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Greater resilience of reef fish assemblages in a no-take reserve compared to multi-use areas of the Gulf of California

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ABSTRACT

Conservation strategies, such as the establishment of Marine Protected Areas (MPAs), aim to safeguard biodiversity and to promote resilience of ecosystems by increasing their capacity to maintain key functions and processes following disturbance. However, the extent to which ecosystems in MPAs exhibit resilience remains debated. To address this question, we evaluated changes in reef fish species and functional diversity over time in relation to environmental and anthropogenic disturbances at multiple locations in the Gulf of California, Mexico. From 2005 to 2017, we assessed reef fish species richness and abundance in three MPAs: one no-take marine reserve (Cabo Pulmo) and two multi-use marine protected areas (MUMPAs: Espíritu Santo and Loreto). To examine change in functional diversity and composition, we calculated three functional diversity indices – functional richness, functional dispersion and functional originality – using six functional traits (size, mobility, activity, gregariousness, water column position, and diet). Species richness, density and functional diversity were maintained over time (resilience) in the no-take marine reserve. In contrast, MUMPAs showed temporal decline in species richness, which translated into decreases in functional richness and increases in functional dispersion. These differences were also observed at the species level: in Cabo Pulmo, only two 'loser' species declined in density, while Espíritu Santo and Loreto showed declines of 12 and 17 species, respectively. The two MUMPAs also shared 9 of the total 22 'loser' species, which are generally abundant and common in the Gulf of California. Density declines were attributed to the combined effect of environmental (sea surface temperature and chlorophyll anomalies) and anthropogenic (fishing, tourism and coastal population density) disturbances. Given the regional decline and the ecological importance of dominant species, long-term decreases in their populations can profoundly modify processes and reef ecosystem services in this region. Thus, local management strategies should be implemented to try to reverse the observed recent decline in fish diversity in MUMPAs.

Keywords: Fish fauna, functional diversity, linear mixed effect models, canonical correspondence analysis, marine protected areas, Mexico.

1. Introduction

Biodiversity loss in reef ecosystems associated with environmental (El Niño events and marine heat waves) and anthropogenic (overfishing, pollution or increase in tourism activities) drivers can result in loss of ecological functions and services (Miller et al., 2011; Mouillot et al., 2013). To cope with these disturbances, biological systems respond to new conditions at individual (physiological acclimatization), population (changes in distribution ranges and demography), and community (ecological reorganization) organization levels (Webster et al., 2017).

At the community level, overlap in species functions (redundancy) allows communities to preserve ecological processes and therefore present high resilience (Figge, 2004; Hooper et al., 2005), defined as the capacity of a system to maintain structure or function in the presence of disturbance (Walker et al., 2007; O'Leary et al., 2017). This 'portfolio effect' is theoretically possible but in practice, it has been difficult to assess resilience in natural communities. To this end, the combination of traditional biodiversity metrics (e.g. species richness) with biological trait analysis (used as a proxy of species functional roles) has become an essential tool to determine the degree of functional redundancy in biotic assemblages, and improve our understanding of the response of ecosystems to disturbance (Hooper et al., 2005; Mouillot et al., 2013).

Conservation strategies involving the establishment of Marine Protected Areas (MPAs) are among the primary means to safeguard biodiversity and to promote resilience of ecosystems by increasing their capacity to maintain key functions and processes following disturbance (Agardy, 1994; Micheli et al., 2014). Different protection schemes involving MPAs have been established around the world, ranging from fishing bans in no-take marine reserves, to the regulation of extractive activities in multi-use marine protected areas (MUMPAs; Agardy et al., 2003; Sala and Giakoumi, 2017). Previous analyses have shown that well-managed no-take marine reserves lead to increased fish abundances and species richness (Lester et al., 2009), whereas studies in MUMPAs have generally demonstrated positive but non-significant outcomes in these ecological indicators (Lester and Halpern, 2008).

The extent to which reef ecosystems in MPAs exhibit resilience to disturbances remains uncertain as a result of the scarcity of analyses of functional diversity change over time, which in turn is due to the difficulty to maintain long-term monitoring and to the lack of continuous data (Edgar and Stuart-Smith, 2014, Fulton et al., 2019). Long-term monitoring programs, such as those in place at temperate reefs in Tasmania since 1992, have shown changes in species richness and increases in functional diversity in studies conducted over decadal periods (A. E. Bates et al., 2014). These changes include effects of tropicalization (rise in temperature and the associated decrease in the concentration of nutrients) that manifest regardless of the different management schemes (no-take marine reserves or MUMPAs). However, even in the presence of these environmental changes, long-term no-take marine reserves present greater stability (low temporal variability) in biological responses to disturbances in comparison with fished sites in Tasmania (A. E. Bates et al., 2014). Interestingly, the biotic response to perturbations can be similar across different level of protection; for example, areas of the Great Barrier Reef showed a general decline in species richness and fish density associated with the impact of tropical cyclone Yasi (2011), followed by recovery of herbivorous/detritivorous and planktivorous fish. This response was similar everywhere, independent of the protection scheme (Bierwagen et al., 2018).

Long-term biodiversity data have also been analyzed in different MPAs of the Gulf of California, Mexico. In 2006, Alvarez-Filip and Reyes-Bonilla showed declines in fish species richness in the Cabo Pulmo MPA between 1987 and 2003, following a severe coral bleaching event caused by the 1997-1998 El Niño and a series of hurricanes that impacted the reef in 2002-2003. These events significantly modified the habitat (coral cover loss > 50%) and caused a decline of associated invertebrates and fishes. However, at the same time fish assemblages showed maintenance in functional diversity, which was attributed to a high degree of functional redundancy. Aburto-Oropeza and collaborators (2011) also reported that fish biomass was similar between Cabo Pulmo, core zones of MUMPAs (including Espíritu Santo and Loreto), and open access sites immediately after the ENSO event, in 1999, but after ten years of protection, in 2009, Cabo Pulmo presented a dramatic increase of fish biomass (463%) and species richness (166%). This positive effect was attributed to social (support of the protection measures by residents, continuous monitoring and application of environmental regulations) and ecological (creation of a large ~ 70 km^2 MPA, good condition of the coral community, high primary productivity and presence of fish spawning areas) factors. Recently, a trophodynamic ECOPATH model based on survey (2017-2018) and published data found evidence that Cabo Pulmo is a relatively mature ecosystem that exhibits high resilience to disturbances, such as coral bleaching and hurricanes, compared to other ecosystems from the Tropical Eastern Pacific (Calderon-Aguilera et al., 2021). By conducting taxonomic, functional and trophic analyses, these studies have shown that the Cabo Pulmo reefs have been resilient since the establishment of the MPA (1995). However, further analyses are necessary to determine if this capacity is maintained through time.

The effectiveness of protection was also evaluated at the Loreto MPA (central Gulf of California) in a continuous time series (1998 to 2010), which found an increase in herbivorous and planktivorous fish biomass in a small no-take zone within the MPA, while the rest of the MPA -where fishing is allowed- did not show significant temporal changes (Rife et al., 2013a). The authors conclude that the management strategies have contributed to maintain the original conditions of fish assemblages, but that it is necessary to promote enforcement to avoid or reduce legal and illegal fishing inside the MPA.

Finally, evaluation of changes in fish assemblages through time (2005 to 2017) in the Espíritu Santo MPA showed that the conservation aims of this MUMPA have not been accomplished because, despite a long-term increase in biomass (associated to a general increase in fish average size) and maintenance in density and functional originality, species richness, functional richness and some species significantly declined due to competitive interactions, habitat loss, and persistence of fishing pressure (Ramírez-Ortiz et al., 2020). Since buffer and no-take zones presented similar results, the authors recommended enforcement of fishing regulations and surveillance in core zones to promote the conservation of fish functional diversity in this MUMPA.

In this paper we evaluated 1) whether fish species richness, density and functional diversity changed through time (2005 to 2017) in one no-take marine reserve (Cabo Pulmo) and two MUMPAs (Espíritu Santo and Loreto) of the Gulf of California, and 2) if changes were associated with environmental or anthropogenic disturbances. This kind of analysis is important considering that the region has been exposed to continuous and intense disturbances, which include high fishing pressure (70% of the fishing activities in México are performed in the Gulf; Cisneros-Mata, 2010; Díaz-Uribe et al., 2013), and accelerated coastal development (Lluch-Cota et al. 2007; Franco-Ochoa et al., 2020), as well as recent increases in sea surface temperature (2013 to 2016: ~ + 2 °C) and declines in primary productivity (~ -1.5 mg/m^3; Gomez-Ocampo et al., 2018). Under these pressures, it is relevant to assess the effects of anthropogenic and environmental disturbances on reef fish functional diversity in MPAs to determine if conservation strategies have been able to mitigate the impacts of these chronic pressures.

To accomplish our goal, we evaluated temporal changes in fish diversity in each MPA. Our premise is that if the area maintained fish species richness, density and functional diversity throughout the study period, it should be considered resilient. If the MPA exhibited changes, we analyzed how variation in the presence and density of common species (those present in > 50% of the surveys) in each MPA contributed to the observed trends in the indices. Finally, we examined the possible role of environmental and anthropogenic variables in explaining temporal population change. We tested the hypotheses that a decrease in fish species richness translates into negative changes in functional diversity independently of the protection scheme, and that the no-take marine reserve Cabo Pulmo and the MUMPAs (Espíritu Santo and Loreto) exhibit similar decline patterns at the assemblage and species level due to a combination of environmental and anthropogenic disturbances that have been observed in the Gulf of California within the last decade.

2. Methods

2.1. Study area

The Gulf of California is a dynamic marginal sea (1,600 km long) of the Eastern Pacific Ocean, considered as a transition zone between tropical and subtropical climate regimes, that is exposed to multi-year processes such as the El Niño–Southern Oscillation (ENSO) and the Pacific Decadal Oscillation (PDO; Lluch-Cota et al., 2013). The Gulf of California is an area of high primary productivity with a latitudinal gradient (highest values in the north compared to the south portion), associated with three main natural fertilization mechanisms: tidal mixing, thermohaline circulation and wind-induced upwelling (Álvarez-Borrego, 2010; Mercado-Santana et al., 2017). Thermohaline circulation is derived from the movement of warmer and less dense surface water (Tropical Surface Water and Gulf of California Water) into the Pacific, that balances with deep colder water (Subtropical Subsurface Water) into the Gulf of California (Castro et al., 2006). This dynamic has profound ecological implications because inflowing deep water has high inorganic nutrient concentrations and it is responsible for the transport of other materials (e.g. larvae and pollutants; Álvarez-Borrego and Lara-Lara, 1991). Upwelling events have a strong effect in the Gulf of California eastern coast were Chlorophyll-a concentration (CHL_a) can exceed 10 mg/m^3, in comparison with the weak effect in the western coast where southeasterly winds and surface sea currents often flow in the opposite direction during summer (July to October) and CHL_a increases only ~ 0.5 mg/m^3 (Santamaría-del-Ángel et al., 1999; Lluch-Cota, 2000; Álvarez-Borrego, 2010).

Biogeographically, the Gulf of California represents the Cortez Province and harbors 698 species out of the 1,139 species registered in the Tropical Eastern Pacific (Robertson and Cramer, 2009), and is also considered a specific marine ecoregion (Cortezian) due to its particular benthic and pelagic biota (Spalding et al., 2007). In the Gulf of California, ten MPAs have been established to protect biodiversity and to control extraction of natural resources in historically important fishing areas (Rife et al., 2013b). For this study, three of them (with different level of protection; Fig. 1) were selected because their fish assemblages have been surveyed for over a decade, and they are relatively close to each other (~ 100km apart) therefore have experienced a similar degree of environmental variability within the study period (Fig. S3). We compiled fish monitoring data from visual censuses performed between 2005 and 2017 at Parque Nacional Cabo Pulmo, a MPA established in the year 1995 with a total area of 71.11 km^2, 35% of which is a no-take zone, and where fishing bans extended to 99.6% of the polygon due to the action of the local community and the support of federal agencies (Aburto-Oropeza et al., 2011).

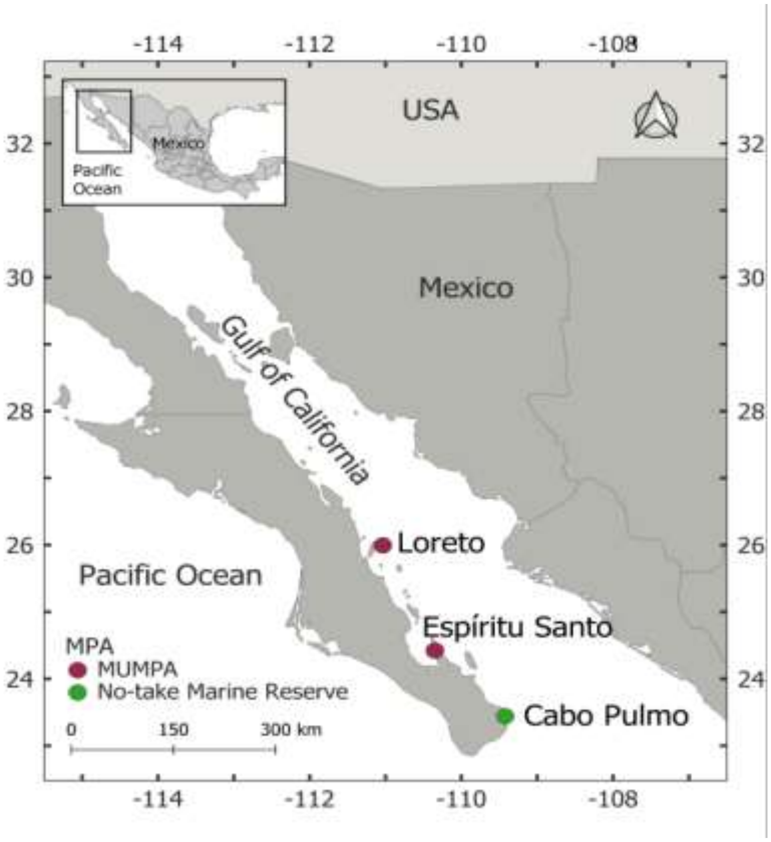

Fig. 1. Study area showing the three MPAs of the Gulf of California where fish surveys were conducted between 2005 and 2017: Cabo Pulmo (N= 144 surveys; 16 sites), Espíritu Santo (N= 320 surveys; 11 sites), Loreto (N= 372 surveys; 47 sites).

In addition, we incorporated into this analysis two MUMPAs that comprise no-take and "buffer" zones where no industrial fishing occurs but some artisanal and recreational fishing activities are allowed (Agardy et al., 2003): a) Parque Nacional

Bahía de Loreto, one of the oldest (1996) and largest MPA in the Gulf of California with a total area of 2,065.8 km^2 but only 0.07% no-take zone (CONANP, 2019); and b) Parque Nacional zona marina del Archipiélago de Espíritu Santo with a total area of 486.54 km^2 (1.4% no-take zone), which was implemented in 2007 (CONANP-SEMARNAT, 2014). The latter was included in the IUCN Green List of Protected Areas in 2018 (IUCN, 2018), and temporal changes of fish functional diversity were previously analyzed by Ramírez-Ortiz and collaborators (2020).

2.2. Data collection

The original dataset included 5,743 transects performed within the depth limits of recreational SCUBA diving (2 to 30 m) in two seasons (cold: January to June, and warm: July to November). Transects that were surveyed closer than 200 m within the same day at a similar depth range were not considered independent and were combined into new sampling units (surveys) following the Reef Life Survey methodology (Edgar and Stuart-Smith, 2014). After this treatment, we obtained a total of 836 surveys that were used to calculate species richness and density (as standardized number of individuals/100 m^2). Before processing, density values were transformed using logarithm base 2 to achieve normality and homoscedasticity. With the information of species richness per survey we constructed species accumulation curves (randomization method) that allowed us to determine that we had a large enough sample (> 80 surveys) to adequately characterize the species pool in each MPA (Fig. S1).

2.3. Data analysis

To determine if fish diversity was maintained (resilience) or if it changed throughout the study period, we analyzed temporal trends in species richness, density, and functional diversity in each MPA following the methods of Ramírez-Ortiz et al. (2020). We classified fish species observed in the field according to the six biological attributes used in previous global and regional analysis (size, mobility, period of activity, aggregation, position in water column and diet) that reflect key aspects of fish ecology

(Olivier et al., 2018). We allocated an alphanumeric code to each species, which corresponds to a particular combination of traits (functional entity, FE; Table 1). These codes were used to construct a matrix of categorical traits that were transformed into a numerical matrix by calculating the paired distances between species using Gower dissimilarity, which allows the use of different types of variables while giving them equal weight (Gower, 1971).

With the dissimilarity matrix we performed a Principal Coordinate Analysis (PCoA) to reduce the trait information by generating orthogonal variables. Additionally, to determine how many dimensions were necessary to build a reliable functional space, we performed the analysis of its quality using the R function 'quality_funct_space' of Maire and collaborators (2015). Based on the low value of the mean squared deviation (mSD= 0.004) between the initial and the scaled functional distance for all MPAs, we chose the first four axes to calculate three functional indices: a) Functional richness – which represents the functional volume occupied by all species of an assemblage; a decrease in this index over time could potentially signal a loss of species with extreme combinations of traits under prevailing environmental conditions, thus leading to more homogeneous assemblages (Mason et al., 2005; Mouillot et al., 2005; Mouillot et al., 2013); b) Functional dispersion – the weighted average distance in functional space of individual species to the weighted centroid of the assemblage, where weights correspond to the abundance or density of each taxon (Laliberté and Legendre, 2010); its low values could be attributed to environmental filtering, since only those species with traits suited for the environment can persist (Bower and Winemiller, 2019); c) Functional originality – the weighted average distance between each species and its closest neighbor within functional space; decreasing values over time indicate increasing functional redundancy (Mouillot et al., 2013).

To determine temporal trends at the community level, we used species richness, density, functional richness, functional dispersion and functional originality as response variables in linear mixed models (LMM) that included year as fixed factor, and site (reefs > 200 m apart) and season (cold and warm) as random variables, to account for spatial and temporal autocorrelation associated with repeated monitoring (Zuur et al., 2009). We present the temporal trends of the five ecological indicators in coefficient graphs that show the standardized values of the estimates, with standard errors and statistical significance.

If the MPA exhibited significant changes in these indices, we assessed how variation at the species level contributed to observed trends. For this, we selected common species as those that were present in over 50% of the total surveys at each MPA (Cabo Pulmo= 21 out of 97 total species, Espíritu Santo= 26 out of 99 total species, Loreto = 27 out of 103 total species), in order to control the influence of zero-density values in short time series (Alvarez-Filip et al., 2015). Then, using data on presence and density (rounded to an integer), we performed individual generalized mixed effect models (GLMM) with binomial and negative binomial distributions, respectively (Zuur et al., 2009). Species with significant increases over time were categorized as 'winners', those without significant changes were called 'neutrals', and fish species with significant decreases were considered 'losers'. These categories were incorporated into PCoA graphs to visualize the distribution of species with significant changes within the functional space, which allowed us to make inferences about the results of temporal community analyses. LMM and GLMM were performed with the "lme4" R package (D. Bates et al., 2014).

To assess the effect of disturbances in species changes over time at each MPA, we analyzed the relationship between environmental/anthropogenic variables and the presence/density of 'winner' and 'loser' species through canonical correspondence analyses (CCAs; Oksanen, 2011). We used the annual presence (number of censuses where a species was registered related to the total surveys per year) and the average annual density (arithmetic mean of a species density at all censuses performed within a year) of 'winner' and 'loser' species at each MPA (Table 1) as response variables in the CCAs, while the explanatory variables included three anthropogenic (fishing pressure, visitors and human population around the MPA) and seven environmental factors: coral cover, hurricanes, photosynthetically active radiation (PAR), chlorophyll-a concentration (CHL_a), particulate organic and inorganic carbon concentration (POC and PIC), and sea surface temperature (SST). More detailed information about these variables is provided in Table S2.

For PAR, CHL_a, POC, PIC, and SST, we calculated annual averages of standardized anomalies (environmental conditions above or below the historic average value) using 204 monthly satellite images (January 2003 to December 2019) downloaded from the OceanColor server of NASA with a spatial resolution of ~ 4km and obtained by the Aqua-MODIS satellite. Subsequently, we matched the annual values of each variable with the study period in which the fish censuses were performed (2005 to 2017) and we considered a lag to the previous year because the effects of these variables on commercially fished species usually manifest between one and ten months later (Marín-Enríquez, 2013) and not immediately. For the estimation of hurricanes we calculated the hurricane hazard index for each year (Table S2; Hernández et al., 2018), while for coral cover we calculated the annual percentage of scleractinian coral cover for all sampled sites in each MPA (more detailed information is provided in Table S2).

Regarding anthropogenic factors, we used the annual reports of catch registered at the closest office to the MPA provided by Comisión Nacional de Pesca (CONAPESCA) and compiled by dataMares (Loreto and Los Cabos; Mascareñas-Osorio et al., 2018) and Universidad Autónoma de Baja California Sur (UABCS; La Paz) as an indicator of fishing pressure. For visitors estimation, we used the number of bracelets sold each year to visitors in the MPA registered by the Comisión Nacional de Áreas Naturales Protegidas (CONANP), while for human population we compiled the number of inhabitants within the municipality adjacent to the MPA obtained from Instituto Nacional de Estadística y Geografía (INEGI) for the years 2005, 2010 and 2015. For visitors and human population, we calculated the values of the missing years in the time series through linear regression constructed from the available data (more detailed information about these variables is provided in Table S2).

To determine if the inclusion of a variable in each CCA was statistically justified, we used the model building process known as "forward stepwise" from the "step" function of the "stats" R package (R core team, 2013). With this method, we started with an unrestricted model (with no variables) and added variables step by step until we had a complex model with the ten disturbances considered in this study. The selection of the best model was based on the Akaike Information Criterion (AIC; Zuur et al., 2009). Once we selected the best models for ‘winners’ and ‘losers’ in presence and density at each MPA, permutation analyses were performed with the "vegan" package (Oksanen et al., 2007) to test the models' significance, the importance of each axis (proportion of variation in the biological data attributable to environmental/anthropogenic factors), and the marginal effects of each included variable. Finally, we plotted CCAs using the "ggplot2" R package (Wickham et al., 2016) with a type 2 scale, which emphasizes the relationship between environmental variables and species (Oksanen, 2011). These graphs allowed us to observe the Chi-square distance between species centroids (whose optimal distribution is given by their presence or average density) and environmental/anthropogenic data vectors with direction towards the maximum change of the associated variable and length given by the correlation with the ordination axes (Hollarsmith et al., 2020; Lara and González, 1998).

3. Results

Temporal analyses revealed non-significant changes in the no-take marine reserve Cabo Pulmo for the five ecological indicators (Fig. 2a), while MUMPAs Espíritu Santo (Fig. 3a; Ramírez-Ortiz et al. 2020) and Loreto (Fig. 4a) showed significant decreases in species richness that translated into less functional richness and higher functional dispersion at the end of the study period. Functional originality showed non-significant changes in all MPAs, which suggests that despite the low functional redundancy, the core ecological trait values have been maintained through time (Table S1).

3.1. No-take marine reserve Cabo Pulmo

The result of non-significant changes in fish diversity at Cabo Pulmo indicates resilience due to the maintenance of species richness and functional diversity in the face of regional disturbances (Fig. S2). This pattern was confirmed at the species level, where the presence of 21 common species was maintained during the study period (Fig. 2b), while for density only six species showed significant changes (two 'winner' and four 'loser' species located close to the functional centroids; Fig. 2c). Density declines in 'loser' species were correlated with measures of anthropogenic disturbances (human population around the MPA and visitors; Fig. 5a), but none of the analyzed variables explained positive changes for ‘winner’ species (Table S4).

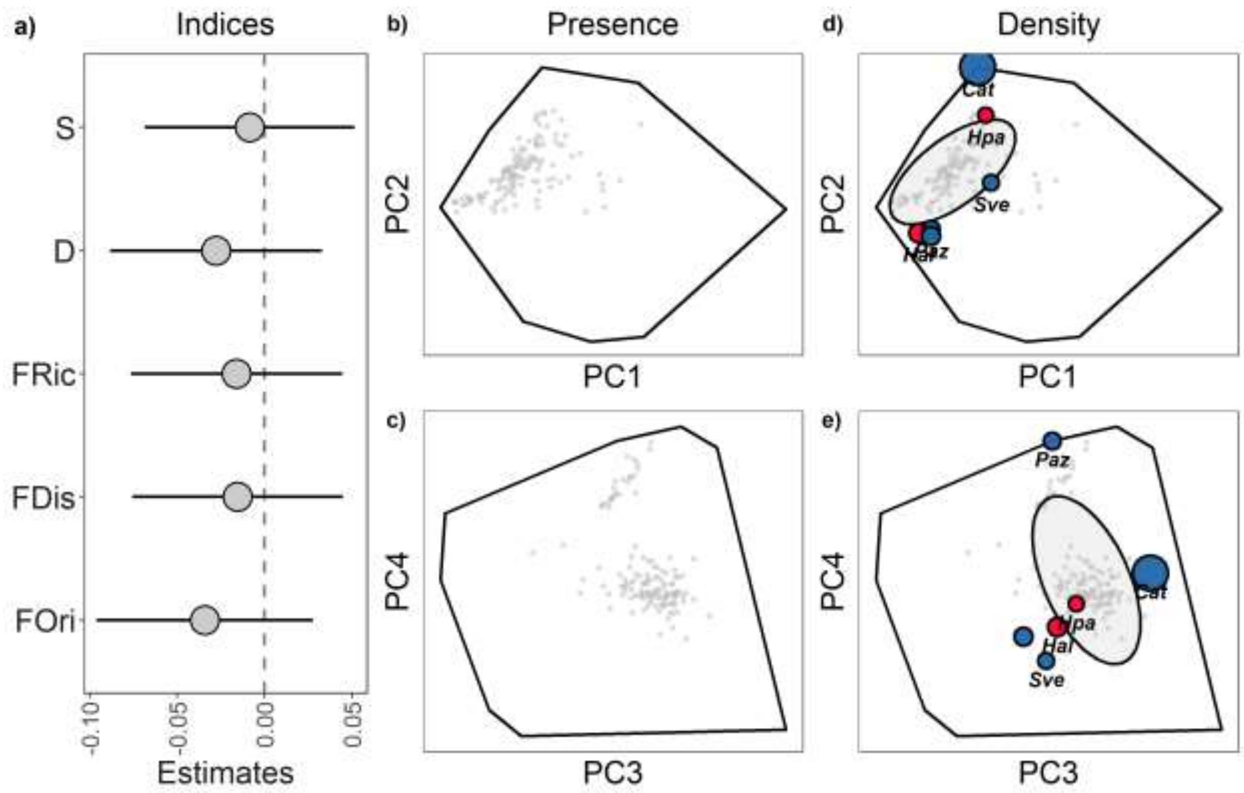

Fig. 2. a) Temporal change of ecological indicators expressed as standardized coefficients (mean ± 95% confidence interval) of LMMs for Cabo Pulmo. Gray circles indicate non-significant change. b and c) Position in the functional space (PC1-PC2 and PC3-PC4) of ‘winners’ (blue), ‘neutrals’ (gray) and ‘losers’ (red) for presence (b) and density (c) models in the no-take marine reserve. Dots’ size is proportional to z-values of the GLMMs, and average-weight centroids (one per transect) are indicated by gray dots; in c, ellipses indicate 95% confidence intervals. Codes of the principal species are included (Table 1).

Note: Cat= *C. atrilobata*, Hal= *Halichoeres sp.*, Hpa= *H. passer*, Sve= *S. verres*, Paz= *P. azaleus*

Table 1. List of common fish species (presence in > 50% of the surveys) registered in the Gulf of California MPAs and analyzed with GLMM for changes in presence (P) and density (D). For each species their code (first letter of the genus and first two letters of the species or first three letters of the genus), functional entity (FE; Olivier et al., 2018), density (average ± SD) and redundancy (species within the same FE) is indicated. Bold letters indicate commercially fished species (Niparajá, 2011). Gray cells indicate species with GLMM validated results: 'winners' (W; significant increase), 'neutrals' (N; non-significant change) or 'losers' (L; significant decrease over time).

Family	Species	Code	FE	Cabo Pulmo	P	D	Espíritu Santo	P	D	Loreto	P	D	Redundancy
Acanthuridae	*Prionurus laticlavius*	Pla	53D41HD	8.26 ± 13.13	N	N	6.31 ± 15.21	N	W	3.15 ± 7.15	W	N	
Blenniidae	*Plagiotremus azaleus*	Paz	21D11FC	3.97 ± 6.67	N	W	0.36 ± 1.13			0.15 ± 0.62			
	Ophioblennius steindachneri	Ost	31D11OM	1.31 ± 2.09	N	N	1.88 ± 5.30			0.43 ± 1.27			
Chaetodontidae	*Johnrandallia nigrirostris*	Jni	32D32OM	1.06 ± 2.81	N	N	2.25 ± 3.60	N	L	0.76 ± 1.67	N	N	
Cirrhitidae	*Cirrhitichthys oxycephalus*	Cox	21D31FC	8.99 ± 11.86	N	N	7.32 ± 14.84	N	L	2.41 ± 4.14	L	L	
Haemulidae	***Haemulon sexfasciatum***	Hse	53N31FC	2.41 ± 16.05			1.82 ± 6.38			2.65 ± 5.07	N	N	
Kyphosidae	***Kyphosus sp.***	Kyp	53D12HD	1.16 ± 3.47			0.54 ± 1.91			0.80 ± 2.11	N	W	
Labridae	***Bodianus diplotaenia***	Bdi	53D11IM	3.41 ± 4.92	N	N	4.01 ± 3.23	N	N	5.20 ± 5.63	N	L	*C. brachysomus, B. polylepis*
	Halichoeres chierchiae	Hal	32D11IM	0.85 ± 1.91	N	L	1.65 ± 10.81	W	N	0.29 ± 0.98			*H. dispilus,H. notospilus, S. inornatus*
	Halichoeres dispilus	Hal	32D11IM	6.12 ± 21.90	N	N	2.72 ± 4.64	W	N	3.82 ± 7.16	N	L	*H. chierchiae, H. notospilus, S. inornatus*
	Thalassoma grammaticum	Tgr	42D11IM	1.37 ± 3.05	N	W	1.74 ± 7.93			0.35 ± 3.27			*H. nicholsi, H. semicinctus, I. pavo*
	Thalassoma lucasanum	Tlu	22D31IM	58.88 ± 68.50	N	N	43.22 ± 57.59	N	L	22.38 ± 27.57	N	L	
Lutjanidae	***Lutjanus argentiventris***	Lar	53N41FC	2.58 ± 13.62			3.89 ± 6.91	N	W	1.28 ± 5.54			
Mullidae	***Mulloidichthys dentatus***	Mde	43N31IM	3.63 ± 14.09			12.86 ± 33.96	N	N	3.52 ± 11.75	L	N	

Family	Species	Code	FE	Cabo Pulmo	P	D	Espíritu Santo	P	D	Loreto	P	D	Redundancy
Pomacanthidae	*Abudefduf troschelii*	Atr	32D42Pk	1.55 ± 5.84			32.03 ± 42.47	N	L	35.23 ± 41.14	N	L	
	Holacanthus passer	Hpa	42D32IS	1.39 ± 1.91	N	L	2.91 ± 2.78	N	N	3.09 ± 4.12	N	L	
Pomacentridae	*Chromis atrilobata*	Cat	22D42Pk	33.22 ± 74.18	N	W	86.66 ± 207.28	N	L	38.71 ± 93.07	N	L	
	Chromis limbaughi	Cli	21D31Pk	0.24 ± 1.86			9.98 ± 34.90	L	L	9.14 ± 22.60			
	Microspathodon dorsalis	Mdo	41D11HD	0.31 ± 1.02			1.00 ± 1.77	L	L	1.28 ± 2.89	N	L	
	Stegastes flavilatus	Sfl	21D11HD	3.21 ± 4.37	N	N	0.55 ± 1.49			0.51 ± 2.76			*S. leucorus, S. rectifraenum*
	Stegastes rectifraenum	Sre	21D11HD	8.69 ± 11.63	N	N	14.71 ± 12.78	N	L	38.90 ± 37.21	N	L	*S. leucorus, S. flavilatus*
Scaridae	***Scarus compressus***	Sca	53D11HD	0.14 ± 0.33			1.21 ± 2.68	N	W	0.38 ± 0.78	N	L	*C. carolinus, S.perrico, S. rubroviolaceus*
Scaridae	***Scarus ghobban***	Sgh	63D11HD	0.55 ± 1.06			3.99 ± 6.13	L	L	1.59 ± 3.06	N	L	
	Scarus perrico	Sca	53D11HD	0.32 ± 0.86			0.58 ± 1.16			0.54 ± 1.05	L	L	*C. carolinus, S.compressus, S.rubroviolaceus*
	Scarus rubroviolaceus	Sca	53D11HD	0.82 ± 3.65	N	N	0.74 ± 1.43	L	L	0.41 ± 0.67	N	L	*C. carolinus, S.compressus, S. perrico*
Serranidae	*Alphestes immaculatus*	Aim	32N11IM	0.02 ± 0.08			0.32 ± 0.63			0.27 ± 0.47	N	N	*Pareques sp.*
	Cephalopholis panamensis	Cpa	42D11FC	0.32 ± 0.62			0.70 ± 0.88	N	W	0.76 ± 1.21	N	N	
	Epinephelus labriformis	Ela	52N11FC	0.55 ± 1.12	N	N	0.68 ± 1.21	N	W	0.37 ± 0.58	N	N	
	Mycteroperca rosacea	Mro	63N11FC	1.41 ± 3.43	N	N	1.14 ± 2.06	L	N	1.38 ± 2.33	N	L	*H. guentherii*
	Cephalopholis colonus	Cco	43D42Pk	9.92 ± 23.55			23.43 ± 52.89	N	N	10.08 ± 18.59	N	W	
	Serranus psittacinus	Sps	32D11FC	0.61 ± 1.06	N	N	0.51 ± 1.19			1.83 ± 3.11	N	L	

Family	Species	Code	FE	Cabo Pulmo	P	D	Espíritu Santo	P	D	Loreto	P	D	Redundancy
Balistidae	***Balistes polylepis***	Bpo	53D11IM	0.58 ± 1.69			1.28 ± 4.58	N	W	1.02 ± 3.16	W	W	*C. brachysomus, B. diplotaenia*
	Sufflamen verres	Sve	43D31IM	1.35 ± 2.67	N	W	0.69 ± 1.45	L	L	0.23 ± 0.92			
Diodontidae	*Diodon holocanthus*	Dho	42N11IM	0.66 ± 2.12			0.76 ± 1.02	L	N	0.98 ± 1.50	N	L	*D. hystrix*
Ostraciidae	*Arothron meleagris*	Ame	42D11IS	0.71 ± 1.38	N	N	0.15 ± 0.36			0.01 ± 0.04			*S. annulatus*
	Canthigaster punctatissima	Cpu	21D11IS	3.07 ± 3.26	N	N	5.83 ± 4.15	N	L	6.41 ± 5.31	N	L	

Note: Functional entities (FE) alphanumeric code can be interpreted by the categories Size (2: 7.1-15 cm, 3: 15.1-30 cm, 4: 30.1-50 cm, 5: 50.1-80 cm, 6: > 80 cm); Mobility (1: low/territorial, 2: medium/within a reef, 3: high/between reefs, 4: very high/widely mobile); Activity period (D: diurnal, N: nocturnal); Gregariousness (1: solitary, 2: living in pairs, 3: small-medium groups 3-50 individuals, 4: large > 50 individuals groups); Position in the water column (1: benthic, 2: bentho-pelagic, 3: pelagic); Diet (H: herbivore/detritivore, IS: invertivores sessile, IM: invertivores vagile, Pk: planktivores, FC: piscivores, OM: omnivores).

3.2. Multi-use areas Espíritu Santo and Loreto

Functional richness decreased significantly in both MUMPAs, and presence declines primarily occurred in species with extreme traits located on the outer margins of the functional space, such as the planktivore *C. limbaughi,* the herbivore/detritivore *S. ghobban*, and the invertivore *D. holocanthus* for Espíritu Santo (Fig. 3b). Moreover, functional dispersion increased, and this change was associated with density declines at species near the 95% confidence interval ellipses of the centroids, such as the reef invertivore *T. lucasanum*, the omnivore *J. nigrirostris*, and the planktivore *A. troschelii* for Espíritu Santo (Fig. 3c), and the planktivore *H. passer* and the piscivore *C. oxycephalus* for Loreto (Fig. 4c; Table 1). By analyzing species identity, we found that Espíritu Santo and Loreto showed overlap in 9 out of the 22 'loser' species (Table 1), which indicates that the decline in these species could be a regional level feature.

Espíritu Santo showed fewer 'winners' (presence: 2 species, density: 6 species) than 'losers' (presence: 7 species, density: 12 species), and most species with significant declines were located towards the edges of the functional space (Fig. 3b; Fig. 3c), suggesting the loss of specialist species. Decreases in presence of commercially fished piscivores (*M. rosacea*) and herbivores/detritivores (*S. ghobban* and *S. rubroviolaceus*) in Espíritu Santo were correlated with negative anomalies of SST (Fig. 5b), while the increase of *H. chierchiae* was correlated with negative anomalies of CHL_a (Fig. 5c; Table S3). In contrast, a functionally redundant of the latter species, *H. dispilus,* also categorized as 'winner' (Table 1), exhibited the opposite pattern (increases in presence associated to positive anomalies in CHL_a; Fig. 5c).

Negative anomalies of CHL_a were associated to density declines of the planktivore *A. troschelii*, invertivores (*C. punctatissima* and *D. holocanthus*), and herbivores/detritivores (*S. rectifraenum, S. ghobban,* and *S. rubroviolaceus*; Fig. 3d). Additionally, anthropogenic disturbances such as increased visitors and human population around the MUMPA (Fig. 5d) coincided with density declines of common species at Espíritu Santo (Table S4).

Furthermore, the density decline of the small piscivore *C. oxycephalus* was associated with coral cover declines, and increased visitors and human population around Espíritu Santo MUMPA (Fig. 5d), while for density ‘winners’ none of the factors considered here was related to positive changes (Table S4).

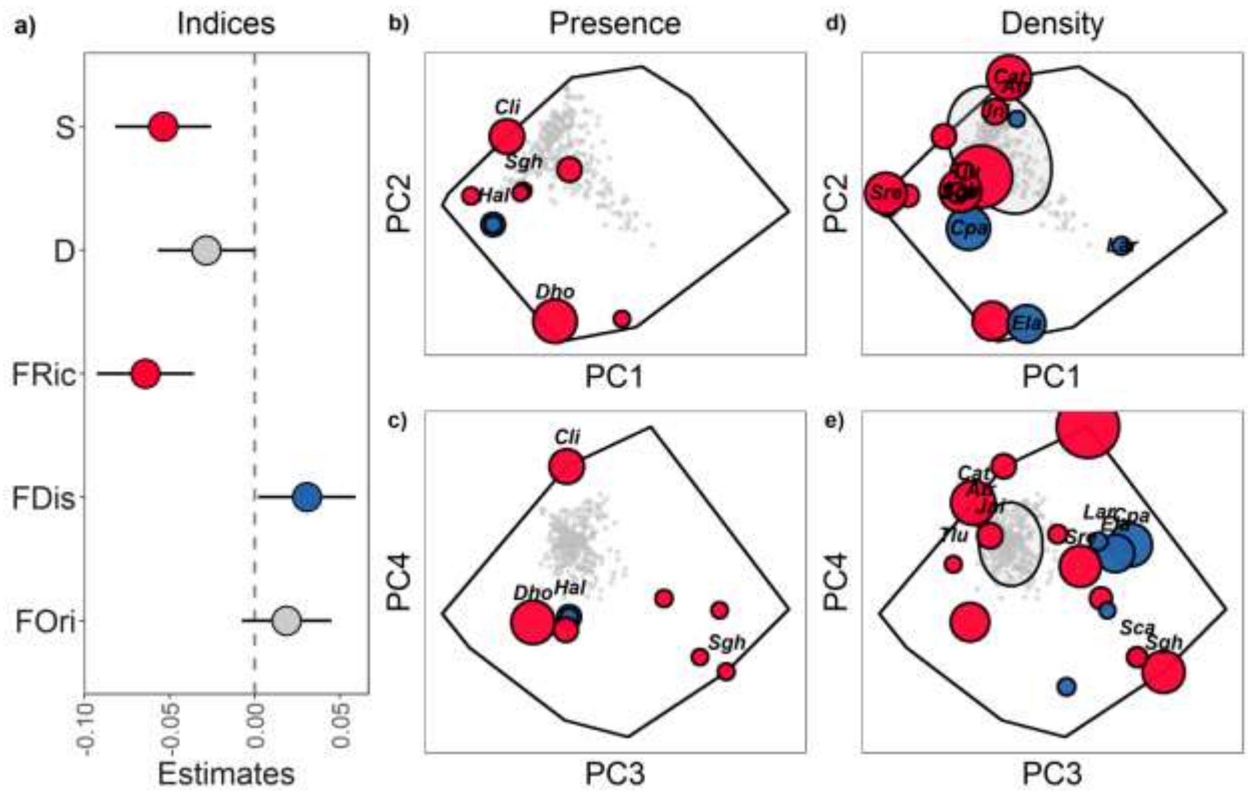

Fig. 3. a) Temporal change of ecological indicators expressed as standardized coefficients (mean ± 95% confidence interval) of LMMs for MUMPA Espíritu Santo. Blue and red circles show significant positive and negative changes, respectively, while gray circles indicate non-significant change. b and c) Position in the functional space (PC1-PC2 and PC3-PC4) of ‘winners’ (green), ‘neutrals’ (gray) and ‘losers’ (red) for presence (b) and density (c) models in the MUMPA. Dots’ size is proportional to z-values of the GLMMs, and the average-weight centroids (one per transect) are indicated by gray dots; in c), ellipses indicate 95% confidence intervals (Ramírez-Ortiz et al., 2020). Codes of the principal species are included (Table 1).

Note: Atr= *A. troschelii*, Cat= *C. atrilobata*, Cli= *C. limbaughi*, Cpa= *C. panamensis*, Dho= *D. holocanthus*, Ela= *E. labriformis*, Hal= *Halichoeres sp*., Jni= *J. nigrirostris*, Lar= *L. argentiventris*, Sre= *S. rectifraenum*, Sca= *Scarus sp.*, Sgh= *S. ghobban*, Tlu= *T. lucasanum*.

Loreto MUMPA also showed a few ‘winner’ species (presence: 2 species, density: 3 species), along with substantial declines in presence (3 species; Fig. 4b) and density (17 species; Fig. 4c) of species located throughout the functional space. This indicates that density decrease in fish occurs in a large number of species and at multiple levels in the functional structure over time. Although none of the analyzed disturbances had a significant correlation with presence (Table S3), CCA (Table S4) showed a combined correlation of environmental (anomalies of SST) and anthropogenic (fisheries and human population around the MUMPA) factors with the density decline of 17 species (Fig. 5e).

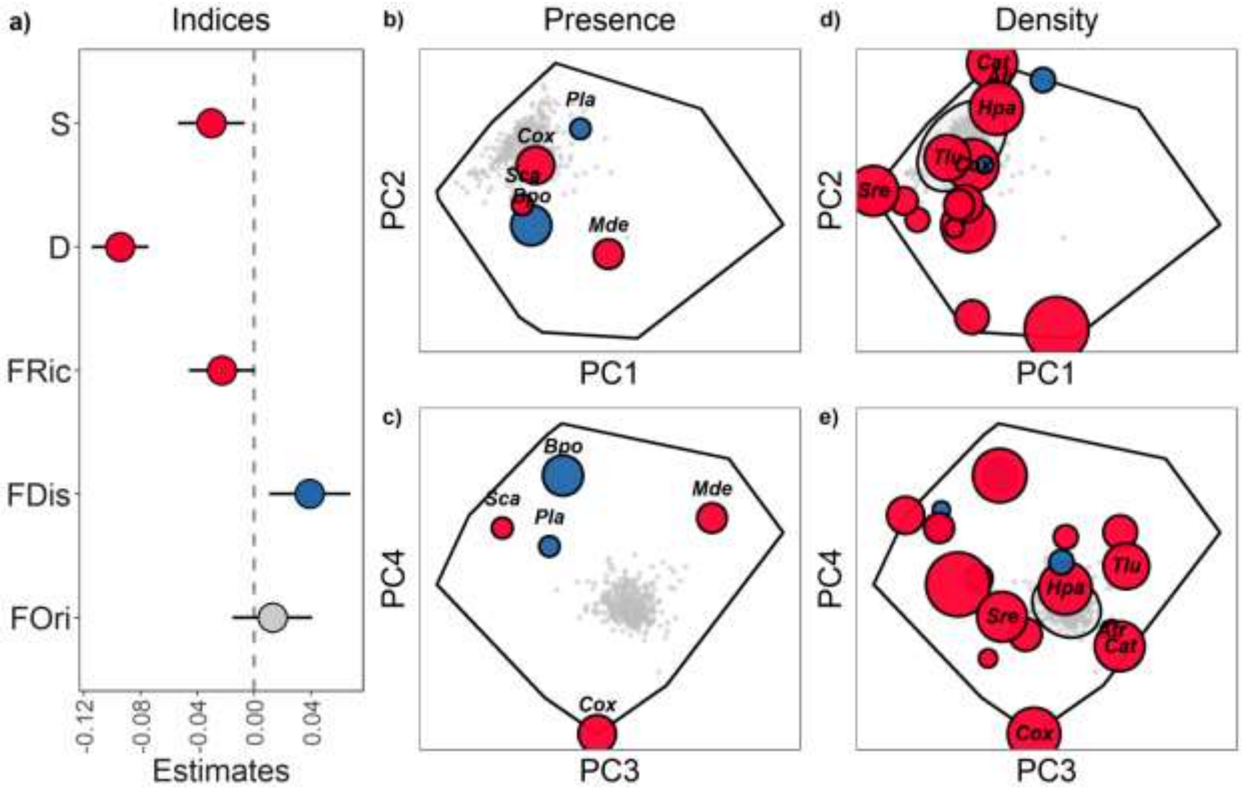

Fig. 4. a) Temporal change of the five calculated indices expressed as standardized coefficients (mean ± 95% confidence interval) of LMMs for Loreto. Blue and red circles show significant positive and negative changes, respectively, while gray circles indicate non-significant change. b and c) Position in the functional space (PC1-PC2 and PC3-PC4) of 'winners' (blue), 'neutrals' (gray) and 'losers' (red) for presence (b) and density (c) models in the MUMPA. Dots' size is proportional to z-values of the GLMMs, and the average-weight centroids (one per transect) are indicated by gray dots; in c, ellipses indicate 95% confidence intervals. Codes of the principal species are included (Table 1).

Note: Atr= *A. troschelii*, Bpo= *B. polylepis*, Cat= *C. atrilobata*, Cox= *C. oxycephalus*, Hpa= *H. passer*, Mde= *M. dentatus*, Pla= *P. laticlavius*, Sre= *S. rectifraenum*, Sca= *Scarus sp.*, Tlu= *T. lucasanum*.

For 'winner' species at Loreto, the commercially fished invertivore *B. polylepis* showed increases in presence associated with negative anomalies of SST and PAR. In contrast, decreases in the number of visitors and human population around the MUMPA were related to increases of the herbivore/detritivore *P. laticlavius* (Fig. 5f).

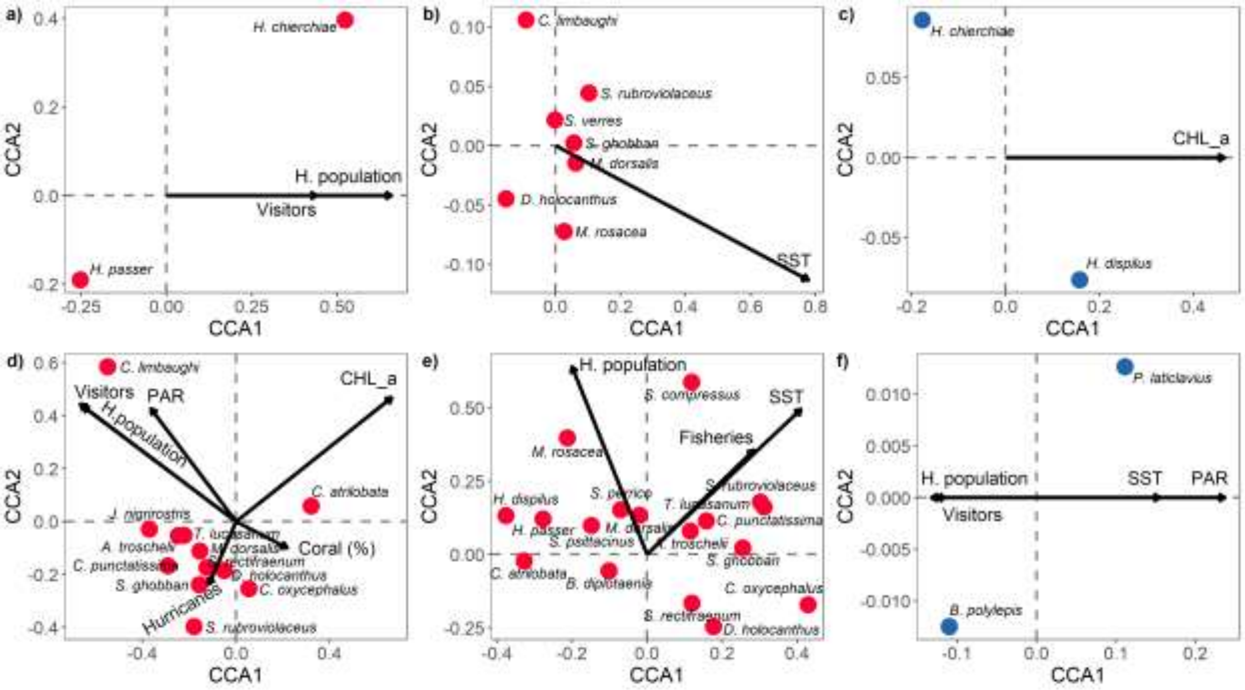

Fig. 5. CCA graphs for ‘losers’ (red) and ‘winners’ (blue) at each MPA where vectors of the disturbances with significant effects are shown: a) ‘losers’ in density for Cabo Pulmo; b) ‘losers’ and c) ‘winners’ in presence, and d) ‘losers’ in density for Espíritu Santo; e) ‘losers’ in density, and f) ‘winners’ in presence for Loreto.

Our findings of maintenance of fish diversity (resilience) at the no-take marine reserve, and declines in species richness that translated into negative changes in functional diversity at the MUMPAs, lead us to reject our hypothesis of similar patterns at the three analyzed MPAs. In contrast with our hypothesized region-wide community changes, patterns of change differed among the three MPAs in this study. These differences were also observed at species level, where Cabo Pulmo had fewer ‘loser’ species than Espíritu Santo and Loreto, whose species declines were related to environmental and anthropogenic disturbances.

4. Discussion

The analysis of fish diversity change over time performed in this study showed that the fully-protected MPA in Cabo Pulmo did not present significant changes in any of the calculated indices, while the partially-protected Loreto and Espíritu Santo showed significant decreases in species and functional richness over the same time period (Fig. 3a; Fig. 4a).

4.1. No-take marine reserve Cabo Pulmo

The result of diversity maintenance in Cabo Pulmo indicate resilience of its reef ecosystem over time, since species and functional diversity did not present significant changes despite the occurrence of a number of environmental disturbances in the region (positive anomalies in SST and negative anomalies in CHL_a), and the increase in human use (Fig. S2). We propose that full protection from intense fishing activities since 1995 in this MPA (Anderson, 2019) has buffered fluctuations in fish diversity, similar to what has been observed in temperate reefs of Tasmania (A. E. Bates et al., 2014).

Considering the multiple disturbances that Cabo Pulmo has faced within the past decade, the observed ichthyofauna functional maintenance is consistent with the previously reported maintenance of energy flows, coral cover and proportional abundance/species/functional characteristics of invertebrates (Calderon-Aguilera et al., 2021). Taken together, these results highlight the effectiveness of conservation efforts that local residents and authorities have performed towards the goal of preserving ecological processes in the northernmost coral reef in the Eastern Pacific (Alvarez-Filip and Reyes-Bonilla, 2006; CONANP, 2006). Since our results for species richness in Cabo Pulmo (non-significant changes; Fig. 2a) are different from the decline reported between 1987 and 2003, as well as from the increase of 166% reported between 1999 and 2009 (Aburto-Oropeza et al., 2011), our study emphasizes the importance of analyzing data sets with longer time scales that allow us to detect patterns in species richness over time, and cautions against conclusions based on particular years that might be atypical.

Alvarez-Filip and Reyes-Bonilla (2006) reported maintenance of fish functional diversity at Cabo Pulmo between 1987 and 2003 due to a high degree of functional redundancy. However, our results allowed us to detect that this pattern was associated with species' presence maintenance (none of the 21 common species presented significant changes; Fig. 2b) or small density changes at the species level, since functional redundancy at the studied MPAs is low and has been maintained over time (Table S1). Regarding density, the increase in visitors and human population around

Cabo Pulmo appeared related to the decrease of *H. passer* (Fig. 5a), an ornamental species protected by the Mexican federal government (Gijón-Díaz et al., 2017). Given that this species also presented density declines in Loreto (Fig. 5e), and that the Gulf of California is the only area in México where there are official capture permits for ornamental species (Gijón-Díaz et al., 2017), these results could indicate a regional population decline caused by fishing pressure at sites outside the MPAs. In the face of these regional declines, management strategies for MPAs, such as the regulation of the number of visitors, enhanced surveillance, and encouragement of good practices amongst tourism operators, are needed to contribute to the conservation of vulnerable/commercially fished species and to the resilience of local reef ecosystems in the near future.

4.2. Multi-use areas Espíritu Santo and Loreto

In contrast to Cabo Pulmo, Loreto and Espíritu Santo MUMPAs exhibited a pattern of decline in species richness that translated into decreases in functional richness. These decreases were associated to presence changes amongst species with extreme traits located towards the limits of functional space (Fig. 3b; Fig. 4b), since loss of species with non-extreme traits does not affect values of this index (Mouillot et al., 2013; Villéger et al., 2008). Analyses of temporal changes in species presence showed that most 'loser' species were rare (present in < 50% of the total surveys) and that some of them had unique functional roles (e.g. deep-water planktivore *C. limbaughi* for Espíritu Santo and coral-associated small carnivore *C. oxycephalus* for Loreto; Table 1). These conditions, in addition to the low functional redundancy with non-significant changes (Table S1), potentially limit functional compensation and the maintenance of ecosystem processes through time (Hooper et al., 2005; Mason et al., 2005).

Temporal changes in fish diversity at MUMPAs were also detected for functional dispersion, where the significant increase of this variable reflected density declines of species with trait values near the centroids of the functional space (Fig. 3c; Fig. 4c). Nine out of the 22 density 'loser' species found in the study (Table 1) were shared by both MUMPAs (Espíritu Santo and Loreto), which may indicate a regional decrease of these species. Moreover, some of them are among the most abundant and frequent reef fish species in the Gulf of California (e.g. *A. troschelii*, *C. atrilobata*, *S. rectifraenum* and *T. lucasanum*; Fernández-Rivera Melo et al., 2018; Sánchez-Caballero et al., 2017). Given the large-scale decline and the ecological importance of these dominant species, long-term decreases in their populations could have large impacts on community structure (e.g. cascading effects), ecological processes, and the flow of reef ecosystem services in the central Gulf of California region (Avolio et al., 2019; Villéger et al., 2010).

Loss or reduced abundance of dominant species is often an outcome of environmental and anthropogenic global changes (Avolio et al., 2019). Our results of species density declines at MUMPAs associated to a combined effect of environmental (anomalies of SST and CHL_a) and anthropogenic (fisheries, visitors and human population around the MUMPA) factors (Fig. 5d; Fig. 5e) are consistent with these global trends. From 2013 to 2016 the California Current showed CHL_a negative anomalies (~ -1.5 mg/m^3) and SST increases up to 2 °C (~ + 1.2 °C in the present study; Fig. S2) in some areas (Gomez-Ocampo et al., 2018). These anomalies were associated to a shift from cold to warm phase in the northeast Pacific Ocean, which caused greater stratification in the water column and decline of primary productivity and phytoplankton biomass (Gomez-Ocampo et al., 2018). Since low primary productivity is generally associated with decreases in the abundance of ichthyofauna (Legendre and Michaud, 1999; Bainbridge et al., 2018), this event could explain the negative trends observed for common species in both MUMPAs (Fig. 5d; Fig. 5e), as well as the general significant decline in fish density at Loreto (Fig. 4a).

Loreto also showed density decreases in large herbivore/detritivore functional entities (Family Scaridae) which are locally consumed, as well as in regional commercially fished species (e.g. *B. diplotaenia* and *M. rosacea*; Table 1; NIPARAJÁ, 2011), associated with an increase of human population and fishing activity (Fig. 5e). Since increasing fishing pressure was observed around this MUMPA (Fig. S2), in addition to reports of illegal fishing inside it (Rife et al., 2013a, 2013b), reinforcing management strategies such as surveillance and the application of fishing regulations could prevent direct (local decline or loss of commercially fished species) and indirect (abundance increase of low-trophic level species, such as herbivorous fish and invertebrates) effects of overfishing and their consequent changes in ecosystem processes (e.g. high bioerosion rates in coral colonies; Alvarado et al. 2016). The expansion of no-take zones from 0.07% to 3% in 2019 represents an additional strategy to address the management problems identified in Loreto MUMPA, including ongoing overfishing (CONANP, 2019; Rife et al., 2013a).

The result that Espíritu Santo presented non-significant density declines (Fig. 3a) and less 'loser' species than Loreto, despite a higher fishing pressure around it (Fig. S2), might be attributed to effective management and governance, which has resulted in the recent addition of this MUMPA to the IUCN Green List of Protected Areas (2018) based on the evaluation of the five previous years (Ramírez-Ortiz et al., 2020). Nonetheless, Espíritu Santo showed significant effects of coral cover loss and increase of visitors and human population on the density decline of 12 species (Fig. 5d). Thus, effort and resources should be focused on further improving local management (e.g. through implementation of coral restoration programs, regulation of the number of visitors, and surveillance of no-take zones) with the goal of reversing the observed decline for some species over the last decade.

Some commercially fished 'winner' species showed density increases (*C. panamensis*, *E. labriformis* and *L. argentiventris*; Fig. 3c), supporting benefits of the partial protection in Espíritu Santo, consistent with trends reported after a similar time period elsewhere (13.1 ± 2 years from the establishment of an MPA; Babcock et al., 2010). But since none of the analyzed variables explained positive density changes, this potential effect of protection needs further investigation (Table S4). In this MUMPA, we found evidence of ecological reorganization, for example the density declines of the herbivores/detritivores *S. rubroviolaceus* and *S. ghobban,* which we attributed to interspecific competition considering they share most of the biological traits with the 'winner' species *S. compressus* (*S. ghobban* only differs in the maximum size trait; Table 1; Ramírez-Ortiz et al., 2020). In addition, we observed asynchronous responses to disturbance: presence increase of two functionally redundant species, *H. chierchiae* and *H. dispilus* (Table 1), associated with contrasting anomalies in CHL_a; *H. chierchiae's* increase was associated with negative anomalies in this variable, while the *H. dispilus'* was associated to positive anomalies (Fig. 5c). Variable responses to environmental change of species that share similar biological traits could contribute to resilience of ecological processes. Altogether, these results highlight the importance of biological trait analyses to detect functional redundancy and to evaluate possible consequences of ecological reorganization on reef resilience.

5. Conclusions

Long-term surveys and diversity analyses show that the fully-protected reefs of Cabo Pulmo appear resilient due to maintenance of fish diversity and limited species-level changes over the years. By contrast, MUMPAs showed biodiversity loss at the community and species level within the study period, associated to environmental anomalies of SST and CHL_a (previously reported for the California Current), as well as anthropogenic disturbances related to increases in visitors, human population and fishing pressure around Espíritu Santo and Loreto. Despite the documented degradation of reef ecosystems within MUMPAs, density increases in some commercially fished species suggests some beneficial effects of partial protection. Considering changing conditions since 2005, full protection appears to be more effective than partial protection in maintaining functional diversity of reef fish communities and promoting ecological resilience in Gulf of California reef ecosystems.

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