

Slow recovery of reef fish populations in an isolated marine reserve

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Abstract

Geographic isolation is an important yet underappreciated factor affecting marine reserve performance. Isolation, in combination with other factors, may preclude recruit subsidies, thus slowing recovery when base populations are small and causing a mismatch between performance and stakeholder expectations. Mona Island is a small, oceanic island located within a partial biogeographic barrier - 44 km from the nearest Puerto Rico shelf. We investigated if Mona Island's no-take zone, the largest in the U.S. Caribbean, was successful in increasing mean size and density of a suite of snapper and grouper species 14 years after designation. The La Parguera Natural Reserve (LPNR) was chosen for evaluation of temporal trends at a fished location. Despite indications of some fishing within the no-take area, a reserve effect at Mona Island was evidenced from increasing mean sizes and densities of some taxa, and mean total density 36% greater relative to 2005. These results should be viewed cautiously, however, as our design lacks seasonal replication within 2005 and 2010. The largest predatory species remained rare at Mona, preventing meaningful analysis of population trends. At LPNR, most commercial species (e.g., lane snapper, schoolmaster, mahogany snapper) did not change significantly in biomass or abundance, but some species (yellowtail snapper, hogfish), increased in abundance owing to strong recent recruitment. This study documents slow recovery in the Mona NTZ that is limited to smaller sized species, highlighting both the need for better compliance and the substantial recovery time required by commercially valuable, coral reef fishes in isolated marine reserves.

Resumen

El aislamiento ecológico es un factor importante pero poco apreciado que afecta el rendimiento de las reservas marinas. El aislamiento puede impedir que lleguen subsidios del reclutamiento, lo que ralentiza la recuperación cuando las poblaciones ya de por sí son pequeñas y provoca un desajuste entre el desempeño y las expectativas de los interesados. La isla de la Mona es pequeña y oceánica ubicada dentro de una barrera biogeográfica parcial, a 44 km de la plataforma más cercana de Puerto Rico. Investigamos si la zona de no pesca (NTZ por sus siglas en inglés) alrededor de la Isla de la Mona logró aumentar el tamaño promedio y la abundancia de un conjunto de especies de pargos y meros 14 años después de su designación. La Reserva Natural de la Parguera (LPNR) fue elegida para evaluar las tendencias temporales en un lugar con pesca. Las métricas de ensamblaje de peces recolectadas en las inmersiones por buzos se evaluaron con PERMANOVA multivariado basado en modelos mixtos multifactoriales. Las percepciones del esfuerzo de pesca y la aplicación de cumplimiento de regulaciones en ambas AMP se recopilaron mediante entrevistas con los pescadores. A pesar de las indicaciones de que hay actividad de pesca dentro del área de no pescar, se evidenció un efecto de la reserva en la Isla de la Mona por el aumento en el tamaño y en la abundancia de algunos peces, con una abundancia media 36% mayor que en 2005. Sin embargo, estos resultados deben considerarse cautelosamente ya que nuestro diseño carece de replicación temporal en 2005 y 2010. Las especies depredadoras más grandes siguen siendo raras en Mona, lo que impide un análisis significativo de las tendencias de sus poblaciones. En LPNR, la mayoría de las especies comerciales (por ejemplo, pargo arrayado, pargo amarillo, pargo ojón) no cambiaron significativamente en biomasa o abundancia, pero algunas especies (colirrubia, capitán) aumentaron en abundancia debido a un evento fuerte de reclutamiento reciente. Este trabajo demuestra que la recuperación en la NTZ de la isla de la Mona

es lenta y se limita a especies de tamaños más pequeños, destacando tanto la necesidad de un mejor cumplimiento con las regulaciones como el tiempo requerido para una recuperación sustancial por los peces de arrecifes de coral con valor comercial en reservas marinas más aisladas.

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Introduction

As in tropical regions worldwide, overfishing of Caribbean coral reefs continues to undercut their functional and productive potential (Hughes et al. 1999; Appeldoorn 2008; Mumby 2009), with the greatest deleterious effects on fish biodiversity and biomass found closest to centers of high human population density (Mora et al. 2011; Cinner et al. 2016; Quimbayo et al. 2018). Given the degree to which coastal communities rely on fish for food security and accessible income (Béné et al., 2010), management for sustainable catch is both an ecologically and socioeconomically-relevant task.

Spatial management schemes, specifically no-take reserves, protect the integrity of marine ecosystems by preserving intact all abiotic and biotic components (Lubchenco et al. 2003). Properly designed and managed marine reserves can bolster fish abundance and species diversity (Russ & Alcala 1996; Halpern & Warner 2002; Garcia-Charton et al. 2008; Lester et al. 2009), protect and increase spawning stock biomass (Bohnsack 1994; Aburto-Oropeza et al. 2011; Hackradt et al. 2014), increase trophic position of consumer species (Dell et al. 2015), maintain live coral cover (Selig & Bruno 2010), and perhaps most importantly preserve ecosystem resilience to future disturbance (Appeldoorn, 2011). The success of a no-take marine protected area (MPA) depends largely upon its size (Dahlgren & Sobel 2000; Halpern 2003), age (Russ & Alcala 2003; Claudet et al. 2008), isolation from similar benthic habitats (Gaines et al. 2010), and degree of enforcement (Pollnac et al., 2010). Meta-analysis by Edgar et al. (2014) found that MPAs that were no-take, well enforced, old (more than 10 years), large (greater than 100 km²), and isolated by habitat discontinuities were most effective, but possessing at least four of these characteristics was sufficient to realize substantial gains in fish biomass. Yet, while isolation on a local scale can be beneficial in terms of limiting anthropogenic influence (Cinner et al. 2016, 2018) and stemming emigration of adult fish outside of reserve boundaries (Edgar et al. 2014), isolation on a

geographic scale can limit the flow of larval recruits, thereby slowing population growth, especially when base populations are small (Swearer et al. 1999; Sale et al. 2005; Sandin et al. 2008; Quimbayo et al. 2018). Isolated fish populations may also have lower natural genetic diversity relative to better-connected counterparts, which can lead to detrimental effects associated with genetic drift and inbreeding (Pérez-Ruzafa et al. 2006).

In Puerto Rico, the Mona and Monito Island no-take zone (NTZ), established in 2004, is the largest NTZ in the U.S. Caribbean (Schärer et al. 2014). The NTZ encircles both islands and encompasses coral reef and colonized hardbottom habitats within a total area of 81 km². Mona Island's platform is surrounded on all sides by deep water (> 500 meters), and lies 44 km distant from the nearest shallow coral habitat (Johns et al. 2002). The Mona Passage is recognized as a partial biogeographic barrier limiting the regional distribution and gene flow of some species between the western and eastern Caribbean (Lessios et al. 1984; Dennis et al. 2005; Taylor & Hellberg 2006; Beltrán et al. 2017, Baums et al. 2006). Several studies have indicated limited population connectivity of reef organisms at Mona with populations in the Dominican Republic (Cowen et al. 2006), or on the Puerto Rican platform (Pagán-López 2002, Rojas Ortega and García Sais 2004).

The objective of this study was to assess the effectiveness of the Mona Island NTZ by evaluating changes in the biomass and density of a suite of snapper and grouper species after 14 years of no-take designation. The most recent assessment conducted in 2009 found increased densities of small-sized predators after five years of designation (Mateos-Molina et al. 2014). Larger, more commercially valuable snapper and grouper species showed no significant reserve effect in either mean biomass or density. The authors mentioned insufficient recovery time, low compliance rates, and spillover of fish into then-fished areas as potential reasons that a clear reserve effect was not observed. Given that the Mona NTZ now approximates four of five criteria deemed important for success by Edgar et al. (2014), with compliance

untested, we also assessed whether the prediction of increased biomass from that study occurred, or whether geographic isolation and small population size might be ecological impediments to recovery. With these connectivity characteristics, we expected that, with other factors held constant, recovery of snapper and grouper populations in the Mona NTZ would be substantially slower than in a less isolated reserve.

With no area currently open to fishing on Mona's insular platform, there is no control area with the same degree of isolation and habitat complex to compare with a fished area. Instead the La Parguera Natural Reserve (LPNR), located on the southwest coast of the main island, was selected to measure temporal changes in biomass and density at a fished site. Considering site differences in habitat composition, fish species composition, and degrees of larval connectivity, fish population metrics between the two MPAs are not directly comparable (Schärer-Umpierre 2009). Rather, trends from the LPNR were sought to interpret the relative strength of fishing pressure and recruitment isolation on the temporal changes of commercial species in the Mona NTZ. We expect the LPNR, despite high rates of exploitation (Pittman et al., 2010), to have higher recruitment rates given its larger size (324 km²), and greater degree of larval subsidy from the adjacent areas on the Puerto Rican platform (Beltrán et al., 2017; Cowen et al., 2006; Pagán-López 2002).

A secondary objective of this study was to assess the potential impacts of marine activities related to fishing around the Mona NTZ through a limited series of scaled stakeholder interviews. Perceptions of enforcement, compliance, and fishing effort were collected to ascertain perceived rates of fishing mortality within the NTZ, past and the present. Survey responses regarding fishing activity provided a means to better evaluate factors affecting recovery, as even small amounts of fishing can be consequential for populations of long-lived, late-maturing fish species (Little et al. 2005; Claudet et al. 2010; Jupiter et al. 2012). Concurrent interviews conducted with fishers in the LPNR yielded information on perceptions of

resource use, as well as rates of law enforcement and compliance with fishery regulations, such as minimum size restrictions and seasonal fishing bans.

Materials and Methods

2.1 Study sites

2.1.1 Mona Island

Mona Island is a 5,500-hectare uplifted carbonate terrace situated to the west of Puerto Rico in the Mona Passage, a deep straight characterized by strong northward and southward currents (Johns et al. 2002). Mona Island is partially encircled on the East, South, and West by a coral reef and colonized hardbottom habitat complex (Fig. 1a), has a few, small areas of nearshore seagrass beds, and entirely lacks mangroves (Schärer-Umpierre 2009). The northern coast is characterized by steeply sloping hardbottom habitat with little to no coral cover. Highest live coral cover and fish species richness are found at depths of 15-30 meters off the southwest coast of the island (Bruckner and Hill, 2009; García-sais et al., 2008). Hardbottom and coral reef habitats surveyed by Schärer-Umpierre (2009) averaged 10.3% live coral cover (ranging from 0% to 55%), while the dominant live substrate in these habitats was macroalgae (36.2%). *Orbicella* spp. comprise the most abundant coral genera within the reserve, however colony density and size decreased markedly during recent bleaching events and disease outbreaks (Bruckner & Hill 2009). Published fish species richness is lower at Mona (261 species) than on the Puerto Rican platform (453 species) (Dennis et al. 2005) likely due to the size differential of the two platforms, differences in available nursery habitat, and low frequency of larval immigration to Mona (Baums et al., 2006; Beltrán et al., 2017; Rojas Ortega and García Sais, 2004; Sandin et al., 2008).

Mona Island has long been the target of commercial and recreational fishing activities of varying intensities. Nearshore fishing yields from Mona appear to have peaked in the 1960's and 1970's with intense spearfishing of grouper spawning aggregations (Suarez-Caabro and Rivas 1976). By 1980, Mona's

Nassau grouper (*Epinephelus striatus*) aggregation had been fished to elimination, and commercial fishing trips to the island slowed in the years thereafter due to declining catches (Colin, 1982; Matos et al., 2011; A. Maldonado, pers. comm.). In 2004, a no-take zone (NTZ) was established around most of the island as a special zoning area within the existing MPA (DNER 2004). This original design restricted all fishing activity within 0.5 nautical miles from shore except for a swath on the west coast. In 2007 the boundary of the NTZ was extended to the 100-fathom depth contour to protect multi-species spawning aggregation sites (Schärer et al. 2010), but still excluded habitats off the western coast (DNER 2007). More recently, in 2010, regulations were amended again to include the western area in the NTZ resulting in the current 81 km² ring that extends to one nautical mile from shore around both Mona and Monito Islands (Fig. 1a) (DNER 2010).

2.1.2 La Parguera

Without a fished, control site on the Mona insular platform, the La Parguera Natural Reserve (LPNR) was chosen for evaluation of temporal trends at a fished location. This area of the Puerto Rico insular shelf is 10 km wide and contains one of the most well-developed reef systems on the island (Morelock et al. 1977). The shoreline and nearshore islands are fringed with mangroves adjacent to extensive seagrass beds, both of which are important nursery and foraging grounds for local fish species (Rooker 1995; Aguilar-Perera 2004; Burke et al. 2009). Multiple studies have documented cross-shelf ontogenetic migrations in La Parguera with movements generally occurring from seagrass to mangroves to reefs (Aguilar-perera et al., 2008; Appeldoorn et al., 2009; Cervený et al., 2010).

Recently, a multi-year survey of fish assemblage distribution and structure within the LPNR was conducted (Pittman et al., 2010). This survey, composed of 1,167 belt transects completed between 2001-2007, found low numbers of commercially important species (particularly snapper, grouper, and large parrotfish) relative to baseline data collected in 1980-1981 (Kimmel 1985). Nassau grouper (*Epinephelus*

striatus) sighting frequency declined from 34% in 1980-1981 to only two individuals sighted between 2001 and 2007. Similarly, the sighting frequency of all other snapper and grouper species declined over this period. Over the course of the later study, however, small grouper (*Cephalopholis fulva* and *C. cruentata*) mean biomass and density increased, potentially reflecting indirect trophic effects caused by the prior removal of larger predators (Stallings, 2008).

The LPNR has never had areas protected from fishing pressure despite attempts to establish spatial regulations (Aguilar-Perera et al. 2006). Historically, fishing pressure in the LPNR has been high with a variety of gears employed (e.g. traps, gillnets, trammel nets, hook and line, speargun) (Valdés-Pizzini & Schärer-Umpierre 2014). Total reported catch in LPNR has declined steeply in recent decades as has the number of licensed commercial fishers (Matos-caraballo & Agar 2010), although increases in the number of recreational anglers has also been noted (García-Sais et al., 2006).

2.2 Sampling Design and Data Collection

Species densities and estimated lengths in both MPAs were collected via underwater visual census during timed, 10-minute, 30 x 2-m belt transects. Following each belt transect, a 10-min roving survey was conducted to better detect wary and less abundant large-bodied species. In all surveys, divers enumerated snapper and grouper species and estimated fork-lengths (FL) into 5-cm interval bins. Snapper and grouper species counted in both previous studies of the Mona Island NTZ were included in surveys: *Lutjanus mahogoni*, *L. apodus*, *L. jocu*, *Cephalopholis fulva*, *Epinephelus guttatus*, *E. striatus*, *Mycteroperca venenosa*, and *M. tigris*. The small grouper *C. fulva* was not included in roving surveys at Mona to match baseline effort and because the species was more abundant and therefore comparatively well-represented in belt transects. In the case of the LPNR, given differences in assemblage composition and commercial fishing pressure, the list of surveyed species was expanded to include *Lachnolaimus maximus*, *Lutjanus*

synagris, *L. griseus*, *L. cyanopterus*, and boxfishes (Family *Ostraciidae*). All transects ran parallel to depth contours and were oriented into the direction of prevailing current. If the current was too swift to maintain uniform pacing (~3 m/min), surveys were aborted and attempted later when conditions were favorable. Likewise, if underwater visibility was less than 4 m at a transect location, the survey was cancelled and postponed until water clarity improved. Roving transects proceeded in the direction of the prevailing current to increase the total area surveyed. To better detect transcription errors from field sheets to the database data were entered weekly. After all data were collected and entered to a database in excel (.xlsx), quality control checks were conducted to identify data entry and any formatting errors.

Data collection at Mona Island followed protocols utilized in the 2005 baseline survey of the NTZ (Schärer-Umpierre, 2009). Prior analyses of species' densities from that study showed significant spatial variation within the NTZ between areas of differing geomorphology, depth and habitat. To separate these potential sources of variance and account for the west coast fished area existing until 2010, the sampling frame was divided into three zones, East, South, and West, containing three, four, and two sites, respectively (Fig. 1b). Each 500-m radius site included nine locations selected randomly from Schärer-Umpierre's (2009) sampling points, for a total of 81 points where transects were performed. This sample size was chosen based on the results of a power analysis considering estimates of variance and density gains found by Mateos et al. (2014) after five years of NTZ designation. Sampling sites were separated by at least one kilometer to maintain independence according to published home range sizes of common Caribbean reef fish (Appeldoorn et al., 2009; Hitt et al., 2011; Kramer and Chapman, 1999). To provide greater temporal resolution to the statistical design, data from 2010 (Mateos-Molina et al., 2014) were incorporated into the analysis. For compatibility, data from 108 random belt and roving transects conducted in 2010 were assigned to spatially corresponding 500-m sites. The overall proportion of depths (5 – 25m) sampled in 2005 was maintained in the composition of points randomly chosen for 2017 surveys. Point

selection was limited to hardbottom and coral reef habitats delineated from the habitat map of the Mona insular shelf (minimum mapping unit 100 meter²) produced for the baseline study (Schärer-Umpierre 2009).

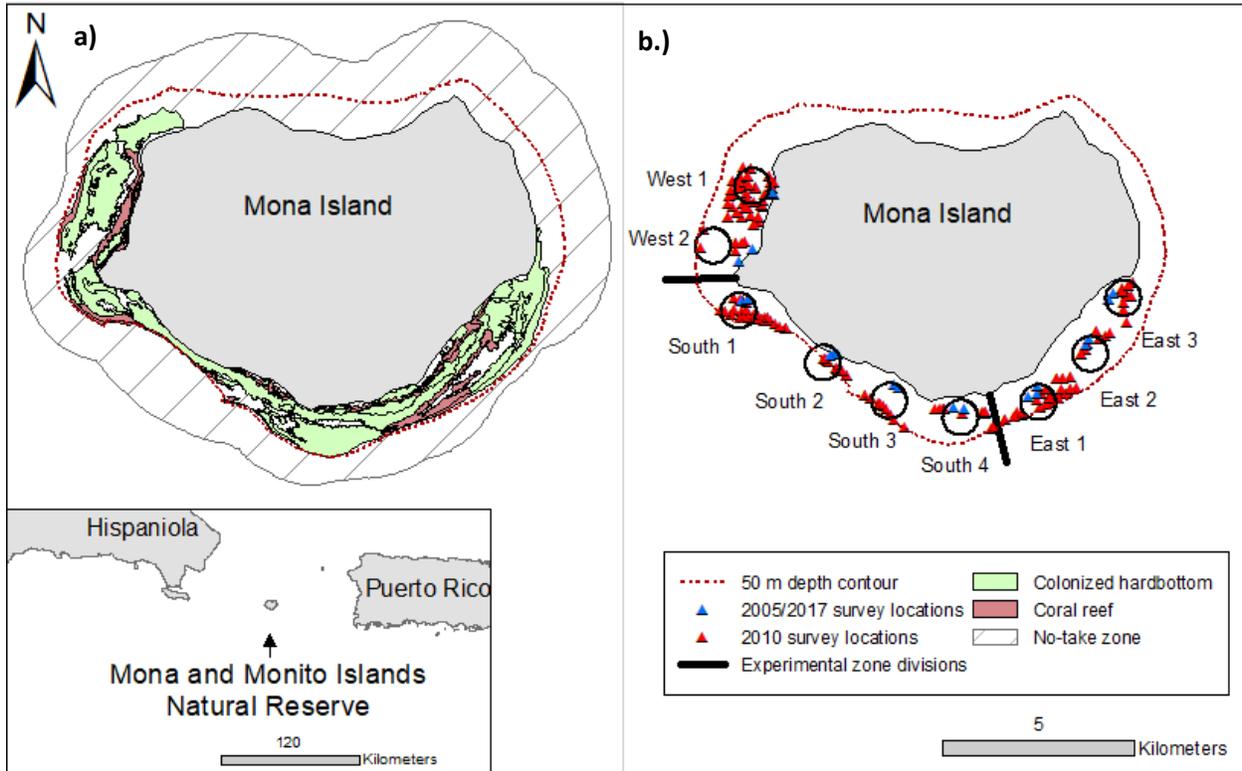


Fig.1. Maps of the Mona Island study area showing current NTZ boundary with coral reef and colonized hardbottom habitat extent (a), and 500 meter – radius experimental sites with nested survey points sampled in 2005, 2010, and 2017 (b).

Sample locations in the LPNR were based upon reef sites with fixed transects sampled previously with four temporal replicates yearly as part of the the Coral Reef Ecosystem Studies (CRES) program between 2004 and 2007 (Nemeth & Appeldoorn 2009). The experimental design used for this study consisted of three zones and 11 sites encompassing 110 total sampling points (Fig. 2b). Inner and mid-shelf forereef zones contained five and three, two-kilometer long (curvilinear distance) sites respectively centered upon original CRES reef sites and delimited in width and maximum depth by the extent of each forereef. Sites were delineated based upon a 4-m resolution, LiDAR-produced bathymetric map of the

region and a habitat map of LPNR (minimum mapping unit of 100 meter²) (Battista, 2016; Kendall et al. 2001). Sampling in the LPNR and Mona NTZ took place twice in 2017, spring and winter, to account for potential seasonal effects and to avoid temporal pseudo-replication (Hurlbert 1984).

To reduce surveyor bias and improve diver’s fish species identifications (Kadison et al. 2002; Yulianto et al. 2015), data collectors were required to conduct a minimum of 10 training dives and three fish-model calibration dives (Rooker & Recksieck 1992) prior to sampling. Following each dive, divers reviewed and discussed their size estimates and tested species identifications.

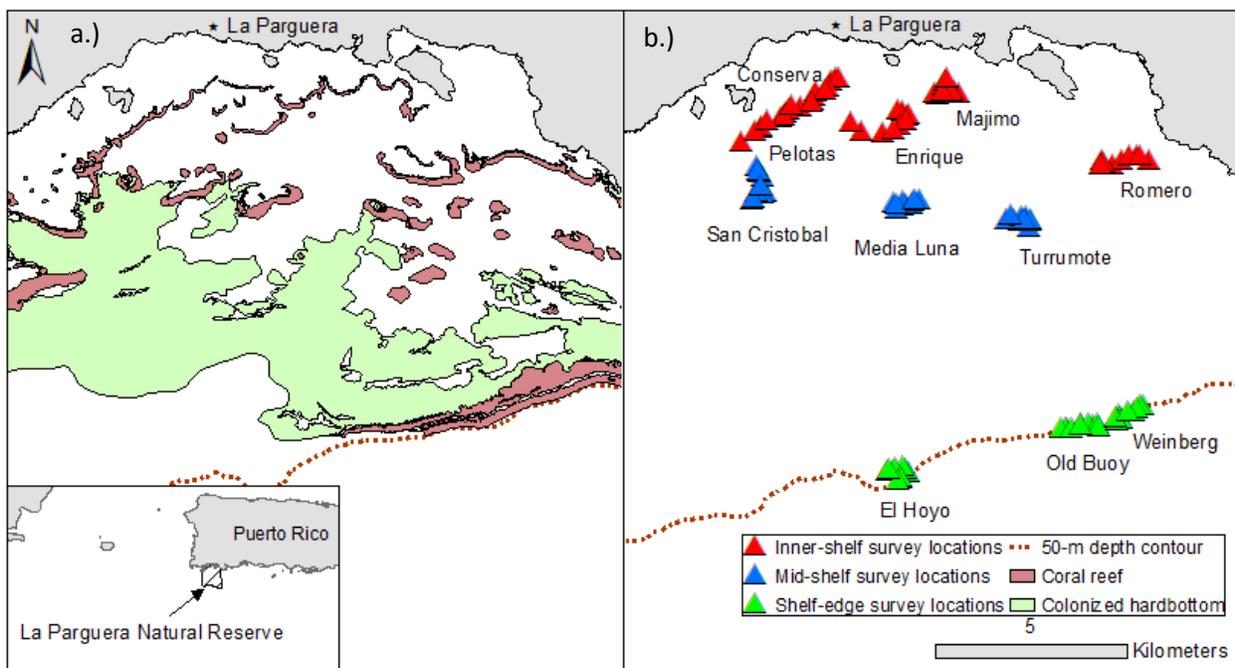


Fig. 2. Maps of the LPNR showing colonized hardbottom and coral reef habitat extent with 50-meter depth contour a.), and survey locations within each experimental zone (eg. inner-shelf, mid-shelf, shelf-edge).

Scaled stakeholder surveys were conducted with local fishers to provide an indication of perceptions of compliance, enforcement, and status of fish populations at Mona Island and within the LPNR. Interviewees were current and former commercial and recreational fishermen selected from recommendations provided by patriarch fishers and captains that commonly visit both reserves. Survey

responses were scored to evaluate assumptions of potential impacts due to directed fishing intensity in both MPAs.

3.3 Statistical Analyses

Analyses were conducted on belt transect and roving survey counts and size estimates over three time periods (2005, 2010, and 2017) within the Mona NTZ. LPNR analysis was conducted upon data collected during two periods: period 1 encompassing surveys from 2004, 2005, 2006, and period 2 containing 2017 data. Estimated FL were converted to weights with species-specific length-weight conversion parameters from Fishbase (Froese and Pauly 2018).

Differences in biomass and density were assessed with permutational multivariate and univariate analysis of variance (PERMANOVA) in Primer v. 7 (Anderson et al. 2008). Multivariate tests were conducted upon on Bray-Curtis dissimilarity matrices of square root-transformed data standardized by sample totals. Square root transformation of multivariate data was used to down-weight more abundant taxa and therefore better represent rarer species in analysis. Given that a significant PERMANOVA result may indicate differences in centroid locations, group dispersions, or both, multivariate dispersions were tested for homogeneity via the PERMDISP function to complement the interpretation of any location effects (Anderson & Walsh 2013). In some cases, dummy variables were added prior to matrix construction to allow for the calculation of dissimilarities between roving samples that returned zero fish (Clarke et al. 2006). Similarity percentage analysis (SIMPER) was applied to identify the species contributing most towards the significant multivariate differences. Species with the largest dissimilarities, that contributed to 30 % or more of cumulative between-group dissimilarity were selected for univariate analysis. Multivariate trends in square root-transformed biomass and density were visualized with principle coordinates analysis (PCoA) overlain with species-response vectors.

Univariate PERMANOVA was performed upon Euclidean distance matrices of total density, total biomass, as well as the density and biomass of species contributing most to multivariate trends. Only species with samples size of at least 80 individuals were included in this analysis in order better control for precision and accuracy of estimated population parameters (Kritzer et al. 2001). Density and biomass of sexually mature individuals (length greater than length at maturity) were tested for temporal variation when sample sizes allowed. The need for transformation of univariate data to meet the assumption of homogeneity of group variances was assessed with Levene's test in R (package: 'car' ; Fox et al. 2011). In cases of heterogeneous variance, a corrective transformation was applied (square root or fourth root for density, and $\log(x+1)$ for biomass). If heterogeneity remained after transformation, analysis was conducted on untransformed data but results were evaluated at the more conservative probability level of $p < 0.01$ (Underwood 1997).

Size distributions of species that contributed most to the differences in each MPA were also tested by year to interpret the results of species-specific univariate tests of fish size and density. In the case of the Mona NTZ, FL data were pooled from roving and belt surveys by year as the proportion of sampling effort divided between survey types was constant . Fish FL data in LPNR was only collected within belt transects. The shape of the length-frequency distributions between years and sampling periods were compared with the two-sample Kolmogorov-Smirnov goodness-of-fit test and relative locations of each distribution were compared with the Mann-Whitney U test on ranks. Probability density plots of FL were used to visualize and standardize differences due to sample sizes and to differentiate between changes in distribution shape and location effects (Langlois et al. 2015).

In LPNR, transect sizes employed during sampling period 1 (2005-2007) were different than in period 2 (2017) (25 x 4 m vs 30 x 2 m, respectively). Therefore, density and biomass were standardized

by using values on a per meter-squared basis. Roving data from LPNR was not included in the analysis of biomass or density because roving surveys were not conducted previously.

No direct comparisons were made between the data collected at the Mona Island NTZ and LPNR because ecosystems at the two locations differ considerably (Dennis 2000; Dennis et al., 2005; Schärer-Umpierre 2009). Due to the lack of fished and unfished reference areas at Mona and LPNR, respectively, no control sites were assessed. Instead, inferences about the condition of fish assemblages in each location and the performance of the Mona NTZ are based upon MPA-specific analyses of temporal trends.

Results

4.1 Mona Island

Multivariate analysis

Multivariate PERMANOVA of grouper and snapper assemblage data at Mona Island NTZ had significant main effects by period in the densities of species surveyed in belt transects and roving counts (Pseudo- $F = 5.10$, $p < 0.01$; $F = 4.05$, $p < 0.01$) (Table 1a, b). There was also a significant effect by period on roving biomass (PERMANOVA, Pseudo- $F = 3.30$, $p < 0.05$), but not transect biomass. Pairwise tests showed significant differences in multivariate transect density and biomass between 2005 and 2010 (Table 1a), as well as a significant difference in roving survey density and biomass between 2005 and 2010 and between 2005/2010 and 2017 (Table 1b.). Dispersions differed significantly by sampling period across biomass and density in roving surveys (PERMDISP, $F = 8.65$, $p < 0.01$; $F = 13.74$, $p < 0.001$), with 2005 exhibiting the greatest group dispersion in both cases. No temporal dispersion effects were identified from transect data, although dispersions were significantly different by zone and by site.

SIMPER analysis of species contributions to the observed differences between survey periods indicated that the schoolmaster (*Lutjanus apodus*) was the largest contributor to multivariate dissimilarities in roving surveys, contributing an average of 45% and 40% to total dissimilarity in square-root transformed density and biomass, respectively (Appendix A). Between 2005 and 2017, schoolmaster contributed an increasing percentage of within-period similarity in density of roving transects, from a contribution of 26% in 2005, to 73% in 2010, to 75% in 2017. Red hind (*Epinephelus guttatus*) contributions to similarity in density for roving surveys decreased from 53% in 2005, to 8% in 2010, to 5% in 2017. Mean total dissimilarity in roving density (92%) and biomass (93%) was greatest between 2005 and 2017.

Principle coordinates ordination (PCO) of Bray-Curtis dissimilarities in density of roving surveys explained 88.9% of the total variation between zones and periods (Fig 3a). PCO1 accounted for 56% of total variation and was driven primarily by dissimilarities *E. guttatus* density between 2005 and 2010. PCO2, explained 32.9% of the total variation and was driven by dissimilarities in *Lutjanus mahogoni*, *L. apodus*, and *M. venenosa* density between 2005 and 2017.

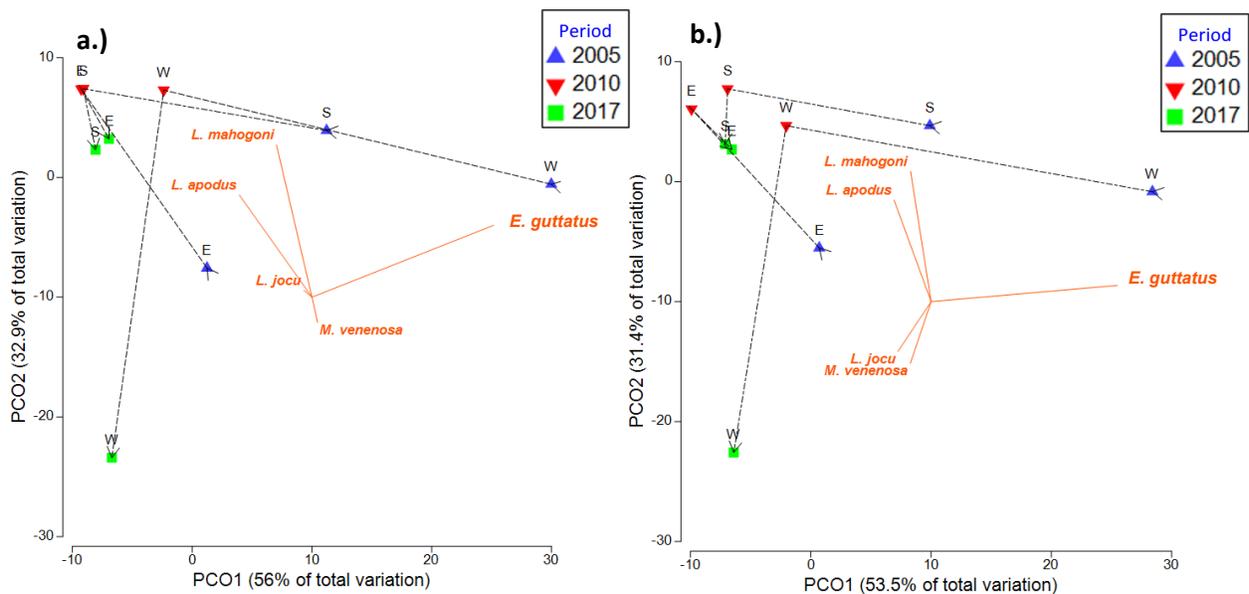


Fig. 3. Principle coordinates ordination plots (PCO) based upon Bray-Curtis dissimilarities of square-root-transformed density (a) (fish/survey) and biomass (grams/survey) (b) from roving surveys, showing centroids by zone and period overlain with species correlation vectors (Pearson > 0.2).

Dissimilarities between years were dominated by differences in density and biomass of *Cephalopholis fulva*, which represented an average of 65% and 48% respectively (Appendix B). Within-year average similarity was also highest for *C. fulva* in both metrics. Average densities for the other species were substantially lower; when their contributions to pairwise year-similarities were combined they approximated to that of *C. fulva*.

Table 1. Results of multivariate PERMANOVA based upon Bray-Curtis dissimilarities of snapper and grouper root-transformed biomass and density from belt transects (a), and roving surveys (b), conducted within the Mona Island no-take zone in 2005, 2010, and 2017.

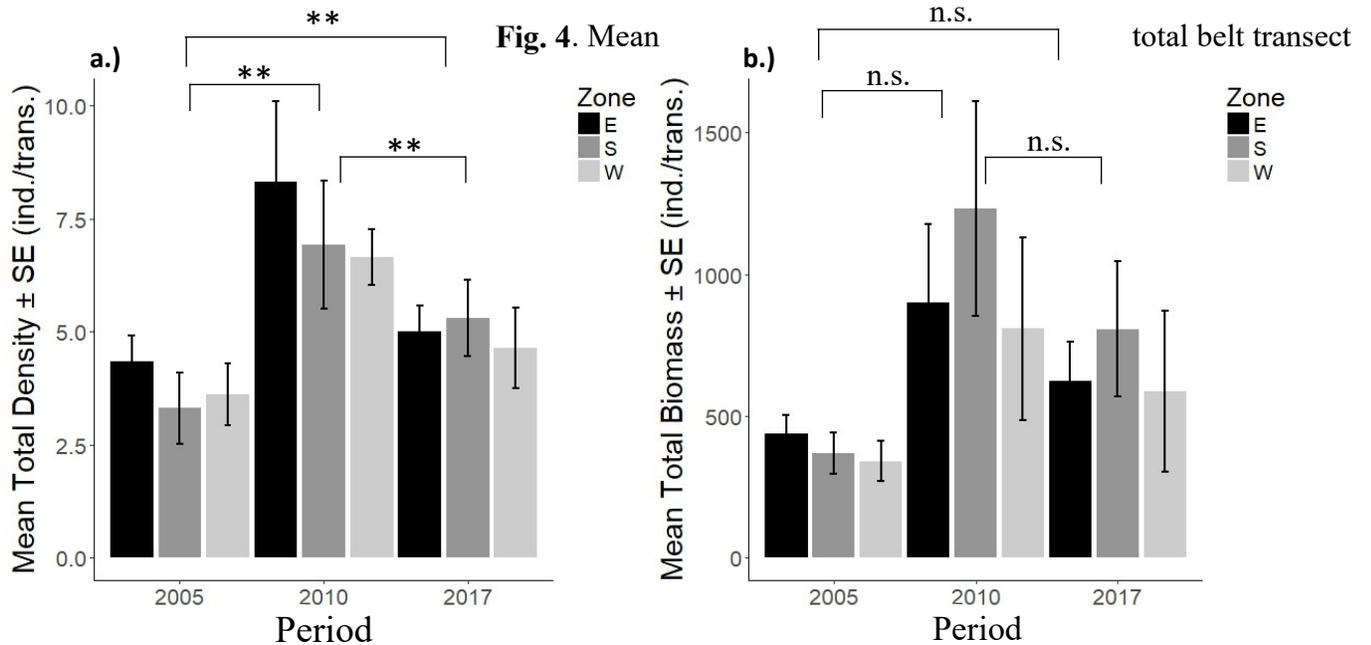
a.) Transects		Density			Biomass			
Source of variation	<i>df.</i>	<i>MS</i>	Pseudo- <i>F</i>	Unique perms	<i>df.</i>	<i>MS</i>	Pseudo- <i>F</i>	Unique perms
Period	2	3646.3	5.10**	9950	2	2166.4	1.07	9944
2005 vs. 2010	1	8101.6	9.70 ***	9955	1	4960.8	2.40 *	9935
2005,2010 vs. 2017	1	1444.6	1.78	9951	1	3648.3	1.80	9937
Time(Pe)	1	170.58	0.29	9968	1	2052.9	1.22	9950
Zone	2	5095.8	2.43	9945	2	6830.2	1.44	9935
Site(Zo)	7	1959.7	3.25 *	9956	7	4213.1	2.45	9950
Zo x Pe	4	1332.5	1.28	9943	4	1774.9	0.81	9921
Si(Zo) x Pe	12	658.75	1.12	9944	12	1580.1	0.93	9924
Zo x Ti(Pe)	2	875.58	1.51	9957	2	2720.1	1.62	9951
Si(Zo) x Ti(Pe)	6	580.53	0.80	9896	6	1683.4	0.87	9878
Residual	313	727.68			313	1934.5		
Total	349				349			
b.) Roving surveys		Density			Biomass			
Source of variation	<i>df.</i>	<i>MS</i>	Pseudo- <i>F</i>	Unique perms	<i>df.</i>	<i>MS</i>	Pseudo- <i>F</i>	Unique perms
Period	2	16375	4.05 **	9949	2	13413	3.30 *	9956
2005 vs. 2010	1	20743	6.22 ***	9943	1	16096	4.83 ***	9944
2005,2010 vs. 2017	1	9100.3	2.70 *	9957	1	7898.2	2.36 *	9954
Time(Pe)	1	279.51	0.23	9966	1	379.36	0.42	9969
Zone	6	5688.1	4.58 **	9939	2	5925.8	0.87	9949
Site(Zo)	2	4536.5	0.79	9943	6	6406.4	6.79 ***	9937
Zo x Pe	4	5888.7	1.20	9929	4	5267.8	1.07	9942
Si(Zo) x Pe	12	4210.4	3.53 *	9943	12	4110.4	4.62 **	9935
Zo x Ti(Pe)	2	1839.8	1.55	9954	2	1774.5	2.01	9960
Si(Zo) x Ti(Pe)	6	1154.4	0.36	9899	6	846.66	0.27	9896
Residual	298	3215.7			298	3192.7		
Total	333				333			

^a Level of significance: * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$.

Univariate analysis

Univariate PERMANOVA of total snapper and grouper biomass and density by year found no significant differences in biomass or density of roving surveys, nor biomass in transects. A significant effect was however detected in transect density ($F = 17.71, p < 0.001$), with all pairwise tests between years also significant. These responses corresponded to a 75 – 117% increase in total density between 2005 and

2010, a 25 – 35% decrease between 2010 and 2017, and an overall 27 – 45 % increase from 2005 to 2017 (Fig. 4).



density (fish / 60 m² transect) and biomass (grams / 60 m² transect) by year and zone from the MNTZ, with standard error bars indicated. Level of significance indicated: * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$.

Univariate PERMANOVA of species-specific metrics revealed a significant, 45-76% decrease in the mean density of red hind (*E. guttatus*) in roving transects between 2005 and 2017 (Pseudo- $F = 7.95$, $p < 0.05$) (Appendix E). No significant trends were detected between 2005 and 2010, or 2010 and 2017, or in mean total biomass of the species for any period. Low sample size ($n = 32$) and high variance in the mean density of large, sexually mature red hind precluded further analysis, however mean density was 28% greater in 2017 relative to 2005 (Fig. 8). A significant effect by year was also found in the density of coney (*C. fulva*) in belt transects (Table 3). Pairwise tests found a significant 28 – 54% increase in mean density between 2005 and 2010 ($t = 5.93$, $p < 0.01$), and a significant 33 – 51% increase between 2005 and 2017 (t

= 2.36, $p < 0.05$)(Appendix D). No significant difference was detected in coney density between 2010 and 2017. Despite attempts at corrective transformation, heterogeneous variance between years could not be eliminated for several taxa (Table 3).

Table 2. Univariate PERMANOVA results table of total snapper and grouper density and biomass from belt transects and roving surveys conducted in the Mona NTZ in 2005, 2010 and 2017.

Source of variation	Transects			Roving Surveys	
	<i>df.</i>	Total density (Pseudo - <i>F</i>)	Total Biomass (Pseudo - <i>F</i>)	Total density (Pseudo - <i>F</i>)	Total biomass (Pseudo - <i>F</i>)
Period	2	17.71 ***	1.94	1.87	0.28
2005 vs. 2010	1	23.07 ***	6.59 *	0.20	0.006
2005,2010 vs. 2017	1	0.31	0.10	2.57	0.72
Time(Pe)	1	0.08	0.86	1.30	6.72 *
Zone	2	0.64	3.15	0.88	0.28
Site(Zo)	7	3.99	0.48	8.54 *	3.63
Zo x Pe	4	0.39	1.39	1.40	1.28
Si(Zo) x Pe	12	0.60	0.51	1.48	0.96
Zo x Ti(Pe)	2	0.31	0.44	0.24	0.36
Si(Zo) x Ti(Pe)	6	0.58	1.91	0.28	0.52
Residual	313				
Total	349				
Transformation		√	log(x+1)	√	none

^a Level of significance: * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$.

Table 3. Results of univariate PERMANOVA of selected species biomass and density from transects and roving surveys conducted within the Mona NTZ in 2005, 2010, and 2017. Pseudo-*F* values shown from pairwise PERMANOVA by sampling period.

Transects	Species	2005 vs 2010 (Pseudo- <i>F</i>)	(2005,2010) vs 2017 (Pseudo- <i>F</i>)	Transformation	
Transects	Density	<i>C. fulva</i>	15.30 ***	0.11	√
		<i>L. apodus</i>	3.29	2.00	none
		<i>L. mahogoni</i>	0.16	0.09	none
	Biomass	<i>C. fulva</i>	0.03	1.50	$\log(x+1)$
		<i>L. apodus</i>	2.28	0.01	none
		<i>L. mahogoni</i>	0.51	0.41	none
Roving surveys					
Roving surveys	Density	<i>E. guttatus</i>	4.50 *	7.95 *	none
		<i>L. apodus</i>	0.05	0.21	none
		<i>L. mahogoni</i>	1.22	0.15	none
	Biomass	<i>E. guttatus</i>	3.47	1.92	√
		<i>L. apodus</i>	0.02	0.17	none
		<i>L. mahogoni</i>	1.24	4.21	none

^a Level of significance: * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$.

4.2 La Parguera Natural Reserve

Multivariate analysis

A significant interaction effect was detected between factors ‘site’ and ‘period’ from the LPNR ($F = 2.45$, $p < 0.0125$) (Table 4), with all but one reef site (Romero) showing significant differences in multivariate density between periods in pairwise PERMANOVA (Table 5). Significant differences in multivariate biomass were found between periods at all reef sites except Turrumote (Table 5), with the largest relative variation between periods found at El Hoyo.

Table 4. Summary of multivariate PERMANOVA results of commercial species density (fish/m²) and biomass from belt transects conducted within the La Parguera Natural Reserve.

Source of variation	Density			Biomass		
	<i>df</i>	<i>MS</i>	Pseudo- <i>F</i>	<i>df</i>	<i>MS</i>	Pseudo- <i>F</i>
Period	1	634.88	12.12 ***	1	1280.2	6.49 ***
Year(Pe)	2	18.019	1.17	2	21.472	1.22
Zone	2	276.87	3.24 **	2	240.44	1.07
Site(Zo)	8	74.557	5.37 ***	8	210.73	5.19 ***
Time(Yr(Pe))	9	11.848	1.29	9	34.211	0.72
Zo x Pe	2	61.93	1.65	2	148.19	0.88
Zo x Yr(Pe)	4	9.8758	0.83	4	37.582	1.40 *
Si(Zo) x Pe	5	31.987	2.45 *	5	165.53	4.29 ***
Si(Zo) x Yr(Pe)	10	11.574	1.27	10	22.751	0.48
Zo x Ti(Yr(Pe)))	18	11.218	1.23	18	39.246	0.82
Si(Zo) x Ti(Yr(Pe))	47	9.0887	1.00	47	47.884	1.05
Residual	690	9.1169		690	45.726	
Total	798			798		

^a Level of significance: **p* < 0.05; ***p* < 0.01; ****p* < 0.001.

Table 5. Summary of pairwise PERMANOVA of square root transformed multivariate density and biomass by reef site between sampling periods (eg. 2004-2006 vs 2017) from the La Parguera Natural Reserve.

Zone	Reef site	Density	Biomass
		Pseudo- <i>F</i>	Pseudo- <i>F</i>
Inner	Pelotas	11.33 *	7.37 *
	Enrique	16.39 *	15.04 *
	Romero	2.56	5.08 *
Mid	Turumote	15.97 *	2.63
	Media Luna	5.47 **	2.95 *
	San Cristobal	32.59 **	7.14 *
Shelf-edge	Weinberg	15.06 **	11.39 ***
	El Hoyo	45.98 *	51.12 *

^a Level of significance: **p* < 0.05; ***p* < 0.01; ****p* < 0.001.

PCO plots based on Bray-Curtis dissimilarities in density by factors ‘Zone’ and ‘Period’ showed greater separation between period 1 (2004-2006) and period 2 (2017) than among the centroids from either

period (Fig 5a,c; Fig 6a). The first two axes of the PCO for inner-shelf sites by period explained 74.4% of total variation in density (Fig 5a). Species response vectors based on Pearson correlation coefficients > 0.2 showed *O. chrysurus* and *L. maximus* contributed most to density dissimilarities between periods at the inner-shelf sites with 21.96% and 12.81% average dissimilarity, respectively (Fig. 5b). Within the Romero reef site, cross period density dissimilarity contributions were greatest from *C. cruentata* (9.46 %) and *L. synagris* (7.63 %), corresponding to decreasing trends in both cases. The PCO plot for mid-shelf sites by period explained 88.3% of the total variation in density (PCO1: 63%; PCO2 25.3%) (Fig 5c). Separation between periods along PCO1 was driven largely by an average 33.8 % dissimilarity in *O. chrysurus* density (SIMPER), primarily from San Cristobal (Fig. 5c,d), corresponding to a net increase. Other top contributors were *L. apodus* (11.69% dissimilarity) and *C. cruentata* (9.34% dissimilarity) with both species' correlation vectors indicating between-period decreases at Media Luna. Variation between periods at the Turrumote reef site was most influenced by a 5.69 % dissimilarity (increase) in *L. maximus* density. Shelf-edge variation in multivariate density was divided nearly equally between average dissimilarity between sites (64.08 %), and similarities between periods (64.92%) (Fig 6a). Inter-site dissimilarities were largest for *C. cruentata* (18.54%) and *C. fulva* (12.72 %), with densities for these species most dissimilar between El Hoyo and Weinberg. As with inshore zones, *O. chrysurus* contributed the most (21.80%) to dissimilarities in density at shelf-edge sites between periods, with an associated mean increase.

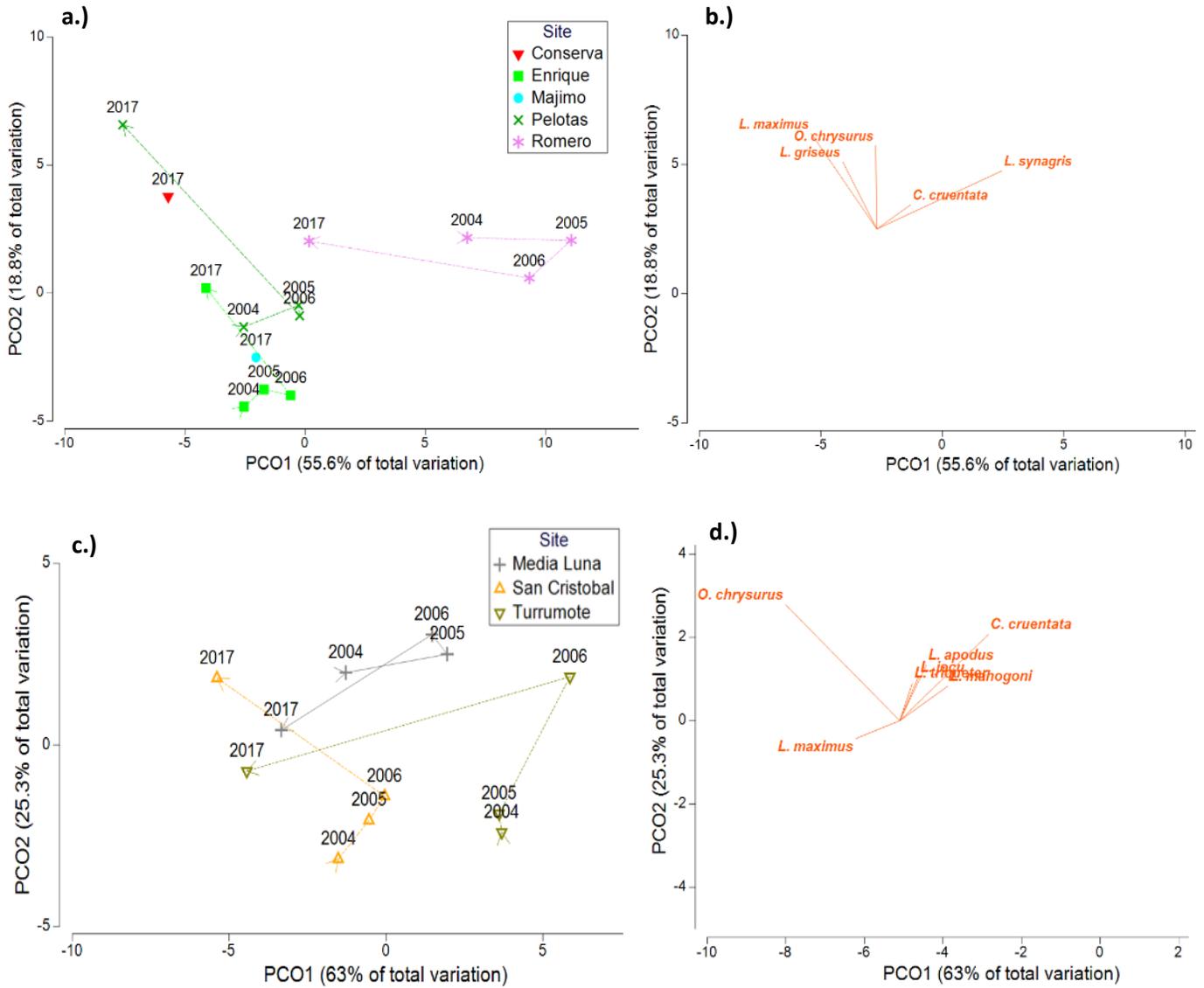


Fig. 5 Principle coordinate ordination plots showing centroids of root-transformed commercial species density (fish/m²) from LPNR by year from inshore sites (a) and mid-shelf sites (c). Adjacent plots (b, d) show corresponding response vectors (Pearson > 0.2) from top contributing species indicating direction and magnitude of contributions to dissimilarities between periods (2004-2006, 2017).

Univariate analysis

Univariate permutational analysis of variance showed a significant 75 - 113% increase in the total mean density of commercial species between periods in the LPNR ($F = 3.39$, $p < 0.05$), with no significant overall differences in biomass ($F = 2.97$, $p > 0.05$; Table 6). A significant interaction of factors ‘Site’ and

‘Period’ was detected for both metrics. Pairwise tests of mean total density by ‘Site x Period’ returned significant increases in total commercial density for four reef sites: Enrique, Pelotas, El Hoyo, and San Cristobal. Likewise, with the exception of Pelotas, biomass at these sites increased significantly.

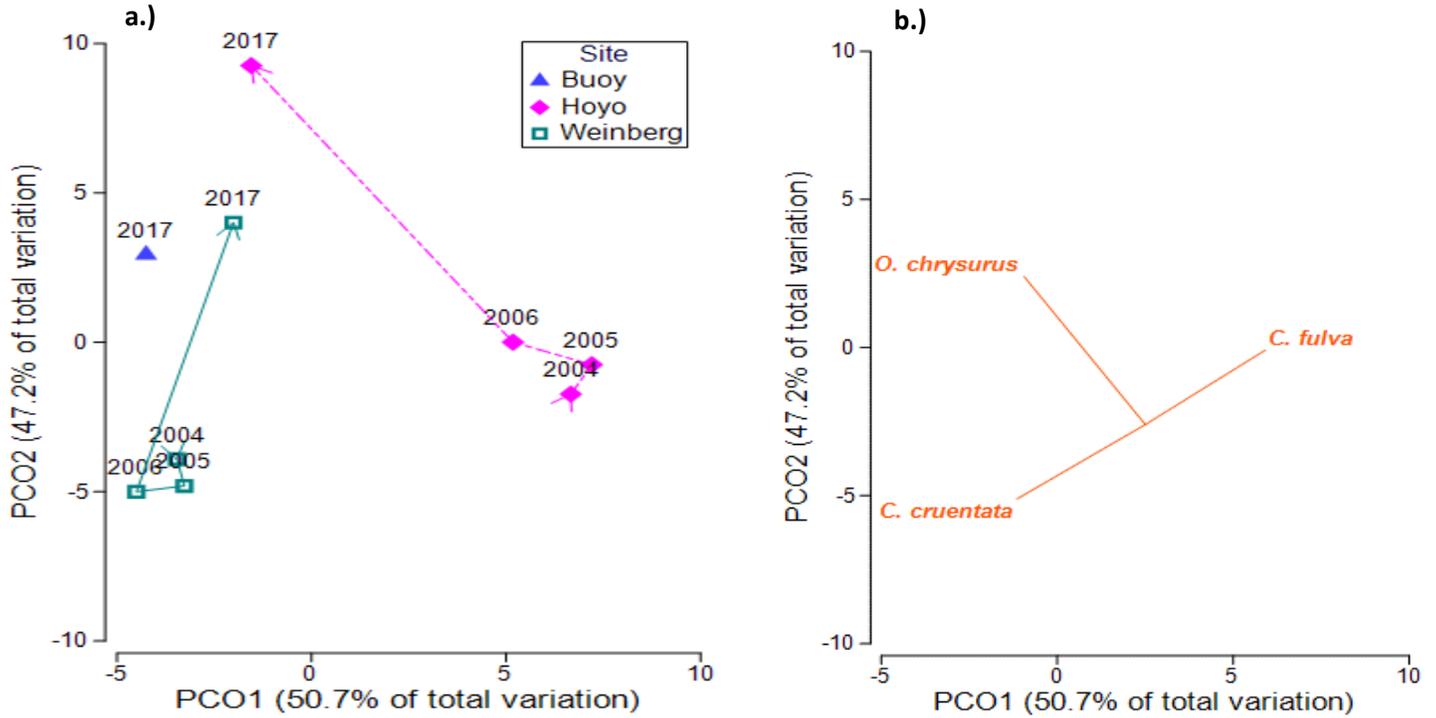


Fig. 6 Principle coordinate ordination plots showing centroids of root-transformed commercial species density from the LPNR by year from shelf-edge sites (a), with species response vectors indicating direction and magnitude of top species' contributions to dissimilarities (Pearson > 0.2) (b).

Table 6. Summary of univariate PERMANOVA results of total density (fish/m²) and biomass (g/m²) of commercial species in the LPNR.

Source of variation	d.f.	Total density (Pseudo - <i>F</i>)	Total Biomass (Pseudo - <i>F</i>)
Period	1	3.39 *	2.97
Year (Pe)	2	0.84	2.44
Time(Ye(Pe))	9	3.42 **	1.27
Zone	2	1.51	0.48
Site(Zo)	8	5.33 **	6.80 **
ZoxPe	2	0.26	0.43
Si(Zo)xPe	5	5.25 **	5.46 **
Enrique (Pd. 1 vs Pd. 2)	1	3.18 *	3.74 *
Pelotas (Pd. 1 vs Pd. 2)	1	3.65 *	2.89
El Hoyo (Pd. 1 vs Pd. 2)	1	2.88 *	3.21 *
San Crist. (Pd. 1 vs Pd. 2)	1	3.56 **	3.06 *
ZoxYe(Pe)	4	0.92	2.98
Si(Zo)xYe(Pe)	10	1.36	0.37
ZoxTi(Ye(Pe))	18	0.97	0.55
Si(Zo)xTi(Ye(Pe))	47	0.97	1.40
Res	690		
Total	798		
Transformation		√√	log(x+1)

^a Level of significance: **p* < 0.05; ***p* < 0.01; ****p* < 0.001.

Species-specific univariate tests of top contributing species biomass and density revealed significant, period-scale differences for *O. chrysurus*, *L. maximus*, and *C. fulva* (Table 7). Yellowtail snapper (*O. chrysurus*) exhibited a 150 – 239 % increase ($F = 14.54$ ***, $p < 0.001$) in total mean density, and a 117 - 189 % increase ($F = 13.32$, $p < 0.001$) in total mean biomass between periods (Appendix F), with the largest gains in both metrics observed at San Cristobal. The hogfish, *L. maximus*, increased in total mean density by 405 - 807%, and total mean biomass by 215 – 523% (Appendix F), while the coney, *C. fulva*, increased in total mean density by 10 – 126 % (Appendix G). Hogfish mean density gains were strongest at Pelotas as was the magnitude of change in mean biomass, while coney mean density increased

most at Weinberg. Levene’s test of the homogeneity of group variances detected between-period heterogeneity for multiple species’ metrics (Table 7).

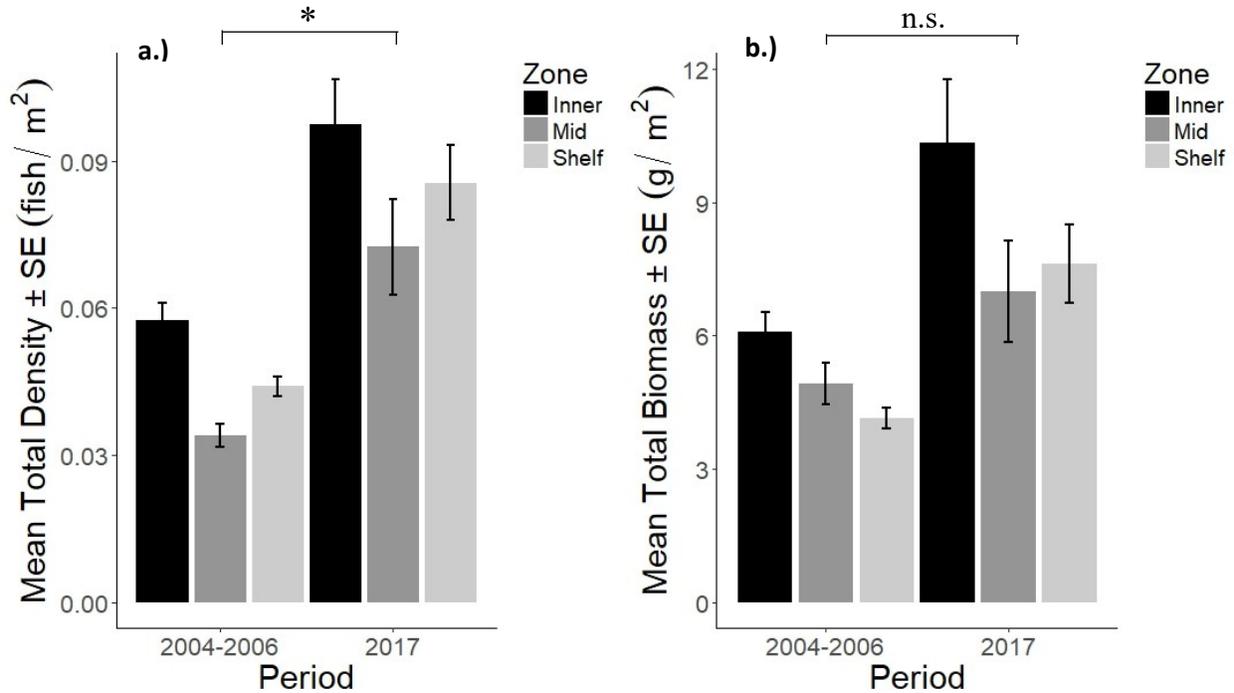


Fig. 7. Mean total commercial species density (fish/m²) (a), and biomass (g/m²) (b) from the LPNR by sampling period (2004-2006, 2017) and cross-shelf zone (inner-shelf, mid-shelf, and shelf-edge) with standard error margins indicated. Level of significance for period-wise comparisons: * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$.

Table 7. Results of species-specific univariate PERMANOVA of density (fish/m²) and biomass (g/m²) between sampling periods (2004-2006, 2017) in LPNR.

	Species	Pseudo- <i>F</i> (Period)	Mean change (%)	Levene's test - <i>F</i> (Period)	Transformation
Density	<i>O. chrysurus</i>	14.54 ***	+ 192 %	0.020	√√
	<i>C. cruentata</i>	1.50	--	111.64 ***	none
	<i>L. maximus</i>	6.92 **	+ 580 %	413.37 ***	√√
	<i>L. apodus</i>	2.21	--	45.08 ***	√√
	<i>C. fulva</i>	3.73 *	+60 %	4.49 *	√
	<i>L. synagris</i>	0.82	--	48.79 ***	none
	<i>L. mahogoni</i>			0.10	none
Biomass	<i>O. chrysurus</i>	13.32 ***	+ 151 %	237.14 ***	log(<i>x</i> +1)
	<i>C. cruentata</i>	2.91	--	314.72 ***	none
	<i>L. maximus</i>	6.22 **	+ 345 %	307.69 ***	none
	<i>L. apodus</i>	1.19	--	0.162	none
	<i>C. fulva</i>	0.62	--	2.19	none
	<i>L. synagris</i>	0.97	--	63.30 ***	log(<i>x</i> +1)
	<i>L. mahogoni</i>	0.74	--	18.92 ***	none

^a Level of significance: **p* < 0.05; ***p* < 0.01; ****p* < 0.001.

^b -- indicates no significant change

4.3 Species size distributions

Four species sampled within the Mona NTZ and seven species sampled within LPNR were selected for size distribution analysis based on a minimum sample size of 80 individuals. In the Mona NTZ, size distributions differed significantly in location and shape between baseline and current surveys (2005 vs. 2017) for three of four taxa (Table 4). For *E. guttatus* and *L. apodus*, mean FL increased significantly between 2005 and 2017 (Mann-Whitney $U = 370.5$, $p < 0.001$; $U = 10209$, $p < 0.01$) (Table 8, Figure 8). *E. guttatus* mean FL increased 24-30% over this period, while *L. apodus* mean FL increased by 11-17%. *C. fulva* was the only species examined from the Mona NTZ that decreased in mean FL between 2005 and 2017 ($U = 53679.8$, $p < 0.0001$), from 16.79 cm (± 0.33) to 14.99 cm (± 0.26).

Table 8. Results of the two-sample Kolmogorov-Smirnov test of the equality of size distributions between 2005 and 2017 from the Mona NTZ, and Mann-Whitney U test for location effects in species FL distributions.

Species	Kolmogorov-Smirnov	Mann-Whitney U
<i>E. guttatus</i>	p < 0.01	p < 0.001
<i>L. apodus</i>	p < 0.05	p < 0.01
<i>C. fulva</i>	p < 0.0001	p < 0.0001
<i>L. mahogoni</i>	p = 0.41	p = 0.10

Size distribution trends at Mona Island between 2005 and 2010, and 2010 and 2017 were less defined for all species. For *E. guttatus*, the shape and location of length distributions were not significantly different between 2005 and 2010, however the period from 2010 to 2017 saw a significant increase in mean FL and an increasingly left-skewed size distribution (Fig. 8). The size distribution of *L. apodus* in 2010 differed between years in shape, but mean FL differed only in 2017 when a significant increase was observed. The Kolmogorov-Smirnov test could not reliably test differences in the shape of *C. fulva* size distributions between 2005 and 2010, or between 2010 and 2017 due to an abundance of rank ties stemming from 2010 length category delineations. In both cases, though, the Mann-Whitney U test found highly significant, opposing location effects corresponding to a mean decrease of 4.71 cm (± 0.49) between 2005 and 2010, and a mean increase of 2.91 cm (± 0.37) from 2010 to 2017. Length distribution comparisons for *L. mahogoni* returned concurrent differences in shape and location only between 2005 and 2010 ($D = 0.37$, $p < 0.001$; $U = 6850$, $p < 0.01$), with an associated 1.17 cm (± 0.33) mean increase in fork length over this period. Other year comparisons did not reveal subsequent significant changes in the mean size of *L. mahogoni*.

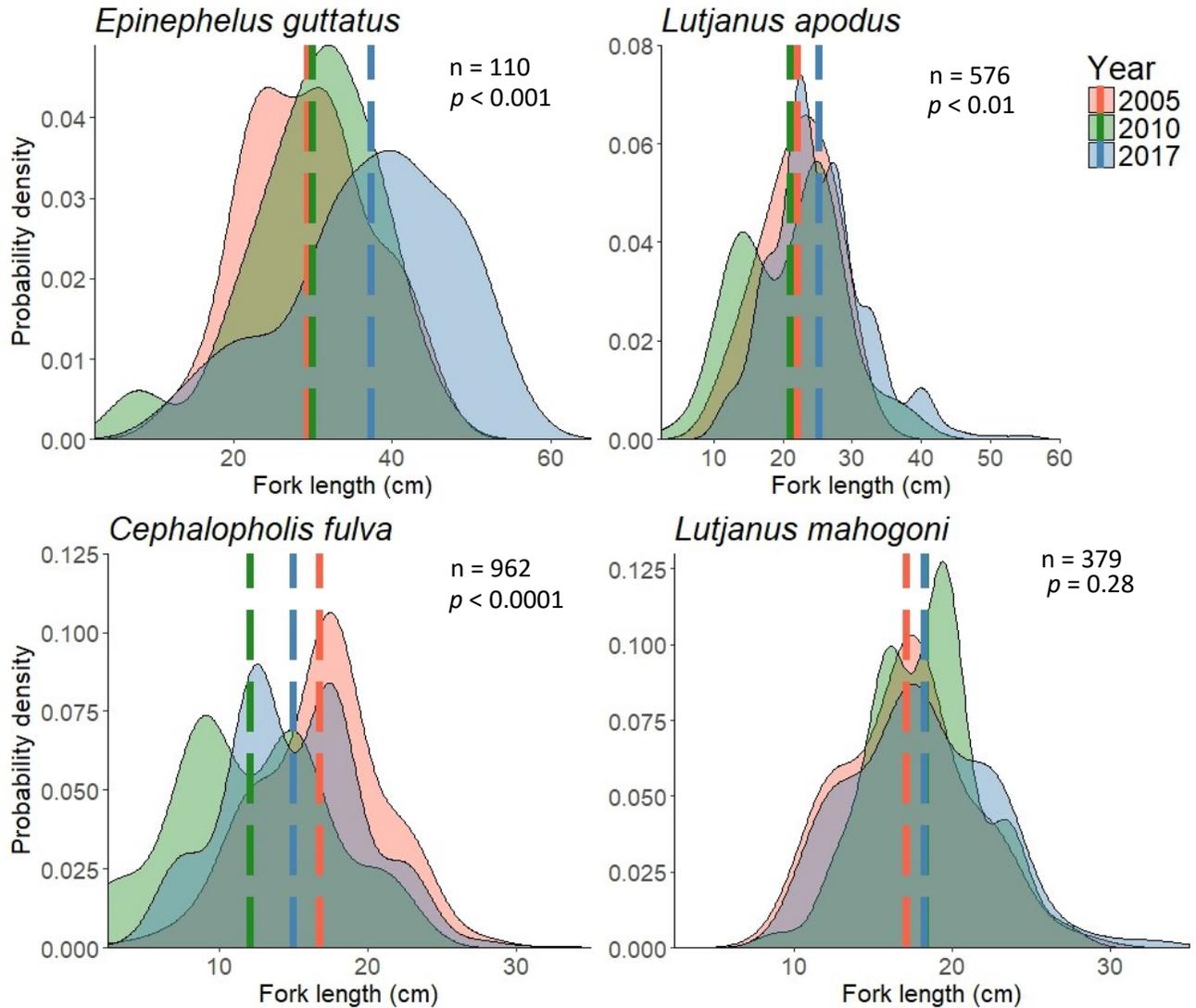


Fig. 8. Probability density distributions of FL estimated for *Epinephelus guttatus*, *Lutjanus apodus*, *Cephalopholis fulva*, and *L. mahogoni* from the Mona NTZ. Dashed lines represent yearly means. P values from Mann-Whitney U tests of mean rank size between 2005 and 2017. Size distributions from LPNR were compared for *O. chrysurus*, *L. apodus*, *L. synagris*, *C. fulva*, *C. cruentata*, *L. maximus*, and *L. mahogoni*. Mean FL decreased significantly between periods for all species except *L. synagris*, which exhibited no significant change (Table 8, Figure 9). The largest relative decrease in FL was estimated for *C. fulva*, which decreased 20 – 25%, from 17.89 cm (± 0.15) to 13.77 cm (± 0.32). Magnitudes of mean decrease, with standard error margins, varied among other taxa: 15 - 21% for *C. cruentata*, 13 -19% for *L. maximus*, 7-13% for *L. apodus*, 7-12% for *L. mahogoni*, and 3-9% for *O. chrysurus* (Fig. 9). Of the taxa

showing significant change in mean size, *L. maximus*, *C. fulva*, *C. cruentata*, and *L. mahogoni* also showed changes in the relative shapes of their size distributions across periods (two-sample Kolmogorov-Smirnov test, Table 8; Figure 9).

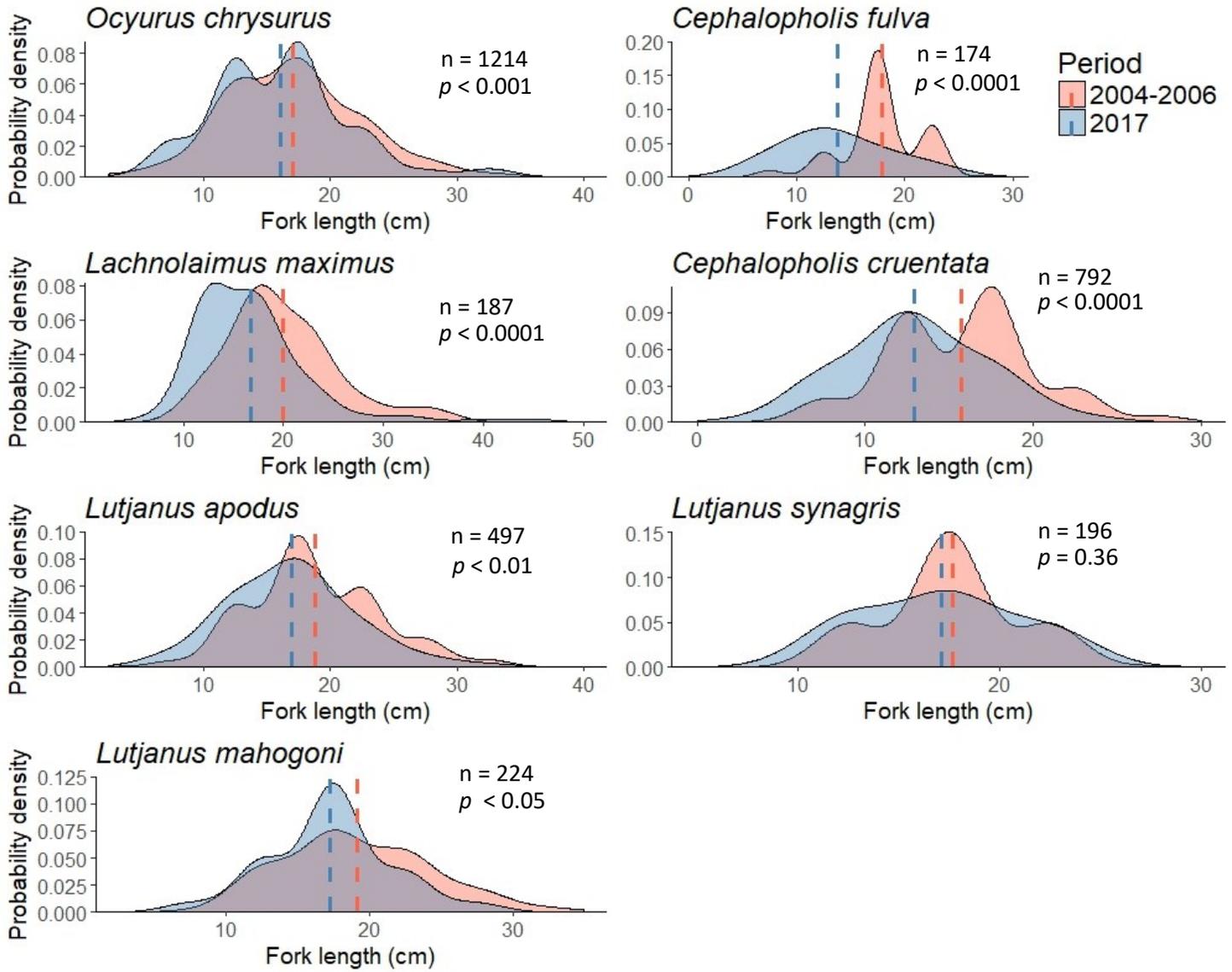


Fig. 9. Probability density distributions of FL of commercial species from the LPNR showing means by period (dashed lines), and *P* values from Mann-Whitney U tests of mean rank size.

Table 9. Results from the LPNR of the two-sample Kolmogorov-Smirnov test of the equality of size distributions between years, and Mann-Whitney U test for location effects on species size distributions.

Species	Kolmogorov-Smirnov	Mann-Whitney U
<i>L. apodus</i>	p = 0.15	p < 0.01
<i>O. chrysurus</i>	p = 0.09	p < 0.001
<i>L. maximus</i>	p < 0.001	p < 0.0001
<i>L. synagris</i>	p = 0.57	p = 0.36
<i>C. fulva</i>	p < 0.0001	p < 0.0001
<i>C. cruentata</i>	p < 0.0001	p < 0.0001
<i>L. mahogoni</i>	p < 0.05	p < 0.05

Fisher Interviews

A total of 8 interviews were conducted opportunistically with current and former fisherman of LPNR and fisherman who fished at Mona Island prior to reserve designation. Primary livelihoods of these men varied, with some currently employed as full-time commercial fishermen and others semi-retired or fishing part-time. Out of the four former Mona Island fisherman, the oldest of these men was 80, the youngest 44 (Appendix J). On average, at their peak, they visited Mona 19.5 times per year to fish commercially, with trips lasting several days. Their primary reported fishing method was with SCUBA and speargun, but also taking conch and lobster. Three of the four men reported decreased abundance of commercially important fish species at Mona now compared to when they began fishing, with the fourth unsure of current conditions but had witnessed a decline during the years he fished. Support for no-take regulations at Mona varied among respondents. Some strongly supported no-take regulations, while others were more skeptical of policy decisions made by the Department of Natural and Environmental Resources

(DNER). The majority of respondents (3 of 4) reported either seeing firsthand or hearing secondhand of fishing within the Mona Island NTZ boundaries. There was weak agreement towards the likelihood of being apprehended for violating no-take regulations at Mona, and no definite sense of social shame associated with such behavior (Appendix J : Q9-10).

Respondents from LPNR were all current commercial fishers who have fished during their entire adult lives (Appendix K). Three of the four currently fish full time, and the other fishes part-time. Three of four reported currently targeting either conch or lobster by SCUBA or freediving, but also opportunistically taking reef fish with speargun. The fourth respondent was a trap fisherman who targets grunts and snapper. There was no clear consensus among respondents on size or abundance trends of commercially valuable fishes or invertebrates. All interviewees perceived a strong enforcement presence in LPNR, with two of four having been fined by the DNER for fishing infractions. There was moderate agreement among respondents (3 of 4) on the existence of social shame regarding illegal fishing activities, and all respondents reported that their friends and family disprove of illegal fishing. Despite the perceived social stigma and perceived likelihood of encounter with enforcement, all interviewees had witnessed illegal take and the majority (3 of 4) believed that other fishers, outside of their social circle, approve of poaching.

Discussion

Our results evidence a weak reserve effect in the Mona NTZ since 2005, acting on the densities and mean FL of some snapper and grouper species; however, the largest taxa showed little or no sign of recovery. Multivariate density effects were driven by increases in smaller predator species, although only one, the coney, increased significantly in mean density. Decreased density and increased mean FL for red hind imply low recent recruitment. However greater density of the largest red hind suggest better adult survival, which may be attributable to no-take protection in habitats closer to shore. Our data suggest that

populations of commercially important species within the Mona NTZ will need substantially more time to show if a reserve effect is causing their recovery but slight positive changes after 14 years of protection are apparent. Results from the LPNR indicate density increases for some species are likely due to recent recruitment (e.g., coney, yellowtail snapper, hogfish). However, decreases in the mean FL of other taxa (graysby, schoolmaster, mahogany snapper), with no density trends, may be explained by historical, size-selective fishing pressure shaping population structures.

We found increases in total density in the Mona NTZ across years owing chiefly to significant increases for coney. Probability density distributions of the FL for this species show a recruitment pulse in 2009-2010 (Fig. 8). This is corroborated by a smaller mean size in 2010 relative to 2005, and a significant increase in density over that period (Table 3). Coney total abundance gains in this particular case are probably not directly related to NTZ protection given the species's history of low commercial fishery targeting (Graham et al., 2003; Jennings and Polunin, 1997) including at Mona (Mateos-Molina et al., 2014). Coney was the only species assessed to show a strong recruitment signal, which may be explained by the species' comparatively large spawning population, earlier age at maturation and frequent spawning events conferring a better probability of successful self-recruitment (Jennings, 2001; Beverton and Holt 1957). In comparison, three species from LPNR (coney, hogfish, and yellowtail snapper) showed trends consistent with recent recruitment pulses (Table 7, Figure 9). The strongest recruitment signal was observed for hogfish, which increased five-fold in mean density and decreased 16-19% in mean fork length. This occurred despite the species having the smallest absolute and proportional density of sexually mature individuals in 2017 ($n = 6$ in 220 transects) (Appendix I). Several explanations for this apparent incongruity are possible: (i) recent environmental conditions were especially favorable for self-recruitment thus improving rates of larval retention, settlement and/or survival and counteracting the limitations imposed by few spawning individuals (Doherty 1994; Bergenius et al. 2002; Sponaugle et al. 2006); (ii) the

spawning population of hogfish in the survey domain is larger than indicated because habitats containing greater densities of sexually mature individuals were not sampled; *(iii)* larval connectivity within a metapopulation on the Puerto Rican platform increased the odds of strong recruitment in the LPNR regardless of the local spawning population size (Cowen et al., 2006; Pagán-López 2002). Regarding point *(ii)*, Pittman et al. (2010) surveyed a wider set of habitat types across the insular shelf and found similarly low numbers of sexually mature individuals ($n = 23$ in 1167 transects). In all likelihood local production and larval-subsidy from nearby areas of the Puerto Rico insular shelf dually contribute to strong recruitment events in hogfish and other reef fishes of the LPNR (Crowder et al. 2000; Cowen et al. 2003; Sale 2004). Larval subsidy into the LPNR would help explain why two heavily fished species (yellowtail snapper and hogfish)(Matos-Caraballo 2007; Ault et al. 2008) showed increased recruitment without significant trends in the densities or sizes of sexually mature individuals. In contrast, only the coney, a minor commercially targeted species with the largest mean density assessed, showed substantial recruitment in the Mona NTZ. These results support the contention that population replenishment at Mona operates according to an entirely different, more restrictive, set of conditions than in the LPNR (Beltrán et al., 2017).

Out of the four species assessed from the Mona NTZ with sufficient sample sizes for individual analysis, red hind is by far the most targeted by fishers and would therefore be expected to show the greatest response to no-take protection (Matos-Caraballo et al. 2006; Matos-Caraballo 2007). That the species increased in mean fork length, but decreased in mean density since 2005 (Appendix , suggests lower recent recruitment. Decreases in density within roving transects from 2005-2017 at several sites (West 1, West 2, South 3, and South 4) (Fig. 1; 3a,b), may also be explained by a displacement of fishing effort following the implementation of no-take regulations in 2004, which left parts of the insular shelf unprotected (DNER 2004; 2007; 2010). Between 2004-2007, a red hind spawning aggregation on the south coast lay outside the 0.5 nautical mile NTZ boundaries, theoretically experiencing greater fishing pressure during this period

as nearby areas were closed (Schärer et al. 2010). This aggregation is located approximately 1 kilometer from the South 3 and South 4 experimental sites, well within the range that red hind are known to migrate for spawning (Nemeth et al. 2007). A displacement of fishing effort into the West zone (open to fishing until 2010) also likely occurred after fishing restrictions were enacted around the rest of the island in 2004. The fact that decreases in mean density are still evident in the population structure 7 years after expansion of the NTZ and closure of the western fished areas supports the notion that red hind recruitment has been low in the intervening years. However, positive trends evidenced in the population structure include a significant change in mean size of + 8.01 cm, and proportional increase of the largest size classes (Fig. 8, Table 8) after 14 years of protection. These differences are similar to a 9.50 cm increase in mean total length recorded at a US Virgin Islands spawning aggregation after 12 years of no-take protection (Nemeth 2005), reflecting better adult survival (a trend not observed in LPNR for any species). With a larger average size, and thereby increased mean fecundity, the odds of good recruitment events become better (Hixon et al. 2014).

Larger sized grouper and snapper species, (*E. striatus*, *M. venenosa*, *M. tigris*, and *L. jocu*), remained rare at Mona, with just 117 individuals sighted in 682 surveys conducted since 2005. Low numbers precluded any meaningful analyses of population trends to evaluate their recovery. However, reports from other regional coral reefs and interviews with elder fishermen suggest that the snapper and grouper assemblage at Mona remains altered. Previously fished taxa at Mona such as the goliath grouper (*E. itajara*) and Nassau grouper were either absent or virtually absent from surveys. Mean density of large grouper as a group was 42% less than estimated at Navassa Island, a similarly isolated, oceanic location west of Hispaniola (Miller & Gerstner 2002). Mean sighting frequency of this group (3.2%) was also substantially lower than reported in other, lightly fished or unfished Caribbean locales such as South Water Caye, Belize (21.0%), the Dry Tortugas, Florida (30.60%), or the Exuma Cays Land and Sea Park, Bahamas

(8.80%) (Chiappone et al. 2000; Ault et al. 2006; Mumby et al. 2012). Similarly, densities of the yellowfin grouper (*M. venenosus*) at Mona were too low for any statistical analyses, yet the species may be showing signs of recovery; mean sighting frequency increased across years from 4.5% in 2005, to 6% in 2010, to 7% in 2017.

Despite increases in total density in the LPNR attributable to greater recruitment for some species, signs of fishing mortality effects on populations are also apparent in our data. Total sample sizes of sexually mature individuals were too low to test for statistical differences between periods for coney, hogfish, and lane snapper, but that fact alone supports the notion that these populations remain overfished. The other species assessed showed no significant trends in mature individual biomass. Large-sized species of epinephelids and lutjanids were exceedingly rare in the LPNR with just 85 individuals sighted in 1219 surveys conducted between 2004 and 2017, precluding species-specific analyses of population trends. However, compared to sighting frequencies collected in 1980-1981, most of these species are now markedly rarer (Kimmel 1985). In 1980 and 1981, Nassau grouper (*E. striatus*) were seen at 34% of coral reef sites; in 2017 sighting frequency at linear reef and shelf-edge reef sites was less than 1%. Red hind (*E. guttatus*) were observed at 64.7% of sites in 1980-1981; in 2017, sighting frequency for the species was 8.2%. During 1980-1981, tiger grouper (*M. tigris*) were seen at 17% of shelf-edge sites. In this study, not a single tiger grouper was observed between 2004 and 2017. While Kimmel (1985) used a different survey methodology, precluding direct comparison of densities, the magnitude of declines suggests that overfishing continues in the LPNR, following island-wide trends (Ault et al. 2008).

Interviews with fishermen indicated a degree of fishing within the Mona NTZ boundaries, corroborating previous reports of non-compliance (Mateos-Molina et al. 2014) and low effectiveness of law enforcement presence (Nemeth 2013; Horadam 2014). Social theory suggests that a fisher's decision to poach is influenced by a variety of factors, but that perceived behavioral controls and social norms weigh

heavily (Bergseth & Roscher 2017). That respondents from the Mona NTZ did not perceive a strong deterrence against illegal take within the NTZ, nor a defined collective stigma, infers that current conditions and attitudes do not foster compliance. The small number of interviews we conducted does not allow for inferences on the extent of fishing within NTZ boundaries, however given the characteristics that limit population replenishment at Mona, any degree of non-compliance could significantly extend recovery time or prevent it entirely (Coleman et al. 2000; Little et al. 2005; Jupiter et al. 2012). Unexpectedly, fisher perceptions of enforcement in the LPNR indicated a higher level of deterrence than at Mona NTZ. This is likely explained by the fact that several agencies with the authority to enforce laws and regulations regularly patrol the LPNR, either at sea or at landing sites, while at Mona, the DNER is the only agency present and does not have a dedicated vessel for at-sea operations (J. Olson, pers. obs.; A. Nieves, pers. comm.). Likewise, there was a consensus of social shame regarding illegal fishing in the LPNR. This may be due to a more cohesive and localized fishing community in the LPNR (Valdés-Pizzini & Schärer-Umpierre 2014), whereas Mona's visitors and former fishermen hail from a wide area of Puerto Rico and therefore may not regularly interact with each other directly (Nemeth, 2013; Suarez-Caabro and Rivas, 1976). Nevertheless, the levels of social shame and perceived probability of apprehension apparently do not completely limit illegal fishing pressure in the LPNR, as all respondents had recently either fished illegally themselves, or witnessed someone else doing so. Reports of illegal take of finfish in LPNR, specifically snapper and grouper during closed seasons, suggests that these management measures likely aren't fully achieving their intended conservation benefits.

The possibility exists that our study lacked sufficient power to detect changes in the population metrics of some species in both MPAs. High and heterogeneous variance between years and periods emerged in the counts and sizes of multiple taxa and may have obscured true reserve effects (Tables 3, 7). One remedy would be to explicitly consider habitat variables within the analysis to better account for fine-

scale population variability. In the case of multivariate comparisons, significant dispersion effects in both MPAs could have led to spurious rejection of null hypotheses given our unbalanced sampling designs (Anderson & Walsh 2013). Future studies of fish assemblages in these MPAs should strive to use a balanced sampling design to avoid this issue. Another limiting aspect of our experimental design is the lack of a control site on the Mona insular platform by which to separate the effects of fishing from environmental and isolation factors. While impossible given the current extent of the Mona NTZ, a nearby control site would have allowed for a more unequivocal assessment of recovery. A lack of seasonal replication in 2005 and 2010 samplings at Mona may have also limited our ability to distinguish seasonal effects from the effects of fishing prohibition. Despite sampling time (season) not being a significant factor in analysis, seasonal processes are well known to shape coral reef ecosystems and may have contributed unexplained variance to our results (Bergenius et al. 2002; Mellin et al. 2007).

The lack of significant trends in the biomass of commercially important species, or in the density or biomass of large sized species in the Mona NTZ is likely reflective of low recovery rates due in part to recruitment isolation. Larval connectivity within a metapopulation is known to be a strong determinant of recovery in marine fishery reserves (Jennings 2001). Well-connected populations are more resilient to fishing pressure and therefore have the potential to recover more quickly once fishing is prohibited (Jones et al. 2009). However, recovery is a dynamic process governed by other factors such as reserve design, the history of biomass depletion (MacNeil et al. 2015), degree of compliance with regulations (Edgar et al. 2014; McClanahan & Graham 2015) and life history characteristics of the species in question (Claudet et al. 2010). Our results suggest that a combination of these features may be responsible for the slow recovery of large sized species in the Mona NTZ. Other studies have estimated 20+ years for predatory fish biomass to reach carrying capacity in high-compliance, tropical and sub-tropical marine reserves of mixed connectivity (McClanahan et al. 2007; García-Rubies et al. 2013; McClanahan & Graham 2015). Russ and

Alcala (2004) estimated 15-40 years for large reef predator biomass to reach carrying capacity in two marine reserves in the Philippines. The two reserves in that seminal study are situated less than 8 km from the mainland. Island biogeographic theory suggests that, other factors notwithstanding, those reserves would have higher rates of larval immigration, and thus faster recovery times than a more isolated one, such as the Mona NTZ (Jennings, 2001; MacArthur and Wilson, 1967). With these points in mind, and in light of our results, it is likely that 14 years has not been sufficient for fish populations at Mona to accrue substantial gains in fish biomass. Additional decades of protection and compliance with NTZ boundaries will be required before recovery is measurable.

Management Implications

Evidence of slow recovery in the Mona NTZ presented here shows that it may be inappropriate to view the reserve in a fisheries management perspective as this will lead to inadequate expectations of its productive capacity. Given the narrow insular shelf with limited coral habitat and infrequency of larval inflow, large-bodied demersal species at Mona likely cannot sustain more than low levels of harvest, once stocks have recovered. Management emphasis for the Mona Island NTZ should instead be framed in the context of marine heritage and biodiversity preservation, with the express benefit of allowing regional long-term genetic connectivity of coral reef species across the Mona Channel.

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Appendices

Appendix A SIMPER results showing top contributors to 90% cumulative dissimilarities in square-root transformed roving survey density (fish/survey) and biomass (g/survey) from the Mona NTZ. Dissimilarities shown between 2005 and 2010 (a), 2005 and 2017 (b), and 2010 and 2017 (c).

a.)		Density				Biomass					
Species	2005		2010	Diss % (85.78)	Contrib.%	Species	2005		2010	Diss % (86.67)	Contrib.%
	Av. Dens.	Av. Dens.	Av. Dens.				Av. Bio.	Av. Bio.			
<i>L. apodus</i>	1.02	1.35	35.32	41.17	<i>L. apodus</i>	14.28	19.08	32.78	37.82		
<i>L. mahogoni</i>	0.82	0.75	21.41	24.95	<i>L. mahogoni</i>	8.60	7.92	17.83	20.58		
<i>E. guttatus</i>	0.36	0.20	18.35	21.39	<i>E. guttatus</i>	7.53	4.45	20.49	23.64		
<i>M. venenosa</i>	0.10	0.09	5.41	6.31	<i>M. venenosa</i>	4.23	4.62	8.51	9.82		

b.)		Density				Biomass					
Species	2005		2017	Diss % (88.59)	Contrib.%	Species	2005		2017	Diss % (89.08)	Contrib.%
	Av. Dens.	Av. Dens.	Av. Dens.				Av. Bio.	Av. Bio.			
<i>L. apodus</i>	1.02	1.02	33.79	38.15	<i>L. apodus</i>	14.28	17.54	32.26	36.21		
<i>E. guttatus</i>	0.36	0.14	20.43	23.06	<i>E. guttatus</i>	7.53	4.03	21.61	24.26		
<i>L. mahogoni</i>	0.82	0.65	20.27	22.88	<i>L. mahogoni</i>	8.60	7.37	16.56	18.59		
<i>M. venenosa</i>	0.10	0.13	7.70	8.69	<i>M. venenosa</i>	4.23	6.21	10.43	11.71		

c.)		Density				Biomass					
Species	2010		2017	Diss % (81.54)	Contrib.%	Species	2010		2017	Diss % (83.96)	Contrib.%
	Av. Dens.	Av. Dens.	Av. Dens.				Av. Bio.	Av. Bio.			
<i>L. apodus</i>	1.35	1.02	38.20	46.85	<i>L. apodus</i>	19.08	17.54	36.93	43.98		
<i>L. mahogoni</i>	0.75	0.65	21.73	26.64	<i>L. mahogoni</i>	7.92	7.37	17.53	20.88		
<i>E. guttatus</i>	0.20	0.14	11.25	13.80	<i>E. guttatus</i>	4.45	4.03	13.01	15.50		
<i>M. venenosa</i>	0.09	0.13	5.30	6.50	<i>M. venenosa</i>	4.62	6.21	8.52	10.15		

^a() Average dissimilarity between years

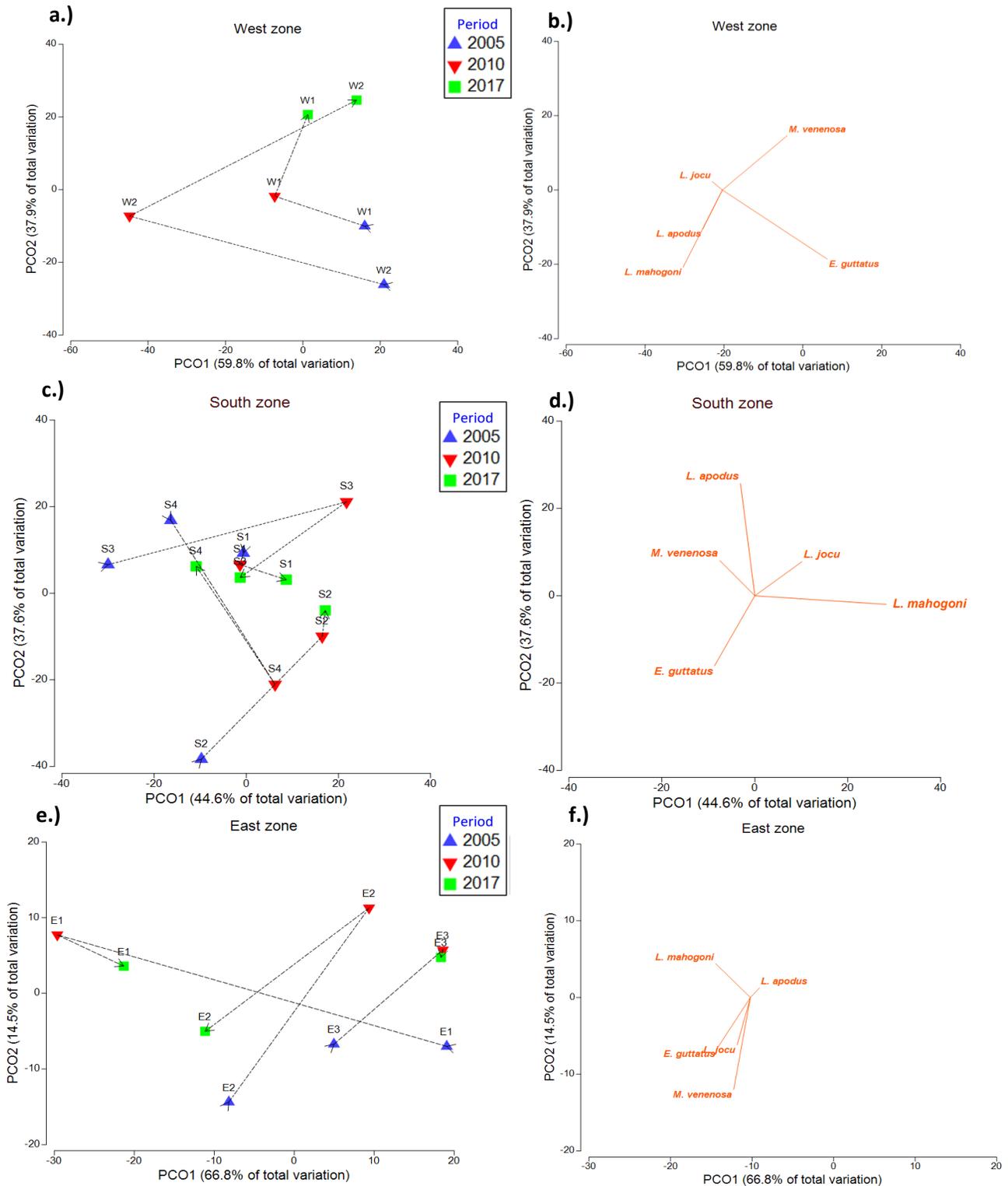
Appendix B SIMPER results showing top contributors to 90% cumulative dissimilarities in biomass (g/m^2) and density (fish/m^2) between cross shelf zones and survey periods in La Parguera (2004-2006, 2017). Species sorted in descending order by percent contribution to total inter-period dissimilarity per metric and zone.

a.) Inner-shelf		Density			Biomass				
Species	Pd. 1	Pd. 2	Diss % (72.81)	Contrib.%	Species	Pd. 1	Pd. 2	Diss % (74.98)	Contrib.%
	Av. Dens.	Av. Dens.				Avg Biom.	Avg Biom.		
<i>O. chrysurus</i>	0.12	0.16	21.96	30.16	<i>O. chrysurus</i>	1.13	1.46	21.46	28.63
<i>L. maximus</i>	0.03	0.08	12.81	17.59	<i>L. maximus</i>	0.35	0.86	13.99	18.65
<i>C. cruentata</i>	0.06	0.03	9.46	12.99	<i>C. cruentata</i>	0.53	0.13	8.5	11.33
<i>L. apodus</i>	0.03	0.04	7.85	10.79	<i>L. apodus</i>	0.38	0.36	8.43	11.25
<i>L. synagris</i>	0.06	0.01	7.63	10.48	<i>L. synagris</i>	0.54	0.13	7.66	10.21
<i>L. griseus</i>	0.00	0.03	3.58	4.92	<i>L. griseus</i>	0.00	0.35	3.58	4.78
<i>L. mahogoni</i>	0.01	0.02	3.27	4.49	<i>L. mahogoni</i>	0.17	0.15	3.46	4.62

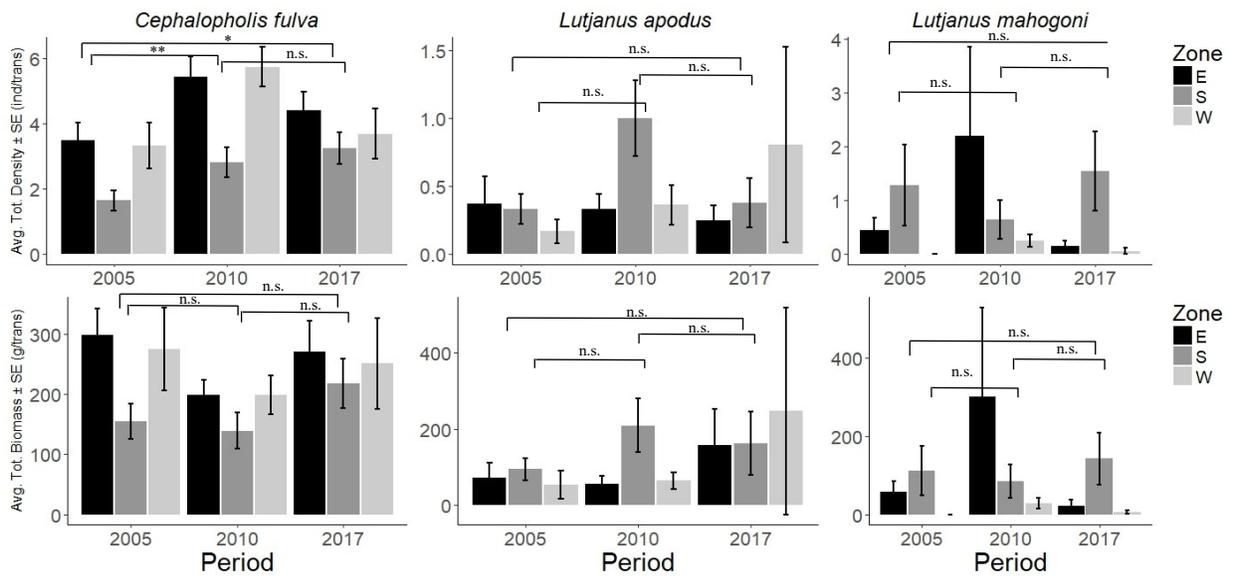
b.) Mid-shelf		Density			Biomass				
Species	Pd. 1	Pd. 2	Diss % (73.85)	Contrib.%	Species	Pd. 1	Pd. 2	Diss % (74.68)	Contrib.%
	Av. Dens.	Av. Dens.				Avg Biom.	Avg Biom.		
<i>O. chrysurus</i>	0.10	0.18	33.83	45.81	<i>O. chrysurus</i>	1.06	1.59	31.61	42.33
<i>L. apodus</i>	0.04	0.04	11.69	15.83	<i>L. apodus</i>	0.52	0.46	13.33	17.85
<i>C. cruentata</i>	0.04	0.01	9.34	12.64	<i>C. cruentata</i>	0.32	0.06	7.50	10.04
<i>L. maximus</i>	0.01	0.03	5.96	8.07	<i>L. maximus</i>	0.13	0.42	7.43	9.94
<i>L. mahogoni</i>	0.02	0.01	5.08	6.87	<i>L. mahogoni</i>	0.29	0.09	5.83	7.81

b.) Shelf edge		Density			Biomass				
Species	Pd. 1	Pd. 2	Diss % (64.92)	Contrib.%	Species	Pd. 1	Pd. 2	Diss % (70.84)	Contrib.%
	Av. Dens.	Av. Dens.				Avg Biom.	Avg Biom.		
<i>O. chrysurus</i>	0.04	0.17	1.41	33.58	<i>O. chrysurus</i>	0.49	1.81	26.32	37.16
<i>C. cruentata</i>	0.13	0.11	1.13	24.68	<i>C. cruentata</i>	1.03	0.67	15.13	21.36
<i>C. fulva</i>	0.05	0.07	0.95	18.97	<i>C. fulva</i>	0.49	0.47	11.69	16.51
<i>L. apodus</i>	0.00	0.03	0.41	5.07	<i>A. quadricornis</i>	0.18	0.06	3.55	5.01
<i>A. quadricornis</i>	0.01	0.01	0.43	4.39	<i>L. apodus</i>	0.03	0.27	3.49	4.93
<i>L. mahogoni</i>	0.01	0.01	0.41	3.82	<i>L. mahogoni</i>	0.11	0.11	2.85	4.02

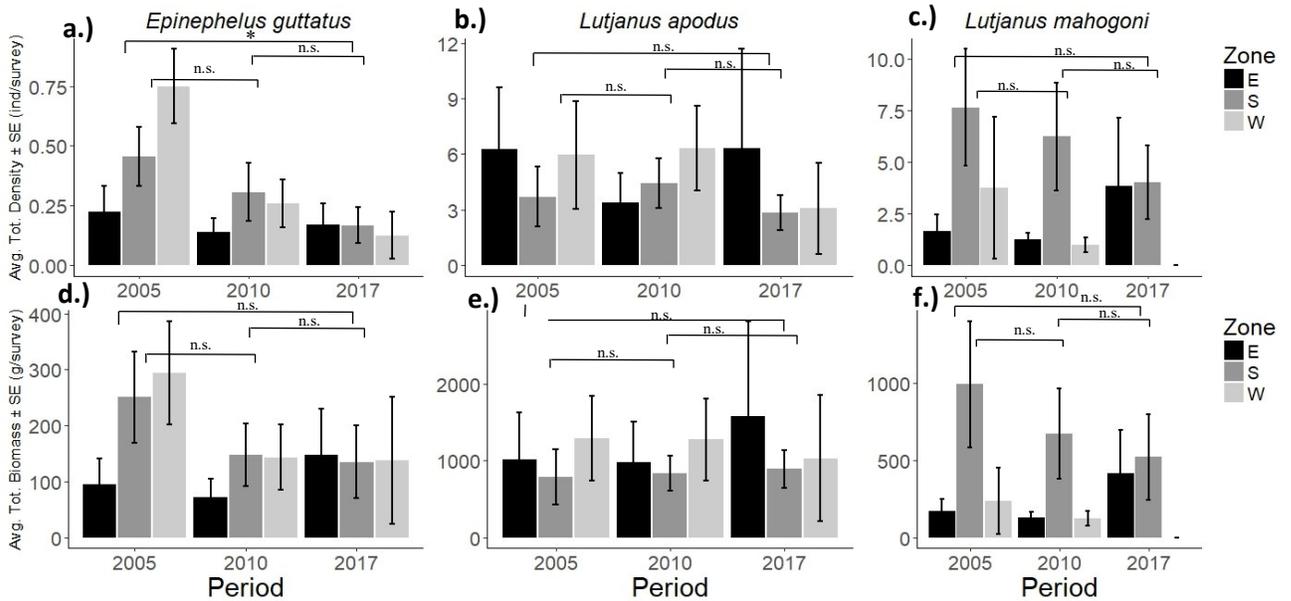
^a() Average dissimilarity between periods



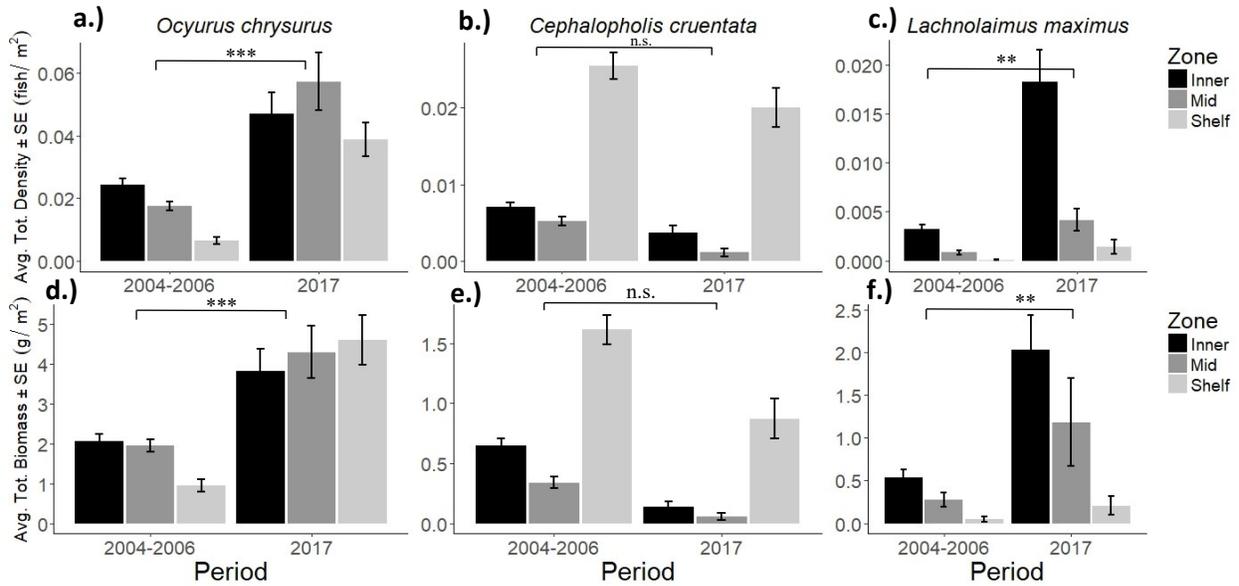
Appendix C Principle coordinates ordination plots (PCO) based upon Bray-Curtis dissimilarities of square-root-transformed density (fish/survey) from roving surveys separated by experimental zone (eg. East zone, South zone, West zone). Centroids by site and period (a,c,e) and corresponding species correlation vectors (Pearson > 0.2) (b,d,f).



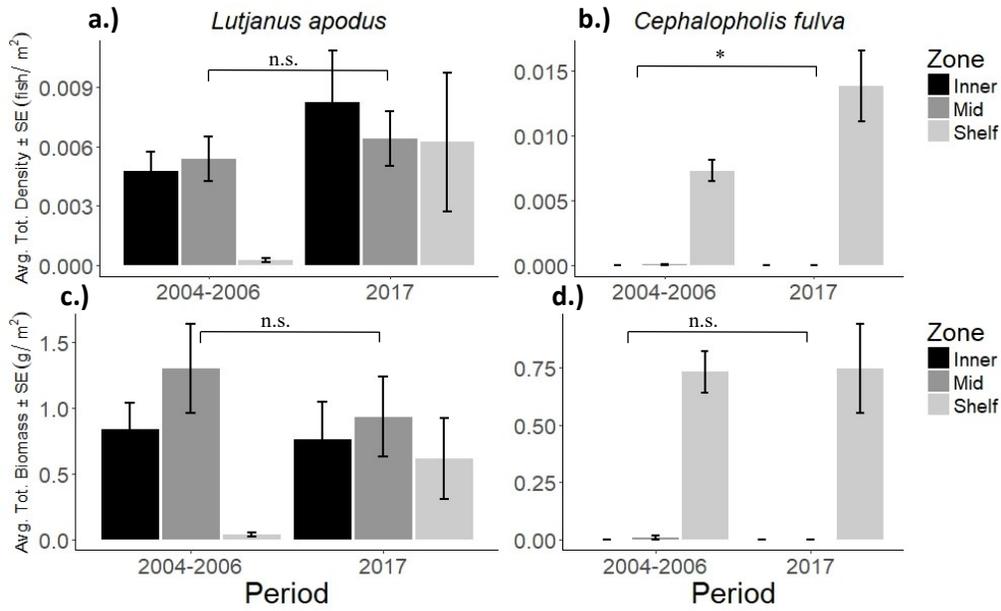
Appendix D Mean total belt transect density (fish/60 m²) (a,b,c) and mean total biomass (grams / 60 m²) (d,e,f) by year and zone from the Mona NTZ for *Cephalopholis fulva*, *Lutjanus apodus*, and *L. mahogoni*. Level of significance from between year, univariate PERMANOVA indicated: *p < 0.05; **p < 0.01; ***p < 0.001.



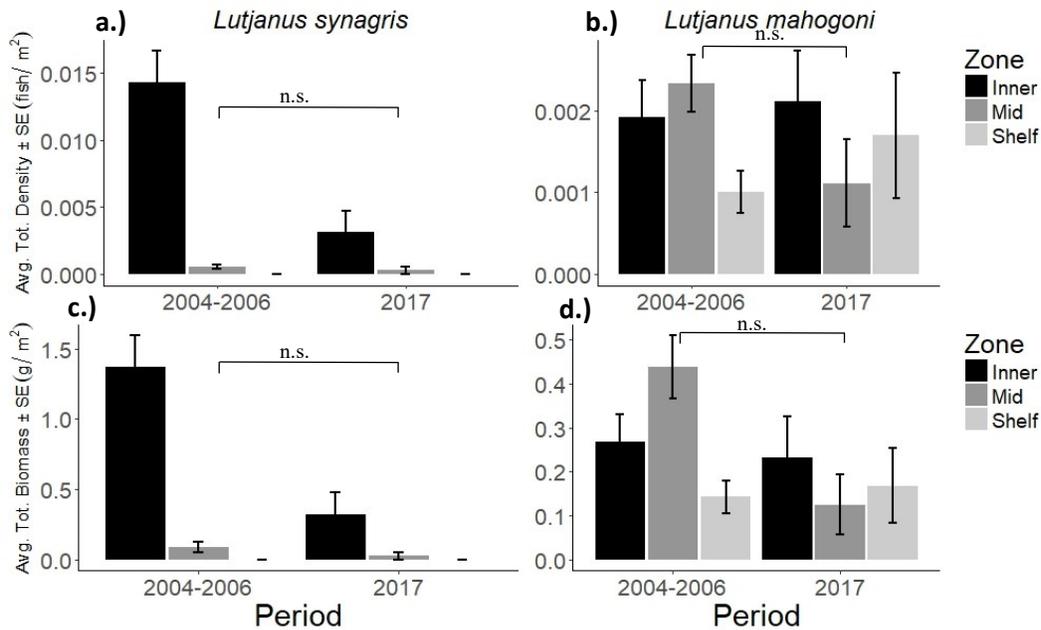
Appendix E Mean total roving survey density (fish/ survey) (a,b,c) and mean total roving biomass (grams / survey) (d,e,f) by year and zone from the Mona NTZ, for *E. guttatus*, *L. apodus*, and *L. mahogoni*. Level of significance from between year, univariate PERMANOVA indicated: * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$.



Appendix F Mean total transect density (fish/m²)(a,b,c), and mean total transect biomass (grams/m²)(d,e,f) for *Ocyurus chrysurus*, *Cephalopholis cruentata*, and *Lachnolaimus maximus*. Results shown by period (2004-2006, 2017), and zone (inner-shelf, mid-shelf, and shelf-edge) from the La Parguera Natural Reserve. Level of significance from between period, univariate PERMANOVA indicated: * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$.



Appendix G Mean total transect density (fish/m²)(a,b), and mean total transect biomass (grams/m²)(c,d) for *Lutjanus apodus* and *Cephalopholis fulva*. Results shown by period (2004-2006, 2017), and zone (inner-shelf, mid-shelf, and shelf-edge) from the La Parguera Natural Reserve. Level of significance from between period, univariate PERMANOVA indicated: *p < 0.05; **p < 0.01; ***p < 0.001.



Appendix H Mean total transect density (fish/m²)(a,b), and mean total transect biomass (grams/m²)(c,d) for *Lutjanus synagris* and *Lutjanus mahogoni*. Results shown by period (2004-2006, 2017), and zone (inner-shelf, mid-shelf, and shelf-edge) from the La Parguera Natural Reserve. Level of significance from between period, univariate PERMANOVA indicated: *p < 0.05; **p < 0.01; ***p < 0.001.

Appendix I Proportion of individuals sighted by period (2004-2006, 2017) from the La Parguera Natural Reserve greater than or equal to the length at maturity (L_m). L_m values taken from Ault et al. 2008.

Species	L_m (mm)	% period 1	% period 2
<i>C. cruentata</i>	165	57.0 (399)	28.2 (26)
<i>C. fulva</i>	185	25.2 (32)	12.8 (6)
<i>L. apodus</i>	145	78.3 (332)	65.8 (48)
<i>L. synagris</i>	206	20.5 (30)	24.0 (12)
<i>O. chrysurus</i>	199	25.6 (210)	18.1 (71)
<i>L. maximus</i>	249	13.3 (11)	5.77 (6)
<i>L. mahogoni</i>	130	78.1 (114)	74.4 (58)

* () indicates number of sexually mature individuals sighted

Appendix J Survey responses from anonymous interviews with former Mona Island fishermen. Surveys conducted between March and July, 2018.

Age:

Respondent a.) 58

Respondent b.) 80

Respondent c.) 44

Respondent d.) 71

1.) How often did you go to Mona to fish? (Trips/year)

Respondent a.) 15 trips/year

Respondent b.) 10 trips/year

Respondent c.) 26 trips/year

Respondent d.) 36 trips/year

2.) What was your primary purpose for visiting Mona?

Respondent a.) fishing

Respondent b.) dive charters/spearfishing early on

Respondent c.) fishing

Respondent d.) fishing

3.) When was your first trip to Mona? Most recent?

Respondent a.) First trip in 1978, last trip in 1995

Respondent b.) First-1956, last- 2018

Respondent c.) First- 1990, last - 2018

Respondent d.) First 1980, last NA

4.) Which areas did you fish?

Respondent a.) Off of Sardinera and Pajaros

Respondent b.) Off of Sardinera, and spur and groove reef off of SE coast

Respondent c.) Sardinera and Pajaros

Respondent d.) NW coast: Punta Arena to north of Punta Capitán

5.) What was your primary fishing method?

Respondent a.) Spearfishing for grouper, but also took snapper and lobster. Mentions spearing Nassau, goliath, and yellowfin

Respondent b.) Spearfishing for grouper, sea turtles. Also took conch and lobster occasionally. Reported dense “schools” of Nassau grouper in 1950s and 1960s.

Respondent c.) Spearfishing, also conch and lobster with lasso

Respondent d.) Spearfishing for grouper, occasionally snapper. Conch and lobster. Mentions spearing a 136 lb goliath grouper

6.) How would you describe the abundance of fish at Mona now compared to before NTZ enactment?

[a lot fewer | slightly fewer | the same | slightly more | a lot more]

Respondent a.) a lot fewer

Respondent b.) a lot fewer

Respondent c.) slightly fewer

Respondent d.) not sure but observed a decrease in the years that he fished

7.) If yes to Q4, how would describe the size of fish at Mona now?

[a lot smaller | slightly smaller | equal | slightly larger | a lot larger]

Respondent a.) not sure

Respondent b.) a lot smaller

Respondent c.) slightly smaller

Respondent d.) not sure

8.) I know the boundaries of the Mona Island No-Take Zone and understand fishing regulations for the island and surrounding waters

[strongly disagree | moderately disagree | neutral | moderately agree | strongly agree]

Respondent a.) strongly agree

Respondent b.) strongly agree

Respondent c.) no response

Respondent d.) strongly agree

9.) If I were to fish within the Mona Island No-take Zone I would face punishment.

[strongly disagree | moderately disagree | neutral | moderately agree | strongly agree]

Respondent a.) neutral

Respondent b.) strongly disagree

Respondent c.) moderately agree

Respondent d.) moderately disagree

10.) If I were to fish within the Mona Island No-take Zone I would face social shame

[strongly disagree | moderately disagree | neutral | moderately agree | strongly agree]

Respondent a.) moderately agree

Respondent b.) moderately disagree

Respondent c.) moderately agree

Respondent d.) strongly disagree

11.) I support the decision of the DNER to prohibit fishing around Mona

[strongly disagree | moderately disagree | neutral | moderately agree | strongly agree]

Respondent a.) moderately disagree, thinks that populations at Mona could sustain some commercial pressure. "All larvae from spawning aggregations lost because no close, fished area for them to settle".

Respondent b.) strongly agree

Respondent c.) strongly agree

Respondent d.) moderately agree but wishes that DRNA would make studies to validate the closure given that he has been forced to sacrifice fishing at Mona.

12.) Have you ever seen someone fishing within the Mona Island No-take Zone?

Respondent a.) No

Respondent b.) Yes

Respondent c.) Yes

Respondent d.) Yes

13.) Do you know anyone personally who's fished in the Mona No-take Zone? If so, were they caught?

Respondent a.) No

Respondent b.) Yes, not caught

Respondent c.) No

Respondent d.) Yes, his cousin. Not caught

Appendix K Survey responses from anonymous interviews with fishermen of the La Parguera Natural Reserve. Surveys conducted between March and July, 2018.

Age:

Respondent a.) 62

Respondent b.) 34

Respondent c.) 45

Respondent d.) 63

1.) On average, how often do you fish in La Parguera? (days/wk)

Respondent a.) 5 days/wk

Respondent b.) 5 days/wk

Respondent c.) 5 days/wk

Respondent d.) 3 days/wk

2.) When did you first begin fishing here?

Respondent a.) 12 years old

Respondent b.) 15 years old

Respondent c.) 14 years old

Respondent d.) 25 years old

3.) What is your primary method of fishing?

Respondent a.) traps, nets

Respondent b.) SCUBA for lobster

Respondent c.) SCUBA for lobster / spearfishing

Respondent d.) gill net, skin diving for conch

4.) Has your primary method of fishing changed?

Respondent a.) Used to fish many more traps. Most of his traps were lost during Hurricane Maria

Respondent b.) No

Respondent c.) No

Respondent d.) Yes, before ear injury he used SCUBA to spearfish, collect conch/lobster

5.) What species do you normally target?

Respondent a.) grunts/snapper

Respondent b.) lobster, reef fish opportunistically

Respondent c.) lobster, reef fish opportunistically

Respondent d.) conch, boxfish, snapper, porgy

6.) Compared to when you began fishing, how would you describe the abundance of fish/conch/lobster in La Parguera now?

[a lot fewer | slightly fewer | the same | slightly more | a lot more]

Respondent a.) the same

Respondent b.) the same

Respondent c.) a lot fewer

Respondent d.) a lot fewer

7.) How would you describe the size of fish in the La Parguera Natural Reserve now?

[a lot smaller | slightly smaller | the same | slightly larger | a lot larger]

Respondent a.) the same

Respondent b.) a lot smaller

Respondent c.) the same

Respondent d.) conch/porgies/grunts smaller | boxfish, yellowtail, lobster the same

8.) Compared to when you began fishing in La Parguera, how many fishermen are there now?

[a lot less | slightly less | the same amount | slightly more | a lot more]

Respondent a.) a lot more

Respondent b.) a lot less

Respondent c.) a lot more

Respondent d.) a lot more

Choose the answer which best describes your response to following statements:

9.) I know the fishing regulations of Puerto Rico regarding closed seasons, minimum sizes, and prohibited species.

[strongly disagree | moderately disagree | neutral | moderately agree | strongly agree]

Respondent a.) strongly agree

Respondent b.) moderately agree

Respondent c.) strongly agree

Respondent d.) strongly agree

10.) My friends and family approve of poaching

[strongly disagree | moderately disagree | neutral | moderately agree | strongly agree]

Respondent a.) strongly disagree

Respondent b.) moderately disagree

Respondent c.) strongly disagree

Respondent d.) strongly disagree

11.) Fishermen I don't know approve of poaching

[strongly disagree | moderately disagree | neutral | moderately agree | strongly agree]

Respondent a.) strongly agree

Respondent b.) moderately agree

Respondent c.) strongly disagree

Respondent d.) moderately agree

12.) If I keep prohibited species, small conch or lobster, or species out of season I will be fined

[strongly disagree | moderately disagree | neutral | moderately agree | strongly agree]

Respondent a.) moderately agree

Respondent b.) strongly agree

Respondent c.) strongly agree

Respondent d.) moderately agree

13.) If I keep prohibited species, small conch or lobster, or species out of season I will face social shame

[strongly disagree | moderately disagree | neutral | moderately agree | strongly agree]

Respondent a.) strongly disagree

Respondent b.) strongly agree

Respondent c.) strongly agree

Respondent d.) moderately agree ("silent shame")

14.) Have you ever seen or heard of poaching? (Taking fish during las Vedas, taking prohibited species , small lobster, conch)

Respondent a.) yes

Respondent b.) yes

Respondent c.) yes

Respondent d.) yes

15.) Do you know of anyone who's poached? If so, were they caught?

Respondent a.) Yes, NA

Respondent b.) Yes, he was caught and fined for spearing 200 lb of red hind at the shelf edge 5 years ago in January.

Respondent c.) Yes, he was caught with 17 undersized lobster. Fined 1000 dollars

Respondent d.) No, NA

16.) Have you ever kept prohibited species, small conch or lobster, or fish out of season?

Respondent a.) No

Respondent b.) Yes, red hind during seasonal closure.

Respondent c.) Yes, undersized lobster

Respondent d.) No
