log_{10} transformed, and normality and homoscedasticity tests were performed (Shapiro-Wilk's and Bartlett respectively; $p \leq 0.05$). For variables that did not meet normality and/or homoscedasticity, non-parametric ANOVAs were considered. For variables with significant differences between seasons and among sites, paired comparisons were performed (*e.g.*, Tukey-Kramer HSD or Wilcoxon test). This was also performed for comparisons among sites regarding the H' index mentioned above.

Rarefaction analysis was performed (H = 0; endpoint = 1000; p = 0.05) to evaluate sampling effort related to species richness for each site and evenness was obtained based on $J = H'/ H'_{max}$ (Pielou, 1966). Beta diversity was calculated as an indicator of species turnover using the Whittaker index, and analysis of similarity (ANOSIM) based on Bray-Curtis distances with 999 permutations was performed to determine statistical differences (Chao, 1984; Magurran, 1988). Due to statistical differences were present in similarity/dissimilarity matrices (see results), Permutational multivariate analysis of variance (PERMANOVA) using pairwise-adonis test based on Bray-Curtis distances (999 permutations) and Bonferroni correction were performed (github.com/pmartinezarbizu/pairwiseAdonis/blob/master/pairwiseAdonis/R/pairwise.adonis.R). Non-metric multidimensional scaling (NMDS) based on ranked Bray-Curtis distance was used as an ordination procedure to illustrate differences among fish assemblages. This ordination method is not susceptible to problems associated with zero truncation. Simultaneously, the dissimilarity matrices were analyzed with a ANOSIM to determine statistical differences, and pair comparisons were performed using pairwise-adonis as mentioned, and comparisons among the number of fish species by guilds was performed by site and marine current. To elucidate segregation/aggregation patterns we used a null model of co-occurrence for CC and NEC assemblages using the algorithm SIM2 and de C-index in the EcoSimR 1.00 (Gotelli, Ellison, 2013; http://www.uvm.edu/~ngotelli/EcoSim/EcoSim.html). Simulation with SIM2 is based on fixed rows and equiprobable columns and randomizes the occurrence of each species among sites. Meanwhile, the C-index allows comparisons among tests by standardizing the effect score scaling the results in units of standard deviations. Significant differences suggest aggregation of species in the assemblage's data, while no statistical differences suggest segregation of species (Gotelli, 2000). Finally, to determine the relationship between seawater conditions and heterogeneity components with the fish assemblages, a multiple regression analysis was performed considering the scores obtained in each site for the first three PCA axes, the variables statistically different (*e.g*., pH, depth, dissolved oxygen, salinity, and temperature) and the assemblage axes values obtained from NMDS. The statistical software used for all the analyses was R (v. 4.1.3, R Development Core Team, 2022), through the libraries R: Vegan, EcoSimR 1.00, iNEXT, rich and PerformanceAnalytics (Rossi, 2011; Gotelli, Ellison, 2013; Hsieh *et al*., 2020; Peterson, Carl, 2020; Oksanen *et al*., 2022).

RESULTS

We found a non-normal distribution for all physicochemical variables of seawater: temperature ($W = 0.786$, $p < 0.001$), pH ($W = 0.860$, $p < 0.001$), salinity ($W = 0.683$, $p < 0.001$), and dissolved oxygen ($W = 0.923$ $p < 0.001$) (Shapiro-Wilks test). We found significant differences ($p <0.05$) between sites considering the changes in seawater conditions related to the effect of the marine currents. In general, CC (December-May) showed significantly lower temperatures compared to NEC (June-November; $x^2 =335.0$; g.l = 7, $p < 0.001$). The pH values presented small differences between currents, however, these small variations produced significant differences among sites and currents ($x^2 = 801.1$, g.l = 7, $p < 0.001$). Salinity showed significantly higher values during CC in comparison to NEC ($x^2 = 3469.4$; g.l = 7, $p < 0.001$). Dissolved oxygen was significantly higher in NEC for all sites, in comparison to CC ($x^2 = 3188.4$, g.l = 7, $p < 0.001$; Tab. 1). The PCA explained 98% of the variation in the first component, resulting in groups differentiated by seasons related to the influence of the annual ocean currents. Regarding the ordination, the first component (PC1) showed high association with dissolved oxygen, the second component (PC2) with temperature, and the third (PC3) with salinity (Fig. 2; Tab. 2).

TABLE 1 | Sea water conditions (physicochemical variables) of reefs (mean ± standard deviation) with pair comparisons (Kruskal-Wallis $p < 0.05$; Wilcoxon, W), in sampling sites regarding seasonality related to the California Current (CC) and the North Equatorial Current (NEC). Caleta de chon CC (A), Caleta de Chon NEC (B), Las Gatas CC (C), Las Gatas NEC (D), Manzanillo CC (E), Manzanillo NEC (F), Zacatoso CC (G), Zacatoso NEC (H). Letters in parenthesis represent groups for paired comparisons. No significant differences are represented by letters in the Tukey-HSD column.

Physicochemical Variables of sea water	Caleta de Chon		Las Gatas		Manzanillo		Zacatoso		Tukey-HSD
	CC	NEC	CC	NEC	CC	NEC	CC	NEC	
	(A)	(B)	(C)	(D)	(E)	(F)	(G)	(H)	
Temperature (°C)	26.40±0.36	29.70±0.23	26.30±0.59	30.00±0.15	26.40±0.08	29.9±0.042	26.9±0.178	29.8±0.039	AC
pH	8.00±0.03	8.00±0.16	7.90±0.04	7.90±0.02	7.90±0.08	7.9±0.073	7.9±0.051	8±0.063	ACG, BDF
Salinity (ppm)	33.80±0.15	33.4±0.02	33.80±0.16	33.40±0.01	33.80±0.15	33.4±0.006	33.8±0.088	33.3±0.004	EG
Dissolved oxygen (%)	109.40±3.87	113.60±1.07	98.00±7.40	112.20±2.61	94.40±6.68	113.3±2.539	101.7±2.509	106.4±1.069	AF, CG, DF

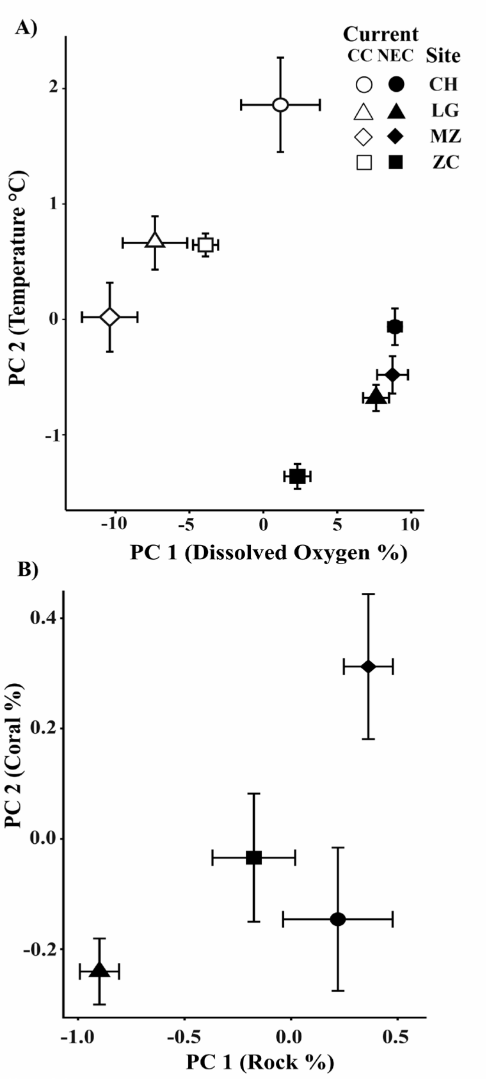

FIGURE 2 | Principal component analysis of (**A**) sea water conditions and (**B**) heterogeneity components in sampling sites for the California Current (CC) and North Equatorial Current (NEC). Sampled sites: Caleta de chon (CH), Las Gatas (LG), Manzanillo (MZ), and Zacatoso (ZC). Horizontal and vertical scatter bars represent 95% of confidence interval.

TABLE 2 | Principal component (PC) analysis of variables of reefs in sampling sites. Bold values represent variables highly related with the PC.

Variables	PC1	PC2	PC3
Cumulative variance (%)	0.983	0.998	1
Temperature	0.162	**-0.966**	0.203
pH	0.003	0.028	0.125
Salinity	-0.028	0.2	**0.971**
Dissolved Oxygen (%)	**0.986**	0.164	-0.006
Cumulative variance (%)	0.625	0.842	0.907
Depth	0.018	0.012	-0.147
Percentage of Sand	-0.003	-0.087	0.317
Precentage of Coral	0.085	**-0.639**	-0.55
Percentage of Rock	**-0.753**	0.453	-0.351
Percentage of Rubble	**0.651**	0.608	-0.298
Rugosity	-0.052	-0.057	-0.053

We found normal distribution for depth (W = 0.976, p < 0.268), while the other physical variables and the substrate diversity did not fit the model of normality (rugosity W = 0.964, p = 0.011; sand W = 0.49, p < 0.001; coral W = 0.555, p < 0.001; rock W = 0.804, p < 0.001; rubble W = 0.755, p < 0.001; substrate diversity W = 0.94, p < 0.001). On the other hand, depth, substrate diversity and rugosity showed homoscedasticity (df = 3, p < 0.529; df = 3, p = 0.18; p = 0.101, respectively) unlike sand (df = 3, p < 0.001), coral (df = 3, p < 0.001), rock (df = 3, p < 0.001), and rubble coverage (df = 3, p < 0.001). CH and ZC are significantly different from LG and MZ (df = 3, F = 14.45, p < 0.001) in depth. On the other hand, LG had higher rugosity (x^2 = 34.094; df = 3; p <0.001) and less substrate diversity (x^2 = 29.494, df = 3; p < 0.001) compared to all other sites. In addition, we found differences between sites: sand (x^2 = 17.90, df = 3, p = 0.0004), coral (x^2 = 35.09, df = 3, p < 0.001), rock (x^2 = 67.82, df = 3, p < 0.001) and rubble (x^2 = 32.04, df = 3, p < 0.001; Tab. 3) (Kruskal-Wallis test). PCA results explained 62% of the variation in the first component (PC1), which is highly associated with rock and rubble, the second component (PC2) explains 21% corresponding to coral (Tab. 2). It is worth mentioning that, in the PCA, LG is the most different site related to lower values in variables such as rugosity, sand, coral, rubble and depth, and the highest value of rock percentage (Tab. 3). Additionally, the variation in terms of standard deviations suggests that LG site was the most seasonally stable in most of the variables in comparison to all other sites (Tabs. 1–3; Fig. 2). Rarefaction analysis suggests that based on the sampling technique (video transects), the sites with the highest species richness were LG and ZC in both seasons with CC and NEC, although in the season with CC, the probability of unrecorded species in these sites is high, since rarefaction curves did not reach the asymptote (Fig. 3).

Based on video transects, a total of 36,282 individuals of seven orders, 26 families, 41 genera and 54 fish species were recorded. The families with the highest number of species were Labridae (9), Pomacentridae (6), and Haemulidae (4). The richness and abundance of the most recorded species was different between season; the most abundant species were *Thalassoma lucasanum* (Gill, 1862), and *Stegastes acapulcoensis* (Fowler, 1944) (Tab. **S1**). In general, the season with CC presented higher richness (54 species) and relative

TABLE 3 | Heterogeneity components of reefs (mean ± standard deviation) with pair comparisons (Kruskal-Wallis p < 0.05; Wilcoxon, W), in sampling sites. Letters in parenthesis represent groups for paired comparisons. No significant differences are represented by letters in the Tukey-HSD column.

Heterogeneity components	Caleta de Chon (A)	Las Gatas (B)	Manzanillo (C)	Zacatoso (D)	Wilcoxon-W
Sand %	9.00±0.155	2.90±0.04	17.70±0.203	9.1±0.174	ABC, BD
Coral %	10.40±0.20	0.70±0.01	19.00±0.262	10.5±0.218	AB, AD
Rock %	44.90±0.39	92.70±0.10	25.90±0.312	46±0.406	AC, AD
Rubble %	26.80±0.37	0.00±0.00	30.90±0.366	27.7±0.382	ACD
Rugosity	1.28±0.16	1.50±0.15	1.26±0.10	1.25±0.16	ACD
Depth (m)	8.80±1.51	6.60±2.45	7.10±1.97	10.3±1.788	AD, CB
Substrate diversity (H’)	0.55±0.08	0.49±0.07	0.60±0.063	0.56±0.080	AD, CD

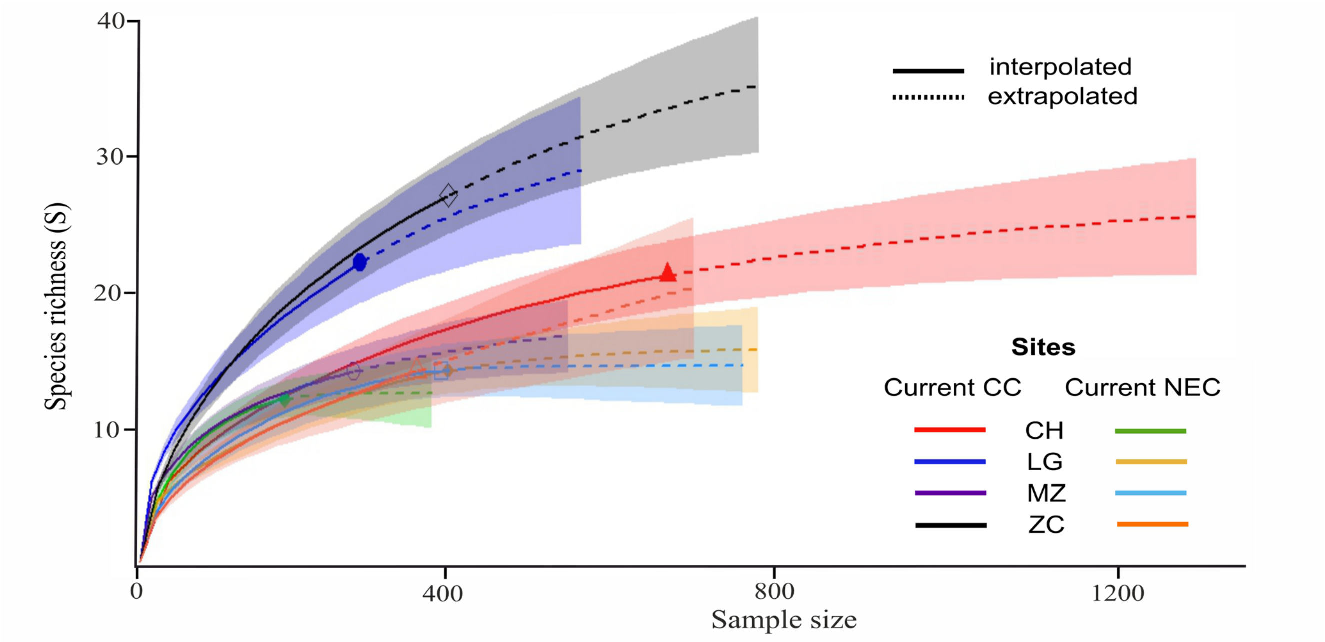

FIGURE 3 | Rarefaction curves of species richness for the California Current (CC) and North Equatorial Current (NEC) in the sampled sites: Caleta de chon (CH), Las Gatas (LG), Manzanillo (MZ), and Zacatoso (ZC). Shaded area represents 95% confidence interval.

abundance in comparison to NEC (36 species). The current with the highest values of evenness was CC (MZ =1; LG = 0.97; ZC = 0.93, and CH = 0.81) in comparison with NEC (MZ = 0.72; LG = 0.66; ZC = 0.66, and CH = 0.79). Regarding Beta diversity, a turnover of species during both seasons was present, and higher values in CC (CC, R = 0.51, p = 0.001; NEC, R = 0.41, p = 0.001).

The NMDS of the fish assemblages suggested differences between the two seasons: CC presented differences in the composition among sites, since ZC and LG did not present shared species. The fish assemblage obtained in NEC, showed greater variation in LG and ZC (Fig. 4). The similarity analysis (ANOSIM) confirmed statistical differences in the fish assemblages (R = 0.47; p = 0.001), and the paired comparisons obtained from the PERMANOVA showed differences among all assemblages by site and season (p > 0.001). Null model tests indicated segregate patterns of species co-occurrence for CC (C-score = 418.72; p = 0.996), and an aggregate pattern for NEC (C-score = 133.77; p < 0.005). The number of species by guilds showed that the number of carnivorous species were greater in all sites in comparison with herbivores, planktivorous and omnivorous (Fig. **S2**). Finally, for the relationship between physicochemical variables of sea water in reefs and fish assemblage structure, the results showed that NMDS1 was correlated with depth, NMDS2 with the percentage of rock cover, and NMDS3 presented the highest correlation values with temperature, dissolved oxygen, and salinity (Tab. 4).

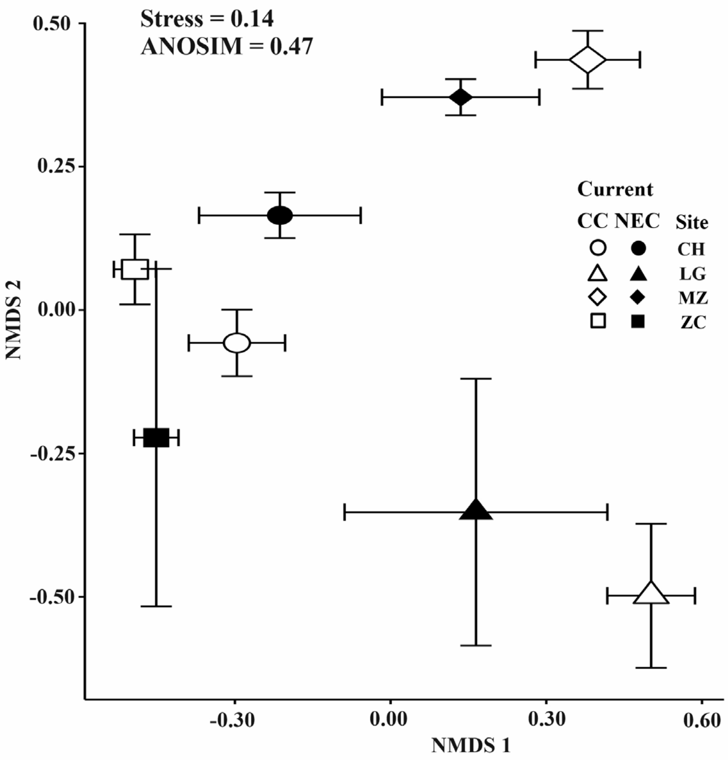

FIGURE 4 | Non-metric multidimensional scaling for fish assemblage data for the California Current (CC) and North Equatorial Current (NEC) in the sample sites: Caleta de chon (CH), Las Gatas (LG), Manzanillo (MZ), and Zacatoso (ZC). Horizontal and vertical scatter bars represent 95% confidence interval.

TABLE 4 | Pearson correlation coefficients (r values) of variables of reefs, PC scores (CPx-SW = Sea water conditions; CPx-HC = Heterogeneity components of reefs) with NMDS axis.

Variables	MSD1	MDS2	MDS3
Temperature	-0.334	-0.119	-0.608
pH	0.024	-0.128	-0.073
Salinity	0.291	0.101	0.593
Oxígeno disuelto (%)	-0.342	-0.249	-0.523
CP1-SW	-0.343	-0.246	-0.529
CP2-SW	0.059	-0.169	0.257
CP3-SW	-0.334	-0.077	-0.553
Depth	-0.489	-0.038	0.055
Percentage of Sand	0.170	0.194	0.007
Percentage of Coral	0.099	0.265	0.033
Percentage of Rock	0.047	-0.465	-0.040
Percentage of Rubble	-0.129	0.182	-0.003
Rugosity	0.221	-0.264	-0.068
CP1-HC	-0.091	0.383	0.024
CP2-HC	-0.113	-0.286	-0.046
CP3-HC	0.126	0.056	-0.012
Substrate diversity (H’)	-0.026	0.299	0.050

DISCUSSION

Since habitat heterogeneity has been proposed as an important factor structuring biological communities, in this study we evaluated fish assemblages in four sites exhibiting different habitat characteristics as components of heterogeneity. According to our hypothesis, the results indicated that fish assemblages were more diverse (species richness and abundance) in sites with greater substrate rugosity and higher variation in seawater conditions. Specifically, we found that substrates such as coral and rock were the most important components related to fish assemblage in the bays of Ixtapa-Zihuatanejo, and seawater conditions presented changes influenced by marine currents (CC and NEC) causing seasonal variations in the studied sites, which in turn were related to fish diversity. For instance, the values of evenness and species richness were higher in CC for all sites in comparison with NEC.

Relationship between water conditions and the structure of fish assemblages is reported for marine and freshwater environments (*e.g.*, Brind'Amour *et al.*, 2005; Santos *et al.*, 2017). The seasonal changes we found in fish assemblage were mostly related to temperature, salinity, and dissolved oxygen. In this sense, the Guerrero State presents constant but lower temperatures (~27°C) in CC related to a cold mass of water that converges and is displaced by Trade Winds (Alvarez-Filip *et al.*, 2006; Barjau *et al.*, 2012). In addition, the influence of the CC in the sampled sites also produced an increase in salinity (~34 ppt), primarily related to the mix of the water column with deeper waters during summer and fall; meanwhile pH is reported in ranges of 7.88–8.37, which in most cases are inversely related to the quantity of carbon dioxide (CO_2), suggesting that if pH values drop below 7.0, the presence and abundance of low tolerant species will decrease (Fiedler, Talley, 2006; Kessler, 2006; Pérez-Moreno *et al.*, 2016; Portela *et al.*, 2016). The values of dissolved oxygen in CC were lower than those for NEC. This could be attributed to an increase in the primary productivity due to marine upwelling and the trade winds throughout the CC, which produces higher diel variation in the consumption of dissolved oxygen by primary producers reducing oxygen concentration at local scale (Fiedler, Talley, 2006; Chiappa-Carrara *et al.*, 2019; Maske *et al.*, 2019).

We also found differences in fish assemblages among sites. Species richness was greater in ZC, followed by LG, CH and MZ in CC season (Fig. 3). This pattern was similar in NEC season, but in this case MZ species richness was higher than CH. LG was the site with the highest rugosity and percentage of rocks, while ZC was the most heterogeneous site based on percentage of rocks (Tab. 3). In marine ecosystems, habitat heterogeneity presents a positive relationship with fish richness and abundance, promoting biotic interactions such as density-dependent processes (Caley *et al.*, 1996; Hixon, Carr, 1997; Ault, Johnson, 1998; Jones, Syms, 1998; Folpp *et al.*, 2020). For example, the number and size of holes on different substrata are most related to abundance in reefs of the Red Sea (Roberts, Ormond, 1987). Moreover, LG is in a cove, while ZC was deepest site. It has been reported that deep reefs provide refuges for numerous shallow water fishes including many species endemic to these habitats (Lindfield *et al.*, 2016), whereas coves can give protection from strong winds and waves promoting habitat stability at local scale (Bejarano *et al.*, 2017; Graham *et al.*, 1997; Karkarey *et al.*, 2020), which might be important for reproduction and foraging sites. Thus, depth and site exposure to winds and waves might be additional habitat factors contributing to the species richness found in ZC and LG sites.

We recorded 54 species in total by using a video-transect technique, of which 32 were registered in both seasons. Previous studies in the bays of Ixtapa-Zihuatanejo based on visual records reported ~50 conspicuous and 108 cryptic species, including pelagic, residents and transient species of soft bottoms (Valencia-Méndez *et al*., 2021), while for other sites of the coast of the State of Guerrero (*e.g*., Bay of Acapulco), 114 species are reported with no mention of whether these were cryptic, conspicuous, or both (Palacios-Salgado *et al*., 2014). Nevertheless, these studies were conducted over 18 years and along a coastline of ~800 km, respectively.

The video-transects sampling technique is used to obtain data on richness and abundance of different taxonomic groups related to reefs (*e.g*., benthos: Ramos *et al*., 2010; fishes: Wartenberg, Booth, 2014), and is considered precise for monitoring conspicuous fishes in terms of richness and abundance, highlighting the implementation in the same sampling area and the experience of the diver (or subaquatic drone operators) to continuously trace the transect with the video-camera in a homogenous manner (Peters, 1991; Rogers, Miller, 2001; Hill, Wilkinson, 2004; Ramos *et al*., 2010; Wartenberg, Booth, 2015). Based on this and in the number of conspicuous species reported for the bays of Ixtapa-Zihuatanejo, we were able to have a good approximation of most conspicuous species using the video-transect technique, which is supported by the rarefaction results obtained for the sampled sites-currents, for which the asymptote was obtained for most of the sites-currents. We must highlight that differences in the fish species richness reported in different regions of the Mexican-Pacific is related not only with the sampling effort, but also to anomalies occurring every 4–5 years due to El Niño Southern Oscillation (ENSO), which can be a veil to elucidate patterns of changes in species richness at local or regional scale (Fiedler, Talley, 2006; Valencia-Méndez *et al*., 2021).

The most abundant species for both seasons and sites were *T. lucasanum*, *S. acapulcoensis*, *Microspathodon dorsalis* (Gill, 1862), and *Abudefduf troschelii* (Gill, 1862). However, our results showed changes in abundance between seasons and among all sites. These species are important biotic components, contributing more than 60% of the total fish biomass in coastal sites for the Tropical Eastern Pacific (Arias-Godínez *et al*., 2019). In the Pacific coasts, these species are associated with rocky reefs and have ecological relevance. For example, *T. lucasanum* feds on eggs and embryos of the other three species mentioned, acting as a density-dependent factor where seasonal changes promote this interaction (Foster, 1987; González-Mendoza *et al*., 2023). On the other hand, most of the sites (excluding CH) presented lower differences in water conditions in NEC, which suggests a more stable season for reproduction of most of the species recorded in this season (*e.g*., *Mulloidichthys dentatus* (Gill, 1862), *Epinephelus labriformis* (Jenyns, 1840), *Caranx caballus* Günther, 1868) (Green, McCormick, 2005; Mair *et al*., 2012; Lucano-Ramírez *et al*., 2019; Ruiz-Ramírez *et al*., 2019).

Based on the feeding habits reported in literature for the recorded fish species, the number of carnivorous species was higher in CC in comparison to NEC in all sites. These seasonal changes can be explained by the relation in temperature and marine upwellings in CC, with an increase in primary productivity and prey abundance (Fulton *et al*., 2005; Dornelas *et al*., 2006; Tian *et al*., 2014; Varela *et al*., 2018). By the other hand, the absence of planktivorous fish species in MZ could be associated to the presence of carnivorous fish species in sites where coral is the dominant substrate, changing the foraging behavior of planktivorous fish (Beukers, Jones, 1998; Bullard, Hay, 2002; Motro *et al*., 2005). Furthermore, the species co-occurrence model indicated a segregated pattern of species in CC, while an aggregate pattern for NEC. This is explained by changes in abundance and presence of 17 different species exclusive for this season (Alvarez-Filip *et al*., 2006; Valencia-Méndez *et al*., 2021). Besides, the beta diversity index showed higher values for CC, indicating high turnover species across sites. This suggests that the fish assemblage can be related with dispersion factors in CC and niche factors in NEC (Fiedler, Philbrick, 1991; Gotelli, 2000; Escalera-Vázquez, Zambrano, 2010).

Our results showed higher abundances of fish associated to changes in water conditions (*e.g*., increase in temperature), which resulted in low differences in the ordination comparing the same sites in different seasons (Fig. 4). The fish species that changed abundance between season were *Halichoeres dispilus* (Günther, 1864), *Thalassoma lucasanum*, *Chromis atrilobata* (Gill, 1862), and *S. acapulcoensis*. These species are reported to increase in abundance with temperature, and they can coexist at high abundances by differences in feeding behavior (Dominici-Arosemena, Wolff, 2006; Sánchez-Caballero *et al*., 2019).

These results provide evidence of the importance of maintaining sites with different substrate composition, depth, and exposure to wind and waves will allow the conservation of fish assemblages dynamics inhabiting seasonal environments in the bays of Ixtapa-Zihuatanejo. The conservation of these sites in the Mexican Tropical Pacific coast lies on the importance as part of a biological corridor, where increasing anthropogenic activities threaten the marine fish diversity.

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REFERENCES

- **Allen GR, Robertson DR.** Fishes of Tropical eastern pacific. Honolulu: University of Hawai'i Press; 1994.
- **Alvarez-Filip L, Reyes-Binilla H, Calderon-Aguilera LE.** Community structure of fishes in Cabo Pulmo reef, Gulf of California. Mar Ecol. 2006; 27(3):253–62. https://doi.org/10.1111/j.1439-0485.2006.00108.x
- **Androulidakis YS, Kombiadou KD, Makris CV, Baltikas VN, Krestenitis YN.** Storm surges in the Mediterranean Sea: Variability and trends under future climatic conditions. Dynam Atmos Ocean. 2015; 71:56–82. https://doi.org/10.1016/j.dynatmoce.2015.06.001

- **Arias-Godínez G, Jiménez C, Gamboa C, Cortés J, Espinoza M, Alvarado JJ.** Spatial and temporal changes in reef fish assemblages on disturbed coral reefs, north Pacific coast of Costa Rica. Mar Ecol. 2019; 40(1):e12532. https://doi.org/10.1111/maec.12532
- **Arreola-Robles JL, Elorduy-Garay JF.** Reef fish diversity in the region of La Paz, Baja California Sur, Mexico. Bull Mar Sci. 2002; 70(1):1–18. Available from: https://www.ingentaconnect.com/contentone/umrsmas/bullmar/2002/00000070/00000001/art00001
- **Ault TR, Johnson CR.** Spatially and temporally predictable fish communities on coral reefs. Ecol Monogr. 1998; 68(1):25–50. https://doi.org/10.2307/2657142
- **Barjau E, Rodríguez-Romero J, Galván F, Gutiérrez F, López J.** Estructura temporal y espacial de la comunidad de peces arrecifales de la Isla San José, Golfo de California, México. Rev Biol Trop. 2012; 60(2):649–67. https://doi.org/10.15517/rbt.v60i2.3957
- **Bejarano S, Jouffray J-B, Chollett I, Allen R, Roff G, Marshell A *et al*.** The shape of success in a turbulent world: wave exposure filtering of coral reef herbivory. Funct Ecol. 2017; 31(6):1312–24. https://doi.org/10.1111/1365-2435.12828
- **Beukers JS, Jones GP.** Habitat complexity modifies the impact of piscivores on a coral reef fish population. Oecologia. 1998; 114:50–59. https://doi.org/10.1007/s004420050419
- **Bowen BW, Rocha LA, Toonen RJ, Karl SA.** The origins of tropical marine biodiversity. Trends Ecol Evol. 2013; 28(6):359–66. https://doi:10.1016/j.tree.2013.01.018
- **Brind'Amour A, Boisclair D, Legendre P, Borcard D.** Multiscale spatial distribution of a littoral fish community in relation to environmental variables. Limnol Oceanogr. 2005; 50(2):465–79. https://doi.org/10.4319/lo.2005.50.2.0465
- **Bullard SG, Hay ME.** Plankton tethering to assess spatial patterns of predation risk over a coral reef and sea grass bed. Mar Ecol Prog Ser. 2002; 225:17–28. https://www.jstor.org/stable/24865392
- **Calderón-Aguilera E, Reyes-Bonilla H, López CON, Pérez RAL.** Los arrecifes coralinos de México: servicios ambientales y secuestro de carbono. Elem Pol Publ. 2017; 1(1):53–62. http://www.lead.colmex.mx/pdfs/elementos-politicas-publicas-ene-abr-2017.pdf#page=55
- **Caley MJ, Carr MH, Hixon MA, Hughes TP, Jones GP, Menge BA.** Recruitment and the local dynamics of open marine populations. Annu Rev Ecol Evol Syst. 1996; 27(1):477–500. https://doi.org/10.1146/annurev.ecolsys.27.1.477
- **Carranza-Edwards A, Gutiérrez-Estrada M, Rodríguez-Torres R.** Unidades morfotectónicas continentales de las costas mexicanas. Anales del centro de ciencias del mar y limnología. 1975; 2:81–88. Available from: http://biblioweb.tic.unam.mx/cienciasdelmar/centro/1975-1/articulo13.html
- **Centeno-García E, Guerrero-Suastegui M, Talavera-Mendoza O.** The Guerrero Composite Terrane of western Mexico: Collision and subsequent rifting in a supra-subduction zone. In: Draut AE, Clift PD, David W, Scholl DW, editors. Formation and applications of the sedimentary record in Arc Collision Zones; Colorado: GSA; 2008. p.276–308.
- **Chao A.** Nonparametric estimation of the number of classes in a population. Scand Stat Theory Appl. 1984; 11(4):265–70. Available from: https://www.jstor.org/stable/4615964?seq=1
- **Chiappa-Carrara X, Enríquez C, Papiol V, Mariño-Tapia I, Reyes-Hernández C.** Pacific Coast of Mexico. In: Sheppard C, editor. World seas: An environmental evaluation. Academic Press; 2019. p.655–71. https://doi.org/10.1016/B978-0-12-805068-2.00045-0
- **Dominici-Arosemena A, Wolff M.** Reef fish community structure in the Tropical Eastern Pacific (Panamá): living on a relatively stable rocky reef environment. Helgol Mar Res. 2006; 60:287–305. https://doi.org/10.1007/s10152-006-0045-4
- **Dornelas M, Connolly SR, Hughes TP.** Coral reef diversity refutes the neutral theory of biodiversity. Nature. 2006; 440(7080):80–82. https://doi.org/10.1038/nature04534

- **Escalera-Vázquez LH, Zambrano L.** The effect of seasonal variation in abiotic factors on fish community structure in temporary and permanent pools in a tropical wetland. Freshw Biol. 2010: 55(12):2557–69. https://doi.org/10.1111/j.1365-2427.2010.02486.x
- **Fiedler PC, Talley LD.** Hydrography of the eastern tropical Pacific: A review. Prog Oceanogr. 2006; 69(2–4):143–80. https://doi.org/10.1016/j.pocean.2006.03.008
- **Finch DM.** Habitat use and habitat overlap of riparian birds in three elevational zones. Ecology. 1989; 70(4):866–80. https://doi.org/10.2307/1941355
- **Folpp HR, Schilling HT, Clark GF, Lowry MB, Maslen B, Gregson M *et al*.** Artificial reefs increase fish abundance in habitat–limited estuaries. J Appl Ecol. 2020; 57(9):1752–61. https://doi.org/10.1111/1365-2664.13666
- **Foster SA.** Acquisition of a defended resource: a benefit of group foraging for the Neotropical wrasse, *Thalassoma lucasanum*. Environ Biol Fish. 1987; 19:215–22. https://doi.org/10.1007/BF00005350
- **Friedman A, Pizarro O, Williams SB, Johnson-Roberson M.** Multi-scale measures of rugosity, slope and aspect from benthic stereo image reconstructions. PLoS ONE. 2012; 7(12):e50440. https://doi.org/10.1371/journal.pone.0050440
- **Fulton CJ, Bellwood DR, Wainwright PC.** Wave energy and swimming performance shape coral reef fish assemblages. Proc Royal Soc B. 2005; 272(1565):827–32. https://doi.org/10.1098/rspb.2004.3029
- **García-Charton J, Pérez-Ruzafa Á.** Spatial pattern and the habitat structure of a Mediterranean rocky reef fish local assemblage. Mar Biol. 2001; 138:917–34. https://doi.org/10.1007/s002270000524
- **Glynn PW, Morales GEL.** Coral reefs of Huatulco, West Mexico: reef development in upwelling Gulf of Tehuantepec. Rev Bio Trop. 1997; 45(3):1033–47. Available from: https://revistas.ucr.ac.cr/index.php/rbt/article/view/21114/21241
- **González-Mendoza T, López-Pérez A, Valencia-Méndez O, Torres-Hernández P, García-Medrano D, Ortiz-Martínez L *et al*.** Nesting sites and parental care in the giant blue damselfish, *Microspathodon dorsalis*. Environ Biol Fish. 2023; 106:79–91. https://doi.org/10.1007/s10641-022-01378-7
- **Gotelli NJ.** Null model analysis of species co-occurrence patterns. Ecology. 2000; 81(9):2606–21. https://doi.org/10.1890/0012-9658(2000)081[2606:NMAOSC]2.0.CO;2
- **Gotelli NJ, Ellison AM.** EcoSimR 1.00. 2013. Available from: http://www.uvm.edu/~ngotelli/EcoSim/EcoSim.html
- **Graham MH, Harrold C, Lisin S, Light K, Watanabe JM, Foster MS.** Population dynamics of giant kelp *Macrocystis pyrifera* along a wave exposure gradient. Mar Ecol Prog Ser. 1997; 148:269–79.
- **Green BS, McCormick MI.** O_2 replenishment to fish nests: males adjust brood care to ambient conditions and brood development. Behav Ecol. 2005; 16(2):389–97. https://doi.org/10.1093/beheco/ari007
- **Greenberg CH, Harris LD, Neary DG.** A comparison of bird communities in burned and salvage-logged, clearcut, and forested Florida sand pine scrub. Wilson Bull. 1995; 107(1):40–54. https://www.jstor.org/stable/4163511
- **Hixon MA, Carr MH.** Synergistic predation, density dependence, and population regulation in marine fish. Science. 1997; 277:946–49. https://doi.org/10.1126/science.277.5328.946
- **Hsieh TC, Ma KH, Chao A.** iNEXT: iNterpolation and EXTrapolation for species diversity. R package version 3.0.0. 2020. Available from: https://sites.google.com/view/chao-lab-website/software/inext?authuser=0
- **Hughes TP, Barnes ML, Bellwood DR, Cinner JE, Cumming GS, Jackson JB *et al*.** Coral reefs in the Anthropocene. Nature. 2017; 546(7656):82–90. https://doi.org/10.1038/nature22901
- **Jackson JB, Kirby MX, Berger WH, Bjorndal KA, Botsford LW, Bourque BJ *et al*.** Historical overfishing and the recent collapse of coastal ecosystems. Science. 2001; 293(5530):629–37. https://doi.org/10.1126/science.1059199
- **Jones GP, Syms C.** Disturbance, habitat structure and the ecology of fishes on coral reefs. Austral Ecol. 1998; 23(3):287–97. https://doi.org/10.1111/j.1442-9993.1998.tb00733.x

- **Kamikuri S, Motoyama I, Nishi H, Iwai M.** Evolution of eastern Pacific warm pool and upwelling processes since the middle Miocene based on analysis of radiolarian assemblages: Response to Indonesian and Central American Seaways. Palaeogeogr Palaeoclimatol Palaeoecol. 2009; 280(3–4):469–79. https://doi.org/10.1016/j.palaeo.2009.06.034
- **Karkarey R, Rathod P, Arthur R, Yadav S, Theo A, Alcoverro T.** Wave exposure reduces herbivory in post-disturbed reefs by filtering species composition, abundance and behaviour of key fish herbivores. Sci Rep. 2020; 10:9854. https://doi.org/10.1038/s41598-020-66475-y
- **Kessler WS.** The circulation of the eastern tropical Pacific: A review. Prog Oceanogr. 2006; 69(2–4):181–217. https://doi.org/10.1016/j.pocean.2006.03.009
- **Lindfield SJ, Harvey ES, Halford AR, McIlwain JL.** Mesophotic depths as refuge areas for fishery-targeted species on coral reefs. Coral Reefs. 2016; 35:125–37. https://doi.org/10.1007/s00338-015-1386-8
- **Levey DJ.** Tropical wet forest treefall gaps and distributions of understory birds and plants. Ecology. 1988; 69(4):1076–89. https://doi.org/10.2307/1941263
- **López-Pérez RA, Calderón LE, Reyes-Bonilla H, Carriquiry JD, Medina-Rosas P, Cupul-Magaña AL *et al*.** Coral communities and reefs from Guerrero, southern Mexican Pacific. Mar Ecol. 2012; 33(4):407–16. https://doi.org/10.1111/j.1439-0485.2011.00505.x
- **Lowe JR, Williamson DH, Ceccarelli DM, Evans RD, Russ GR.** Responses of coral reef wrasse assemblages to disturbance and marine reserve protection on the Great Barrier Reef. Mar Biol. 2019; 166:119. https://doi.org/10.1007/s00227-019-3566-5
- **Lucano-Ramírez G, Robles-Ravelero M, Ruiz-Ramírez S, González-Sansón G, Aguilar-Betancourt C, Perez-Toledo A.** Biología reproductiva de *Mulloidichthys dentatus* (Perciformes: Mullidae) en el Pacífico tropical mexicano. Rev Biol Mar Oceanogr. 2019; 54(1):118–28. https://doi.org/10.22370/rbmo.2019.54.1.1656
- **MacArthur R, Levins R.** The limiting similarity, convergence, and divergence of coexisting species. Am Nat. 1967; 101(921):377–85. https://doi.org/10.1086/282505
- **MacArthur RH, Wilson EO.** The theory of island biogeography. Princeton University Press; 1967.
- **McCoy ED, Bell SS.** Habitat structure: the evolution and diversification of a complex topic. In: Bell SS, McCoy ED, Mushinsky HR, editors. Habitat structure: The physical arrangement of objects in space. London: Chapman and Hall; 1991. p.3–27.
- **Magurran AE.** Ecological diversity and its measurement. Princeton University Press; 1988.
- **Mair JM, Cipriani R, Guzman HM, Usan D.** Fishery of the green jack *Caranx caballus* (Osteichytes: Carangidae) in Las Perlas Archipelago, Pacific Panama. Rev Biol Trop. 2012; 60(3):1271–88. https://doi.org/10.15517/rbt.v60i3.1806
- **Maske H, Escovar E, Sanchez L, Almeda-Jauregui CO, Chapa-Balcorta C, Sosa-Avalos R *et al*.** Zona del mínimo de oxígeno en el Pacífico Mexicano. Estado del Ciclo del Carbono: Agenda Azul y Verde. Programa Mexicano del Carbono Texcoco, Estado de México, México; 2019. Available from: https://pmcarbono.org/pmc/publicaciones/eccm.php
- **Mason NWH, Lanoiselée C, Mouillot D, Wilson JB, Argillier C.** Does niche overlap control relative abundance in French lacustrine fish communities? A new method incorporating functional traits. J Anim Ecol. 2008; 77(4):661–69. https://doi.org/10.1111/j.1365-2656.2008.01379.x
- **McCune B, Grace JB, Urban DL.** Analysis of ecological communities. Gleneden Beach, OR: MjM software design; 2002.
- **Moberg F, Folke C.** Ecological goods and services of coral reef ecosystems. Ecol Econ. 1999; 29(2):215–33. https://doi.org/10.1016/S0921-8009(99)00009-9
- **Morin PJ.** Community ecology. United States: Wiley Blackwell; 2011. https://doi.org/10.1002/9781444341966
- **Motro R, Ayalon I, Genin A.** Near-bottom depletion of zooplankton over coral reefs: III: vertical gradient of predation pressure. Coral Reefs. 2005; 24:95–98. https://doi.org/10.1007/s00338-004-0451-5
- **Nava H, López N, Ramírez-García P, Garibay-Valladolid E.** Contrasting effects of the El Niño 2015–16 event on coral reefs from the central pacific coast of Mexico. Mar Ecol. 2021; 42(2):e12630. https://doi.org/10.1111/maec.12630

- **Nava H, Ramírez MT, Figueroa-Camacho AG, Villegas-Sanchez BM.** Habitat characteristics and environmental factors related to boring sponge assemblages on coral reefs near populated coastal areas on the Mexican Eastern Pacific coast. Mar Biodiv. 2014; 44:45–54. https://doi.org/10.1007/s12526-013-0182-3
- **Nava H, Ramírez-Herrera MT.** Land use changes and impact on coral communities along the central Pacific coast of Mexico. Env Earth Sc. 2012; 65:1095–104. https://doi.org/10.1007/s12665-011-1359-3
- **Oksanen J, Simpson G, Guillaume F, Kindt R, Legendre P, Minchin P *et al*.** vegan: Community ecology package. R package version 2.6-4; 2022. Available from: https://CRAN.R-project.org/package=vegan
- **Palacios-Salgado DS, Ramírez-Valdez A, Rojas-Herrera AA, Amores JG, Melo-García MA.** Marine fishes of Acapulco, Mexico (Eastern Pacific Ocean). Mar Biodiv. 2014; 44(4):471–90. https://doi.org/10.1007/s12526-014-0209-4
- **Paulay G.** Diversity and distribution of reef organisms. In: Birkeland C, editor. Life and death of coral reefs. New York: Chapman & Hall; 1997. p.298–353.
- **Sánchez-Caballero CA, Borges-Souza JM, Ferse SCA.** Rocky reef fish community composition remains stable throughout seasons and El Niño/La Niña events in the southern Gulf of California. J Sea Res. 2019; 146:55–62. https://doi.org/10.1016/j.seares.2019.01.008
- **Santos NCL, Santana HS, Ortega JCG, Dias RM, Stegmann LF, Araújo IMS *et al*.** Environmental filters predict the trait composition of fish communities in reservoir cascades. Hydrobiologia. 2017; 802:245–53. https://doi.org/10.1007/s10750-017-3274-4
- **Pérez-Moreno V, Ramos-López MÁ, Zavala-Gómez CE, Rodríguez MAR.** Heavy metals in seawater along the Mexican Pacific coast. Interciencia. 2016; 41(6):419–23. Available from: https://www.interciencia.net/wp-content/uploads/2017/10/419-PEREZ-41-6.pdf
- **Peterson B, Carl P.** Performance analytics: Econometric tools for performance and risk analysis. R package version 2.0.4. 2020. Available from: https://CRAN.R-project.org/package=PerformanceAnalytics
- **Pielou EC.** The measurement of diversity in different types of biological collections. J Theor Biol. 1966; 13:131–44. https://doi.org/10.1016/0022-5193(66)90013-0
- **Portela E, Beier E, Barton ED, Castro R, Godínez V, Palacios-Hernández E *et al*.** Water masses and circulation in the tropical Pacific of central Mexico and surrounding areas. J Phy Ocean. 2016; 46(10): 3069–81. https://doi.org/10.1175/JPO-D-16-0068.1
- **R Development Core Team.** R: The R project for statistical computing. Vienna, Austria: R Foundation for Statistical Computing; 2022. Available from: https://www.r-project.org/
- **Ramos CAC, Amaral FD, Kikuchi RKP, Chaves EM, Melo GR.** Quantification of reef benthos communities and variability inherent to the monitoring using video transect method. Environ Monit Assess. 2010; 162:95–101. https://doi.org/10.1007/s10661-009-0778-z
- **Roberts CM, Ormond RFG.** Habitat complexity and coral reef fish diversity and abundance on Red Sea fringing reefs. Mar Ecol Prog Ser. 1987; 41:1–08. https://doi.org/10.3354/meps041001
- **Robertson DR, Allen G.** Shorefishes of the Tropical Eastern Pacific online information system. Version 2.0 [Internet]. Balboa: Smithsonian Tropical Research Institute; 2015. Available from: https://biogeodb.stri.si.edu/sftep/es/pages
- **Rogers A, Blanchard JL, Mumby PJ.** Vulnerability of coral reef fisheries to a loss of structural complexity. Curr Biol. 2014; 24(9):1000–05. https://doi.org/10.1016/j.cub.2014.03.026
- **Rossi J-P.** rich: an R package to analyze species richness. Diversity. 2011; 3(1):112–20. https://doi.org/10.3390/d3010112
- **Ruiz-Ramírez S, Pérez-Segoviano AM, Lucano-Ramírez G, González-Sansón G, Flores-Ortega JR.** Reproducción de la cabrilla pinta *Epinephelus labriformis* en la Bahía de Navidad, Jalisco, México. Rev Biol Mar Oceanogr. 2019; 53(3):335–47. https://doi.org/10.22370/rbmo.2018.53.3.1358
- **Safuan M, Boo WH, Siang HY, Chark LH, Bachok Z.** Optimization of coral video transect technique for coral reef survey: Comparison with intercept transect technique. Op J Mar Sci. 2015; 5:379–97. https://doi.org/10.4236/ojms.2015.54031

- **Saleh A.** Soil roughness measurement: chain method. J Soil Water Conserv. 1993; 48(6):527–29. Available from: https://www.jswconline.org/content/48/6/527
- **Spalding MD, Brown BE.** Warm-water coral reefs and climate change. Science. 2015; 350(6262):769–71. https://doi.org/10.1126/science.aad0349
- **Spalding MD, Ravilious C, Green EP.** World atlas of coral reefs. Berkeley: University of California Press; 2001.
- **Stubbs WJ, Wilson JB.** Evidence for limiting similarity in a sand dune community. J Ecol. 2004; 92(4):557–67. https://doi.org/10.1111/j.0022-0477.2004.00898.x
- **Thomson D, Findley L, Kerstitch A.** Reef fishes of the Sea of Cortez: The rocky-shore fishes of the Gulf of California. Revised Edition. University of Texas Press; 1979. p.302.
- **Tian Y, Uchikawa K, Ueda Y, Cheng J.** Comparison of fluctuations in fish communities and trophic structures of ecosystems from three currents around Japan: synchronies and differences. ICES J Mar Sci. 2014; 71(1):19–34. https://doi.org/10.1093/icesjms/fst169
- **Valencia-Méndez O, Rodríguez-Zaragoza FA, Palacios-Salgado D, Ramírez-Valdez A, López-Pérez A.** Biological inventory and latitudinal gradient of the rocky and reef associated fish along the southern Mexican Pacific. Mar Biodiv. 2021; 51:3. https://doi.org/10.1007/s12526-020-01145-w
- **Varela R, Lima FP, Seabra R, Meneghesso C, Gómez-Gesteira M.** Coastal warming and wind-driven upwelling: a global analysis. Sci Total Environ. 2018; 639:1501–11. https://doi.org/10.1016/j.scitotenv.2018.05.273
- **Wang C, Enfield DB.** The tropical Western Hemisphere warm pool. Geophys Res Lett. 2001; 28(8):1635–38. https://doi.org/10.1029/2000GL011763
- **Willig MR, Kaufman DM, Stevens RD.** Latitudinal gradients of biodiversity: Pattern, process, scale, and synthesis. Annu Rev Ecol Evol Syst. 2003; 34:273–309. https://doi.org/10.1146/annurev.ecolsys.34.012103.144032

AUTHORS' CONTRIBUTION

Luis H. Escalera-Vázquez: Conceptualization, Data curation, Formal analysis, Investigation, Methodology, Supervision, Validation, Visualization, Writing-original draft, Writing-review and editing.

Francisco Martínez-Servín: Conceptualization, Data curation, Investigation, Methodology, Project administration, Resources, Writing-original draft.

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The author declares no competing interests.

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