

**Assessing the effects of Mona Island Marine Protected Area on coral reef fishes**

By

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## **Abstract**

No-take marine reserves or no-take zones (NTZ) have become an effective tool for restoring marine populations threatened by overfishing by allowing populations to recover from excessive extraction. In 2004, a NTZ was established within the Mona Island Natural Reserve. The objective of this study is to evaluate the effectiveness of the Mona Island NTZ with respect to coral reef fish populations threatened by overfishing. We used a before-after-control-impact (BACI) design to analyze these effects. Fish abundance and biomass of selected species known to be fishery targets were used as indicators of NTZ effect. Belt transects and roving surveys were used to quantify fish abundances and sizes. Permutational multivariate analyses of variance (PERMANOVA) and SIMPER analysis were carried out to assess spatio-temporal changes between 2005/06 and 2009/10. Significant increases in fish abundance and biomass were observed, suggesting a NTZ effect for important fishery resources.

## **Resumen**

Reservas marinas o zonas de no pesca (ZNP) han llegado a ser una herramienta efectiva para la restauración de poblaciones marinas amenazadas por la sobrepesca. En 2004 se estableció una ZNP dentro de la Reserva Natural de Isla de Mona. El objetivo de este estudio es evaluar la efectividad de la ZNP para proteger poblaciones de peces de arrecife amenazados por la sobrepesca. Se utilizó un diseño antes-después-control-impacto (ADCI) para analizar tales efectos. La abundancia y biomasa de especies conocidas por ser objetivos pesqueros, fueron utilizadas como indicadores del efecto de la ZNP. Transectos de banda y búsquedas aleatorias se utilizaron para cuantificar las abundancias y tamaños de los peces. Se utilizó un análisis de varianza multivariado por permutaciones (PERMANOVA) y análisis de SIMPER para evaluar los cambios temporales entre 2005/06 y 2009/10, y diferencias espaciales entre zona de pesca y ZNP en Isla de Mona. Se observó un incremento significativo en la abundancia y biomasa de peces, sugiriendo un efecto importante de la ZNP para los recursos pesqueros.

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## Introduction

Overfishing is thought to be the most destructive human activity on marine coastal ecosystems, with impacts dating back to historical times (Jackson et al. 2001; Lotze et al. 2006) but accelerating in the past century (McClenachan 2009). The result has been degraded ecosystems and unsustainable fishing (Pauly et al. 2002). Puerto Rico has been no exception, where overfishing has resulted in reduced stocks (Appeldoorn 2008) and environmental degradation is readily apparent (Ballantine et al. 2008; Appeldoorn et al. 2009). Marine reserves or No-Take Zones (NTZs) have been suggested as an effective tool for restoration (Palumbi 2003), biodiversity conservation (Murray et al. 1999; Schrope 2001; Rodrigues et al. 2004) and for fisheries management (Roberts et al. 2001; Claudet et al. 2006). Many examples have already demonstrated increases in abundance and biomass in NTZs (Bohnsack 1998; Halpern 2003; McClanahan & Arthur 2001) and spillover effects into adjacent areas (Roberts et al. 2001), specifically of species threatened by overfishing (Côté et al. 2001; Halpern 2003; Craig & Hastings 2007). Nevertheless, NTZs have not been uniformly adopted. In part this is due to the small number of well-designed studies (Russ 2002) documenting reserve impacts, particularly those incorporating assessments before and after reserve establishment (Willis et al. 2003) or where protection has been effective or operational over sufficient time scales (Appeldoorn & Lindeman 2003), which have resulted in some reports of only slight benefits (Sale et al. 2005). The lack of well-documented studies also reduces the number of regional role models that local managers can use to evaluate potential impacts or illustrate benefits to stakeholders. This situation is particularly evident in the northeast Caribbean (Appeldoorn & Lindeman 2003).

The purpose of this study is to evaluate the effectiveness of a NTZ at Mona Island, Puerto Rico, a remote oceanic island lying in the Mona Channel between islands of Puerto Rico and Hispaniola. Because of its location, the success of the NTZ takes on added importance. On the one hand, on small time scales isolated areas must support fish abundances and age structures sufficient enough to ensure self-recruitment and population persistence (Jones et al. 2007). On the other hand, the Mona Channel is a known partial biogeographic barrier, with north-south currents that divide the eastern and western populations of the Caribbean (Lessios et al. 1984; Dennis et al. 2005; Taylor & Hellberg 2006; Baums et al. 2006; Eytan & Hellberg 2010), and at

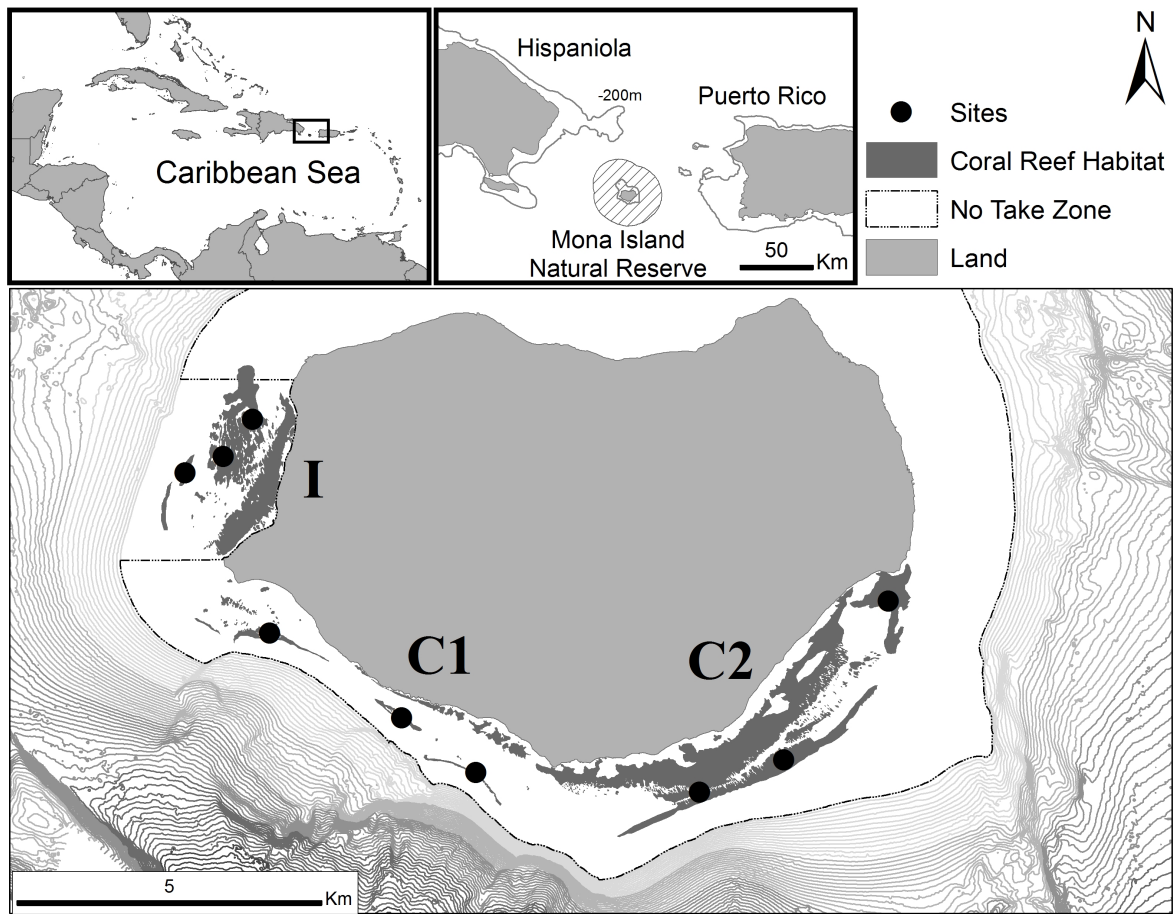
larger time scales the island may serve as a stepping stone in the connectivity of shallow water species in the northeast Caribbean.

To evaluate the Mona Island NTZ, this study concentrates on groupers and snappers. Worldwide, these fishes are among the most heavily exploited in recent years (Pauly et al. 2002) and are believed to be especially sensitive to overfishing (Russ & Alcala 1996; Sadovy & Domeier 2005); therefore they are excellent indicators of the effects of a marine reserve (Mosqueira et al. 2000; Schroeder & Parrish 2005). The NTZ effects were analyzed at the fish assemblage level, applying multivariate methods to several metrics belonging to different groups, and incorporating data from the inception of the NTZ, as well as from fished and non-fished areas.

## **Materials and Methods**

### **Study area**

Located 72 km to the west of Puerto Rico in the Mona Passage, Mona Island Natural Reserve is the largest marine protected area (MPA) in Puerto Rico, with 266 km<sup>2</sup> of seafloor surface area. The MPA includes several habitats: small lagoons of seagrass, shallow fringing reefs, deeper patch and spur-and-groove reefs along the eastern, southern and western shores. This MPA was established in 1986 (Aguilar-Peréa et al. 2006) with the primary aim of protecting marine biodiversity, and favoring social and economic activities linked to the sea, especially recreational and commercial fisheries. A no-take zone (NTZ) was established within of the Mona Island MPA in 2004, extending 0.5 nautical miles (926 m) from shore around the island except a swath on the western coast where fishing is allowed. In 2007 this zone was modified to include areas up to the 100 fathom (182 m) depth contour (DNER 2007). In the NTZ, only fishing is prohibited. Compliance within the MPA is limited due to pressures not only from directed recreational and commercial fishing, but also from hunters, divers and other users.



**Figure 1.** Study area and position of impacted (I) and control (C1 and C2) locations in Mona Island MPA.

### Sampling design and data collection

Surveys used in this study were conducted in autumn and winter during two periods of time: 1) in 2005-06, just after the establishment of the NTZ (Schärer-Umpierre 2009), and 2) four years later, in 2009-10. Three locations within the MPA were considered in this study: two areas within the NTZ (controls), the southwest no-take zone (SWNTZ) and the east no-take zone (ENTZ), and the impacted (fished) area, the take zone (TZ), on the west side of the island. Sampling points per location were chosen randomly within the 10 and 20 m depth range and limited to coral reef habitats. These depth and habitat limits were based on the previous study (Schärer-Umpierre 2009) to maximize the probability of sampling target species while minimizing sampling effort. The following species were selected because of their fisheries importance: *Lutjanus jocu*, *L. apodus*, *L. mahogani*, *Epinephelus guttatus*, *E. striatus*, *Mycteroperca venenosa*, *M. tigris*, *Cephalopholis cruentatus*, *C. fulva*, and *Balistes vetula*.

Underwater visual census (UVC) monitoring techniques were used to provided quantitative assessments of fish abundance, as they have little impact on the ecosystem and are therefore particularly suited for use in marine reserves (Harmelin et al. 1995; Ciriaco et al. 1998). Baseline data for the initial time period, as well as the sampling design and intensity were from Schärer-Umpierre (2009). Briefly, 36 belt transects (30 x 2 m) were sampled by scuba divers within each of the three locations, for a total of 108 transects per time period. Divers swam one way for 8–10 min along each transect identifying and estimating the size of each fish observed within a distance of 2 m on each side of a center line. After each belt transect, a 5-min roving survey was used to help better determine the presence and relative abundance of large and elusive fish species (*L. jocu*, *E. guttatus*, *E. striatus*, *M. tigris*, *M. venenosa*). Divers were trained and the sampling methodology practiced prior to actual sampling to minimize biases inherent in UVC (Kulbicki 1998; Edgar et al. 2004). For this study it was assumed that habitat did not change between the surveyed periods.

## Data analyses

For statistical analyses, fish abundance and biomass were modeled as a function of Year (2 levels, fixed factor), Location (random factor, with 1 impact (I) and 2 control (C) locations) and Site (3 levels, random, nested in Location). The latter represented the grouping of the 36 samples per location into three “sites” based on proximity to assess within location variability. Year was crossed with Location, which allowed the assessment of the contrast of Impact versus Controls (I-v-Cs) and among Controls. As there was only 1 location that was purportedly ‘impacted’ (I), this design is asymmetrical (Underwood 1991, 1994). To estimate positive or negative cumulative effects among the different factors examined (Underwood 1981), the model included all combinations of the factor levels. Given the design, the linear algebraic model is thus:

$$X_{ijz} = \mu + Y_{e_i} + L_{o_j} + Y_{e_i} \times L_{o_j} + S_i(L_{o_j})_{k(j)} + Y_{e_i} \times S_i(L_{o_j})_{ik(j)} + e_{z(ij)}$$

where  $X_{ijz}$  represents the set of abundances observed at the  $z$ th replicate ( $z = 1, 2, \dots, 36$ ) of the  $k$ th level of the nested factor Site ( $S_i$ ) in the  $j$ th level of the factor Location ( $L_o$ ) crossed with the  $i$ th level of the factor Year ( $Y_e$ ).  $\mu$  represents the overall mean abundance vector.  $Y_{e_i}$  represents the effect of the  $i$ th Year ( $i = 1, 2$ ),  $L_{o_j}$  denotes the effect of the  $j$ th Location ( $j = 1, 2, 3$ ), and  $S_i(L_{o_j})_{k(j)}$  corresponds the effect of the  $k$ th level of the nested factor Site in the  $j$ th level of the factor Location ( $k=1,2$ );  $Y_{e_i} \times L_{o_j}$  and  $Y_{e_i} \times S_i(L_{o_j})_{k(j)}$  correspond to the interaction effects of the

factors Year and Location and of the factors Year and Site. Finally,  $e_{z(ij)}$  represents the error term associated with each observation.

With data from a BACI (Before–After–Control–Impact) design, the NTZ effect on the fish assemblage may be identified from differences in the biological and ecological responses of fishes (e.g., abundance, biomass) inside the NTZ location from before to after its establishment compared with such changes from before to after in the impacted location (Underwood 1993). Under this model an effect of the NTZ on the fish assemblage is confirmed if the interaction between Year x Location is statistically significant. Such differences in biological responses across time and between inside and outside the NTZ and within the NTZ were interpreted by pair-wise comparisons conducted on these interaction terms. In order to analyze how the fish assemblage responds to the NTZ, analyses were organized for sets of abundance and biomass data calculated separately for several components of the fish assemblage (see Appendix A): (i) abundance and biomass (per species) for the whole fish assemblage; (ii) abundance and biomass per species size group (small = *C. cruentatus*, *C. fulva*, *L. mahogani*; medium = *L. apodus*, *E. guttatus*, *B. vetula*; large = *E. striatus*, *M. venenosa*, *M. tigris*, *L. jocu*), (iii) abundance and biomass per species by relative life stage based on size, where the absolute size of individuals with each small, medium, and large life stage were species specific and formed by dividing sizes (length or biomass) into three equal classes based on maximum reported size.

Conventional multivariate methods, such as MANOVA, assume normality of errors and are not appropriate when data are highly skewed and contain many zeros. As a consequence, we used the non-parametric permutational multivariate analysis of variance (PERMANOVA; Anderson 2001a; McArdle & Anderson 2001), to test for significance, including interactions. This analysis uses bootstrapping methods to generate means, variances and P-values; these were accomplished with the Primer 6 & PERMANOVA+  $\beta 17$  software (Clark & Gorley 2006, Anderson & Gorley 2007). All PERMANOVAs were performed on untransformed data. Multivariate analyses were based on testing differences in Bray-Curtis dissimilarities (Bray & Curtis 1957). To obtain sufficient statistical power while controlling Type I error (Anderson & Legendre 1999), p-values were generated after 4999 permutations of residuals (Anderson 2001b). When Year x Location interaction terms or associated interactions were significant ( $p < 0.05$ ), a posteriori pair-wise comparison was used to show how each area responded over time. Significant differences between sites over years in a given location (Year x Site (Location)) do not affect the overall NTZ effects and could be attributable to small scale variability in the assemblage of fish, and significant

higher order interactions suggest that the experimental treatments do not operate independently, in any combination (Underwood 1981). In addition, canonical analysis of principal coordinates (CAP) was used to revealed patterns that were masked visualizing the specific multivariate interaction (Anderson & Willis 2003). Both methods again used 4999 random permutations on the same Bray-Curtis dissimilarity values to obtain p-values. For some terms in the analysis, there were not enough units to obtain an acceptable test by permutation, so a p-value was calculated using a Monte Carlo random sample from the asymptotic permutation distribution (Anderson & Robinson 2003). To further understand test results, the percent contribution of each species (SIMPER) was calculated to identify which species were more important in dissimilarity/similarity between sampling times (Clarke 1993).

Lastly, univariate analyses were applied to test NTZ effect on abundance and biomass pooled over all species and also for *C. fulva*, the only species found in more than 50 % of transects across the Locations and Years (see Appendix A). The analysis included each of the different levels, components and techniques as above. Data were initially checked for heteroscedasticity using Cochran's C-test (Underwood 1997). In some cases, data were transform,  $\ln(x + 1)$  for abundance and square root for biomass, to remove heterogeneous variances. When the heterogeneity could not be stabilized through data transformation, untransformed data were used and results were interpreted with more conservative probability level ( $p < 0.01$ ) (Underwood 1997). These were again conducted on dissimilarities, but now based in Euclidean distance. We particularly tested the  $Ye \times Lo_{ij}$  interaction term from a posteriori pairwise comparisons, based on 4999 random permutations. Bar graphs based on non-transformed data were used to illustrate mean abundances and biomass per Location and Year.

## **Results**

### **Fish Assemblage**

Multivariate analysis of the entire fish assemblage revealed variation over time on abundance measured from transects (Table 1). Small-sized species showed a significant difference over time in abundance and a significant multivariate interaction between the factors year (Ye) and location (Lo) (Table 2). Pairwise PERMANOVA detected significant differences over time in control 1 (C1) ( $p < 0.01$ ) and in the zone where fishing continued, known as the impact (I) ( $p < 0.05$ ). Meanwhile, for the relative life stages, medium stages showed significant differences in abundance and biomass over time; while small life stages also showed a

significant difference in abundance over time (Table 2). Also, what seemed an significant effect of protection (Impacted vs. Controls) in the biomass on small life stage over time (Table 2), CAP analysis indicated that I responded more strongly than Cs (Fig. 2), although the higher order interaction (Ye x Si(Lo)) warns us that this interaction is not independent (Underwood 1981).

Table 1. PERMANOVA table of abundance and biomass of whole fish assemblage for each methodology<sup>a,b</sup>.

Source of variation	df	Transects				Roving survey			
		Abundance		Biomass		Abundance		Biomass	
		MS	F	MS	F	MS	F	MS	F
Year	1	19302	4.86 *	6357	1.93	5063	0.80	4914	0.81
Location	2	22684	3.39 *	18803	3.99 *	5648	1.08	5571	1.08
Impact vs.Controls	1	12983	2.51	11477	2.63 *	6939	1.34	6530	1.27
Controls	1	32427	4.00	26160	4.63 **	4371	0.76	4618	0.85
Sites (Lo)	6	3493	1.32	4711	1.63 **	5224	1.07	5145	1.05
Si (I )	2	1515	0.97	2828	1.03	4205	0.87	4536	0.93
Si (Cs)	4	4483	1.41	5653	1.91 **	5734	1.18 *	5450	1.11
Ye x Lo	2	3989	1.54	3299	0.71	6316	1.32	6096	1.22
Ye x I-v-Cs	1	3542	1.24	3253	1.23	4630	0.96	4400	0.88
Ye x Cs	1	4435	1.43	3346	0.67	8025	1.70 *	7810	1.60 *
Ye x Si (Lo)	6	2640	1.27	4631	1.60 *	4789	0.98	4998	1.02
Ye x Si (I )	2	1566	0.87	3930	1.43	4919	1.01	5224	1.07
Ye x Si (Cs)	4	3177	1.44	4981	1.68 *	4723	0.97	4885	1.00
Residual	198	2072		2894		4862		4886	
Total	215								

<sup>a</sup> Untransformed data.

<sup>b</sup> Level of significance: \*P < 0.05; \*\*P < 0.01; \*\*\* P < 0.001.



Table 2. Summary of PERMANOVA results on abundance (A) and biomass (B) calculated by species size and by species life stage for both survey methodologies <sup>a, b</sup>.

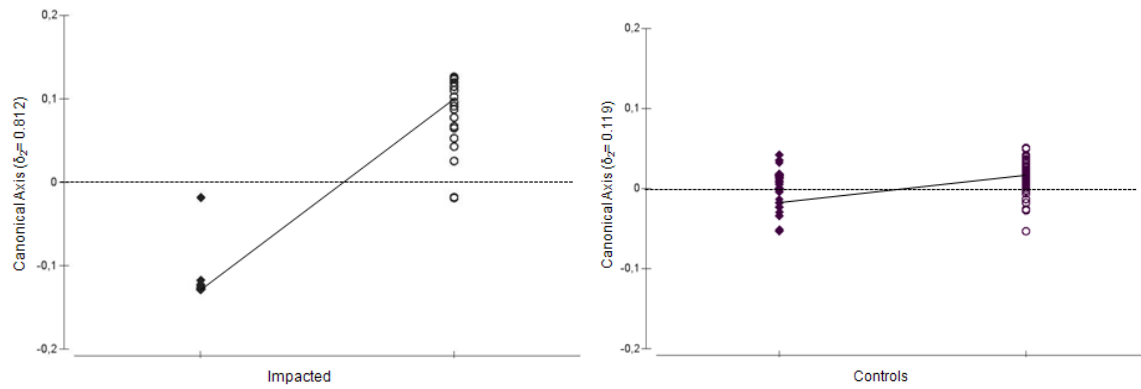
(a) Species size		Transects												Roving survey					
		Small (3 spp.)				Medium (3 spp.)				Large (4 spp.)				Large (5 spp.)					
		A		B		A		B		A		B		A		A		B	
		MS	F	MS	F	MS	F	MS	F	MS	F	MS	F	MS	F	MS	F	MS	F
Year	1	20125	4.56 *	7329	1.75	7932	1.75	7743	1.78	4976	0.95	4954	0.96	4510	0.68	4624	0.71		
Location	2	19945	2.75	16832	4.40 **	12715	2.66 **	13007	2.78 ***	4772	0.97	4833	0.95	5244	1.04	5177	1.02		
Impact vs. Controls	1	11002	2.04	8684	2.44	8129	1.76 *	8052	1.76 *	4815	0.92	4869	0.96	6082	1.23	5834	1.13		
Controls	1	28933	3.33	24978	5.83 **	17312	3.43 **	17971	3.68 **	4730	1.00	4798	0.95	4407	0.86	4504	0.88		
Site(LO)	6	3507	1.92	3823	1.62 *	4782	0.83	4677	1.05	5043	0.98	5079	1.02	5047	1.02	5066	1.02		
Si (I)	2	1680	1.37	2895	1.39	4257	0.79	4272	0.89	5139	1.00	5139	1.03	4956	1.00	4960	0.99		
Si (Cs)	4	4420	2.07	4287	1.72 *	5045	0.84	4879	1.13	4995	0.97	5050	1.01	5127	1.04	5119	1.03		
Ye x Lo	2	4414	2.41 *	4185	1.90	4527	0.78	4343	0.78	5221	1.02	5165	1.00	6603	1.34	6516	1.29		
Ye x I vs. Cs	1	3895	2.11	3607	1.81	5240	1.19	5287	1.17	5555	1.12	5407	1.08	4727	0.87	4732	0.97		
Ye x Cs	1	4918	2.31	4758	2.14	3800	0.63	3388	0.60	4884	0.95	4921	0.96	8479	1.74 **	8303	1.64 **		
Ye x Si (Lo)	6	1831	0.94	2203	0.93	5790	1.31 *	5591	1.25 *	5134	1.03	5148	1.03	4921	0.99	5057	1.02		
Ye x Si (I)	2	1229	0.73	2156	1.03	5386	1.14	5402	1.13	5139	1.03	5139	1.03	5430	1.09 **	5030	1.01		
Ye x Si (Cs)	4	2132	1.02	2226	0.89	5992	1.41	5685	1.32	5131	1.029	5153	1.03	4877	0.99	5071	1.03		
Residual	198	1957		2361		4413		4467		4988		4988		4959		5030			
Total	215																		

(b) Species life stage		Transects												Roving survey					
		Small				Medium				Large				Large					
		A		B		A		B		A		B		A		A		B	
		MS	F	MS	F	MS	F	MS	F	MS	F	MS	F	MS	F	MS	F	MS	F
Year	1	26781	9.55 ***	49347	2.14	12085	3.14 *	12854	3.71 **	4521	0.95	4312	0.92	4639	0.81	4662	0.82		
Location	2	18563	5.37 *	33606	9.71 ***	7442	1.49	7781	1.50	12915	2.68 *	13447	2.88 *	5503	1.03	5553	1.08		
Impact vs. Controls	1	11315	3.52 **	39663	12.17 ***	5953	1.19	5928	1.14	7986	1.60	9656	2.01 **	6219	1.13	6230	1.19		
Controls	1	25874	6.18 ***	27490	6.76 ***	8948	1.67	9659	1.66	17833	3.91 *	17215	3.83 ***	4793	0.89	4881	0.90		
Site(LO)	6	3460	1.34	3462	1.22	5004	1.29	5200	1.28	4826	1.04	4662	0.99	5344	1.08 *	5143	1.04		
Si (I)	2	2003	0.91	2256	0.85	4277	1.17	3953	1.02	5346	1.11	5001	1.02	5247	1.06	4639	0.94		
Si (Cs)	4	4189	1.51 *	4064	1.39	1348	0.08	5823	1.40 *	4566	1.00	4493	0.98	5393	1.09 *	5396	1.09 *		
Ye x Lo	2	2805	0.85	23110	5.29 **	3847	1.20	3464	0.88	4781	0.85	4690	0.87	5724	1.13	5656	1.07		
Ye x I vs. Cs	1	2585	1.35	44471	17.56 **	4043	1.22	3283	0.92	4052	0.70	4298	0.81	4595	0.95	4590	0.90		
Ye x Cs	1	3030	0.73	1649	0.32	3659	1.15	3639	0.85	5511	1.23	5078	1.05	6862	1.30	6730	1.27		
Ye x Si (Lo)	6	3305	1.28	4368	1.54 *	3203	0.83	3940	0.97	5615	1.21 *	5410	1.15	5054	1.02	5285	1.07		
Ye x Si (I)	2	1562	0.71	2633	1.00	3248	0.89	3238	0.84	7856	1.64 **	6586	1.34 **	4583	0.93	5217	1.05		
Ye x Si (Cs)	4	4176	1.50	5235	1.79 *	3181	0.80	4291	1.03	4495	0.99	4821	1.05	5289	1.07	5319	1.08		
Residual	198	2586		2824		3871		4058		4634		4701		4948		4949			
Total	215																		

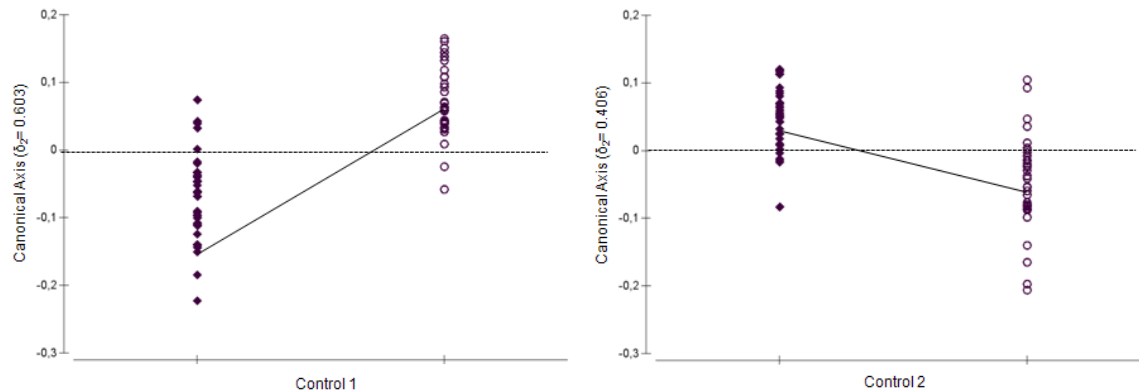
<sup>a</sup> Untransformed data.

<sup>b</sup> Level of significance: \*P < 0.05; \*\*P < 0.01; \*\*\* P < 0.001.



**Figure 2.** Discriminant analysis plots for Impact and Controls based on the Bray-Curtis dissimilarity measure comparing biomass of the small life stage fish at different times: Year 1 (black diamonds) and Year 2 (white circles). There are n= 36 observations in each year in impact, and n=72 observations in each year for Control location.

Data collected in roving surveys, showed a consistent significant year (Ye) x control (Cs) interaction (Table 1 and Table 2) in both abundance and biomass. The pattern was determined by a significantly distinctive performance of the controls over time exemplified by CAP analysis for biomass on the whole fish assemblage (Fig. 3).



**Figure 3.** Discriminant analysis plots for Year x Controls using roving surveys based on the Bray-Curtis dissimilarity measure comparing biomass overall fish at different times: Year 1 (black diamonds) and Year 2 (white circles). There are n = 36 observations in each year in each location.

SIMPER analysis of the data from transects, identified *C. fulva* as the principal contributor to the abundance and biomass of the fish assemblage. Fifty percent of the difference in fish abundance between years was attributed to this species, which doubled its mean abundance from 2005 to 2010. Similarly, *C. cruentata*, *L. apodus* and *L. mahogoni* contributed approximately 10% each to the overall change of fish abundance over time, each also doubling its mean abundance from 2005 to 2010 (Table 3). The higher biomass of these species, and *B. vetula*, in

2010 contributed approximately 20% (each) to the whole biomass dissimilarity found between years. Large species, on the other hand, did not showed large changes over time (Table 3).

Table 3. Results of SIMPER analysis displaying the percentage of contribution in similarity and dissimilarity for the whole fish abundance and biomass per year for both survey methodologies <sup>a,b</sup>.

Species (Transects)	Abundance					Biomass				
	2005		2010		Diss. % (65.21)	2005		2010		Diss % (75.74)
	Av. Abu	Sim. (33.90)	Av. Abu	Sim.% (41.27)		Av. Bio	Sim. % (24.16)	Av. Bio	Sim. % (25.10)	
<i>C. fulva</i>	2.47	68.86	4.69	83.05	51.63	240.3	70.81	217.5	67.55	28.21
<i>C. cruentata</i>	0.79	25.66	0.69	9.17	15.44	67.5	17.97	48.8	7.05	10.94
<i>L. apodus</i>	0.31	3.14	1.32	4.21	13.39	102.1	6.03	261.0	11.48	20.36
<i>B. vetula</i>	0.17	1.14	0.31	2.03	5.30	160.1	3.52	286.8	11.15	21.45
<i>L. mahogoni</i>	0.49	1.00	1.01	1.33	10.19	52.1	1.21	119.6	2.36	8.85

Species (roving survey)	2005			2010			2005			2010		
	Av. Abu		Sim. % (3.02)	Av. Abu		Sim. % (5.78)	Av. Bio		Sim. % (2.07)	Av. Abu		Sim. % (4.06)
			Diss. % (95.47)									Diss. % (96.81)
<i>E. guttatus</i>	0.12	76.32	55.45	0.23	86.83	55.45	53.76	77.8	80.78	87.38	52.74	52.74
<i>M. venenosa</i>	0.06	17.24	21.64	0.11	9.00	21.64	112.82	15.93	245.91	9.71	23.45	23.45

<sup>a</sup> ( ) Averages, Sim. Similarity, Diss. Dissimilarity.

<sup>b</sup> Untransformed data.

In terms of behavior of the locations over years, C1 showed the highest average dissimilarity in abundance (71%) and biomass (77%) which was mostly due to increases in the mean abundance and biomass of *L. apodus*, *C. fulva* and *B. vetula*, and to decreases in *C. cruentata*. A similar pattern was observed at both, I and C2, where the mean abundance and biomass of *C. fulva* increased and that of *C. cruentata* decreased over time. Both species were the most important dissimilarity contributors at these locations. In addition, *B. vetula* and *L. apodus* had a higher mean biomass in 2010 and contributed more importantly to the biomass dissimilarity, 37% and 12% respectively. The roving survey showed mean assemblage dissimilarity close to 97% in abundance and biomass of the large species over time in both C1 and C2 but for very different reasons. At C1 *M. venenosa* (30%) and *E. guttatus* (50%) were the highest contributors to the dissimilarity, followed by *L. jocu* and *M. tigris* (10%), each increasing its mean abundance and biomass over time; C2 presented the same species dissimilarity contribution but driven by a decrease in both abundance and biomass over all species, except *E. guttatus*.

## Univariate Analysis

Permutational univariate ANOVA showed significant differences in abundance within transects over time for the entire assemblage (Table 4), small life stage fish and small-sized

fishes (Table 5). In most cases, the not significant year (Ye) x location (Lo) interaction indicated similar trends by location and the value of the metric was always higher in 2010 (Fig.4). Medium-sized fishes showed significant year (Ye) x location (Lo) interaction (Table 5), and pair-wise tests demonstrated significant differences in C1 ( $p < 0.05$ ) but not for I and Cs. Meanwhile, roving surveys showed a significant year (Ye) x controls (Cs) interaction in abundance and biomass (Table 4); pair-wise tests of abundances demonstrated significant differences over time in C1 ( $p < 0.05$ ), but not C2; however changes in biomass for C1 ( $p < 0.05$ ) and C2 ( $p < 0.05$ ) were significant. Similar effects were found in large-size species and large life stages. In general, fish abundance and biomass were consistently higher in 2010 by total mean abundance and biomass (Fig. 4, Appendix B and C) and by the different groups studied (Fig. 5); except for the interaction Ye x Cs in roving surveys for biomass and abundance, which was higher in 2005 than 2010 at C2 and with opposite effect in C1 (Fig. 4 and 5). The permutational univariate ANOVA for the dominant species, *C. fulva*, revealed significant differences over time for abundance ( $F = 39.7$ ,  $p < 0.05$ ) with larger numbers of individuals at all locations.

Table 4. ANOVA table for permutational univariate analyses of total abundance and biomass for each methodology<sup>a</sup>.

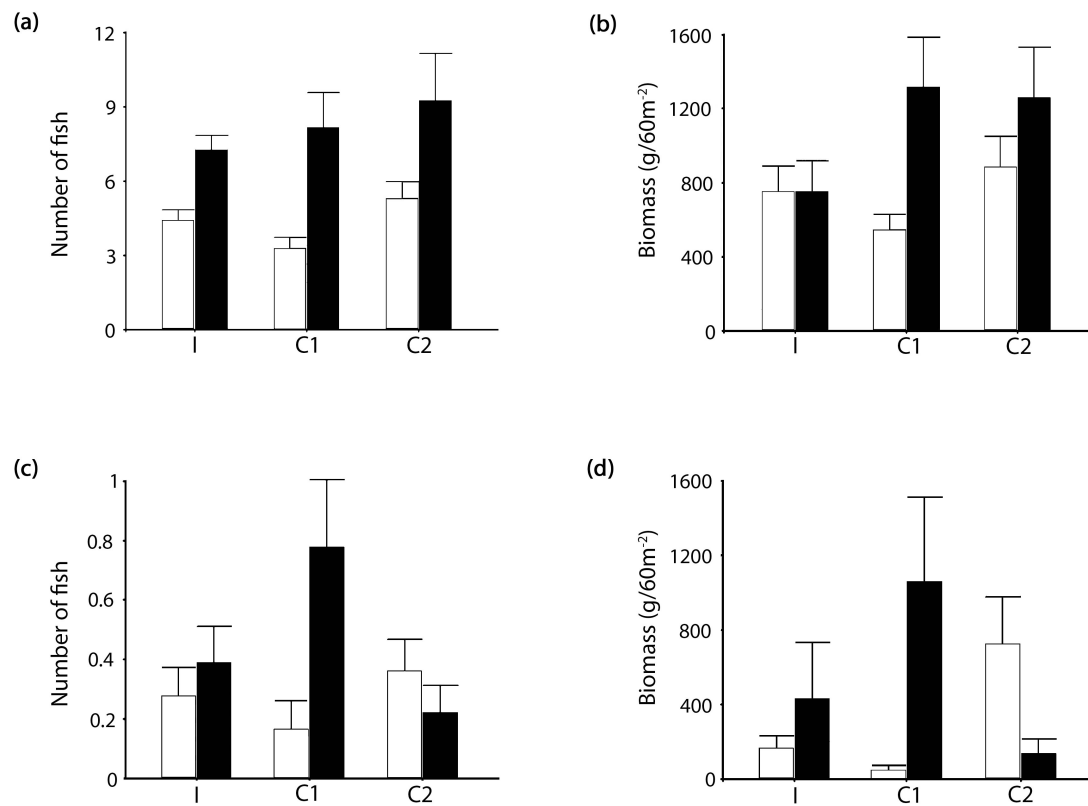
Source of variation	df	Transects				Roving survey			
		Abundance		Biomass		Abundance		Biomass	
		MS	F	MS	F	MS	F	MS	F
Year	1	14.65	57.12 *	1,464.50	2.87	0.40	0.62	2796600	0.24
Location	2	0.89	0.64	295.06	1.62	0.06	1.35	1166100	1.97
Impact vs. Controls	1	0.10	0.10	503.67	2.71	0.00	0.02	1807200	1.92
Controls	1	1.70	0.86	82.55	0.81	0.13	2.61	492820	2.93
Si (Lo)	6	1.41	4.60 ***	182.37	0.80	0.05	0.29	591320	0.26
Si (I )	2	0.27	1.29	344.29	1.98	0.05	0.32	1439300	0.87
Si (Cs)	4	1.97	5.59 ***	101.42	0.40	0.05	0.28	167320	0.06
Ye x Lo	2	509.67	1.56	510.38	1.53	0.65	3.70	11594000	10.03 *
Ye x I-v-Cs	1	798.74	3.84	808.45	2.56	0.02	0.10	44119	0.03
Ye x Cs	1	225.55	0.70	212.30	0.64	1.28	9.75 *	23140000	56.03 **
Ye x Si (Lo)	6	326.94	1.44	333.21	1.48	0.18	1.10	1155200	0.51
Ye x Si (I )	2	0.35	1.64	334.76	1.92	0.27	1.89 *	2640900	1.60
Ye x Si (Cs)	4	0.12	0.33	323.03	1.28	0.13	0.77	412380	0.16
Residual	198	0.31		225.01		0.16		2280200	
Total	215								
Cochran test		C = 0.13		C = 0.12		C = 0.13		C = 0.37	
		p > 0.05		p > 0.05		p > 0.05		p < 0.05	
Transformation		ln(x + 1)		$\sqrt{\quad}$		ln(x + 1)		None	

<sup>a</sup>Level of significance: \*P < 0.05; \*\*P < 0.01; \*\*\* P < 0.001.

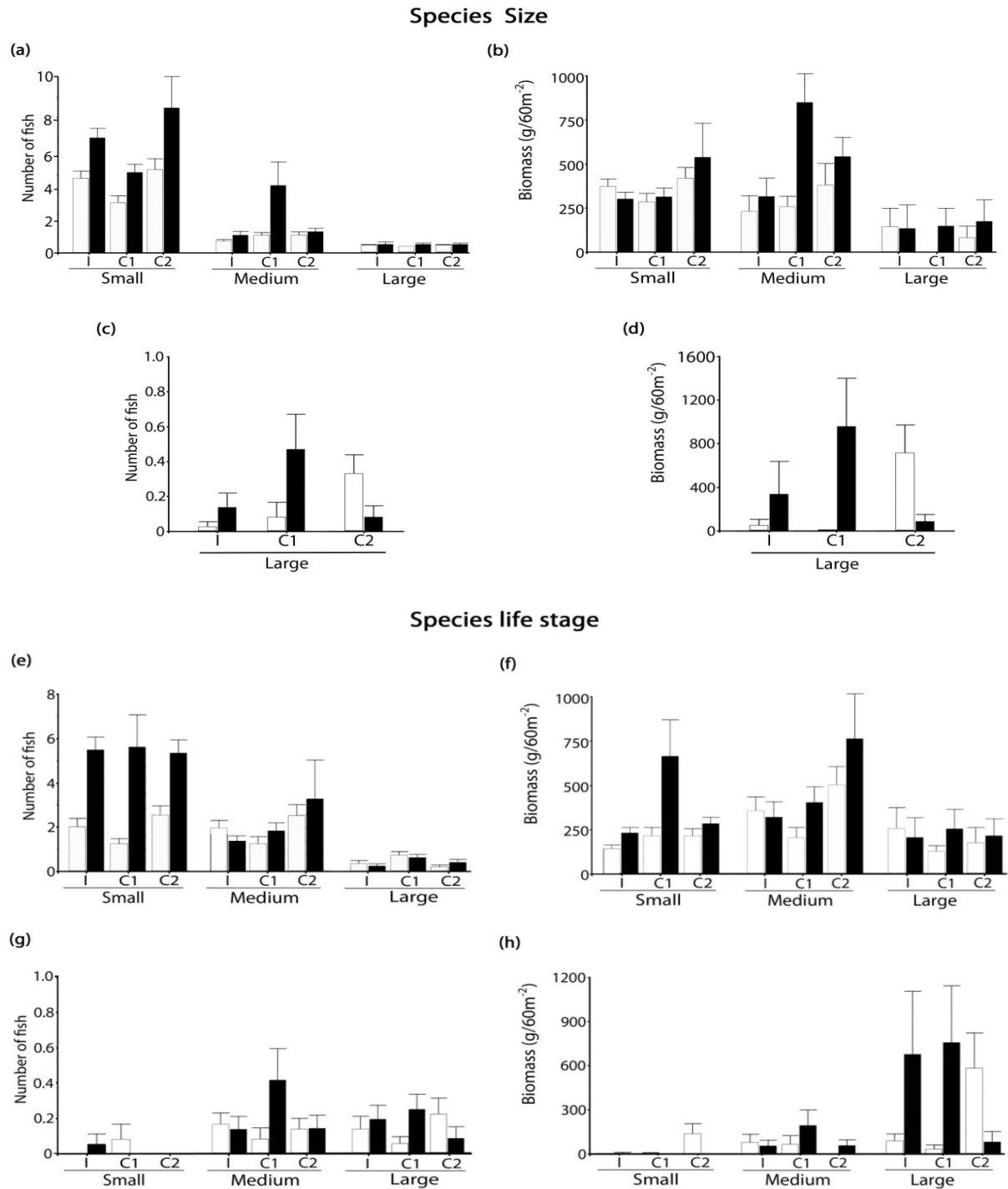
Table 5. Summary of permutational univariate ANOVA results on abundance (A) and biomass (B) calculated by species size and by species life stage for both survey methodologies <sup>a</sup>.

(a) Species size		Transects												Roving survey							
		Small (3 spp.)						Medium (3 spp.)						Large (4 spp.)							
		A		B		A		B		A		B		A		B		A		B	
Source of variation	df	MS	F	MS	F	MS	F	MS	F	MS	F	MS	F	MS	F	MS	F	MS	F	MS	F
Year	1	9.59	1940.10 **	28504	0.20	76.33	1.78	2087.50	9.98	0.29	14.92	302310	2.52	0.37	0.20	2168500	0.19	0.70	2.43	1588800	3.36
Location	2	3.52	2.00	670900	0.91	57.20	23.50 ***	925.77	3.61	0.02	0.11	90955	0.16	1.24	8.25 *	2956100	3.60	1.24	8.25 *	2956100	3.60
Impact vs. Controls	1	1.15	0.85	136190	0.31	45.80	11.30	1742.30	8.38 *	0.01	0.04	68481	0.09	0.17	0.39	190210	1.88	0.17	0.39	190210	1.88
Controls	1	5.91	2.34	1201100	1.13	68.61	24.40 **	130.76	0.35	0.03	1.17	115930	0.79	0.29	0.69	472080	0.21	0.29	0.69	472080	0.21
Site(Lo)	6	1.76	5.62 ***	734050	2.61 **	2.43	0.19	256.60	1.06	0.18	1.36	570960	1.68	Neg	Neg	1214700	0.74	Neg	Neg	1214700	0.74
Si (I)	2	0.23	0.80	80542	1.50	1.68	1.70	29.03	0.15	0.50	2.02	1418900	2.84	0.43	0.78	100740	0.04	0.43	0.78	100740	0.04
Si (Cs)	4	2.52	7.69 ***	1060800	2.68 **	2.81	0.15	370.39	1.40	0.03	0.33	146980	0.56	1.86	8.55 *	11485000	14.83 **	1.86	8.55 *	11485000	14.83 **
Ye x Lo	2	0.00	0.02	145810	2.93	42.96	14.63 **	209.25	0.28	0.02	0.23	119880	0.44	0.02	0.08	191180	0.17	0.02	0.08	191180	0.17
Ye x I vs. Cs	1	0.01	0.04	241220	3.03	18.47	4.94	271.05	0.95	0.01	0.11	208350	1.29	3.69	12.40 *	22773000	66.93 **	3.69	12.40 *	22773000	66.93 **
Ye x Cs	1	0.00	0.00	57297	1.04	67.36	25.83 **	138.55	0.16	0.03	0.30	35879	0.09	0.22	0.52	774250	0.35	0.22	0.52	774250	0.35
Ye x Si (Lo)	6	0.24	0.78	49658	0.18	2.93	0.23	748.99	3.08 **	0.09	0.64	271720	0.80	0.06	0.40	1643500	0.99	0.06	0.40	1643500	0.99
Ye x Si (I)	2	0.59	2.09	38891	0.72	3.60	3.65	527.60	2.64	0.06	0.22	2608	0.01	0.30	0.53	339640	0.14	0.30	0.53	339640	0.14
Ye x Si (Cs)	4	0.07	0.22	55042	0.14	2.60	0.14	859.69	3.25 *	0.10	1.27	406280	1.56	0.42		2205700		0.42		2205700	
Residual	198	0.31		281530		12.86		242.97		0.14		340600									
Total	215																				
Cochran test		C = 0.12		C = 0.74		C = 0.53		C = 0.12		C = 0.54		C = 0.31		C = 0.40		C = 0.34		C = 0.40		C = 0.30	
		p > 0.05		p < 0.05		p < 0.05		p > 0.05		p < 0.05		p < 0.05		p < 0.05		p < 0.05		p < 0.05		p < 0.05	
Transformation		ln(x + 1)		None		None		None		None		None		None		None		None		None	
(b) Species life stage		Small						Medium						Large							
		A		B		A		B		A		B		A		B		A		B	
		MS	F	MS	F	MS	F	MS	F	MS	F	MS	F	MS	F	MS	F	MS	F	MS	F
Year	1	30.37	218.11 **	2216300	2.69	2.853	0.32	1053700	2.4	0.01	0.01	4.97	0.17	0.03	0.15	3795800	0.46	0.03	0.15	3795800	0.46
Location	2	2.29	1.70	1245900	8.59 **	42.21	1.31	2326400	6.6 *	3.48	4.01	152.37	0.63	0.00	0.08	68225	0.10	0.00	0.08	68225	0.10
Impact vs. Controls	1	0.48	0.90	1190800	10.26	14.52	0.68	789530	3.2	1.99	2.69	74.33	0.36	0.00	0.14	16739	0.02	0.00	0.14	16739	0.02
Controls	1	4.11	2.23	1294400	6.73 *	69.6	1.52	3864300	8.9 *	4.98	5.30	231.06	1.33	0.00	0.06	123100	0.25	0.00	0.06	123100	0.25
Site(Lo)	6	1.35	3.06 **	145010	0.50	32.29	1.44	353120	0.6	0.87	1.88	241.89	1.59	0.03	0.47	705700	0.29	0.03	0.47	705700	0.29
Si (I)	2	0.35	0.86	50704	2.16	5.556	2.01	189450	0.8	0.72	1.92	377.75	2.05	0.05	0.68	1136200	0.33	0.05	0.68	1136200	0.33
Si (Cs)	4	1.85	4.03 **	192170	0.46	45.65	1.42	434960	0.6	0.94	1.87	173.96	1.27	0.02	0.35	490460	0.25	0.02	0.35	490460	0.25
Ye x Lo	2	0.28	0.14	823210	2.77	8.975	2.05	439360	1.4	0.54	0.38	29.55	0.08	0.22	2.64	8305600	6.92 *	0.22	2.64	8305600	6.92 *
Ye x I vs. Cs	1	0.11	0.11	347500	3.47	18.24	4.97	844910	3.7	0.26	0.21	58.37	0.22	0.00	0.05	2783000	1.64	0.00	0.05	2783000	1.64
Ye x Cs	1	0.16	0.16	1300900	2.94	0.102	0.02	35723	0.1	0.81	0.87	0.02	0.00	0.43	5.42	13792000	33.48 **	0.43	5.42	13792000	33.48 **
Ye x Si (Lo)	6	2.94	0.49	297560	1.04	4.371	0.20	309860	0.5	1.41	3.06 **	375.92	2.46 *	0.08	1.13	1199200	0.49	0.08	1.13	1199200	0.49
Ye x Si (I)	2	0.27	0.67	8075	0.34	Neg.		181460	0.8	2.39	6.35 **	506.80	2.75	0.09	1.14	2928700	1.19	0.09	1.14	2928700	1.19
Ye x Si (Cs)	4	0.60	1.31	442300	1.06	6.556	0.20	374060	0.5	0.92	1.84	310.48	2.27	0.08	1.12	411530	0.21	0.08	1.12	411530	0.21
Residual	198	0.44		287260		22.38		600960		0.46		150.83				2460900					
Total	215																				
Cochran test		C = 0.12		C = 0.68		C = 0.83		C = 0.55		C = 0.11		C = 0.12		C = 0.14		C = 0.30		C = 0.14		C = 0.30	
		p > 0.05		p < 0.05		p < 0.05		p < 0.05		p > 0.05		p > 0.05		p > 0.05		p > 0.05		p > 0.05		p > 0.05	
Transformation		ln(x + 1)		None		None		None		None		None		ln(x + 1)		None		None		None	
Level of significance: **p < 0.05; ***p < 0.01; ****p < 0.001.																					

<sup>a</sup> Level of significance: \*p < 0.05; \*\*p < 0.01; \*\*\* p < 0.001.



**Figure 4.** Mean (+ SE, n= 36) total abundance and biomass separated by locations over time. (a) abundance in transects; (b) biomass in transects; (c) abundance in roving surveys ; and (d) biomass in roving surveys; bars white = 2005, black = 2010.



**Figure 5.** Mean (+ SE, n= 36) total abundance and biomass by location at each year by species size group (a) in transect abundance, (b) in transect biomass, (c) in roving abundance, and (d) in roving biomass; and by relative life stage (e) in transect abundance, (f) in transect biomass, (g) in roving abundance, and (h) in roving biomass. Grey = 2005, Black = 2010.

## Discussion

The primary effect observed within the Mona Island MPA after four years was an increase in fish abundance at all locations. This increase was of small life stages and primarily of small species. The increase in small life stages suggests that there was significant recruitment occurring across the island during this period. The species showing the greatest increase was *C. fulva*, with *L. mahogoni*, *L. apodus*, *B. vetula* also showing increases.

That recruitment did occur, however, has important implications for the Mona Island MPA. Mona Island is located within a partial biogeographic boundary (Taylor & Hellberg 2006; Baums et al. 2006; Eytan & Hellberg 2010) and surrounded by a topographically forced eddy (Pagan 2002) that may serve to entrain locally spawned eggs and larvae. As a consequence, the populations there are thought to rely on self-recruitment (Rojas-Ortega 2002), although occasional recruitment from Puerto Rico may be possible (Ojeda-Serrano 2002) especially for winter spawners, such as groupers (Baums et al. 2006). The occurrence of substantial recruitment occurred suggests that either there is sufficient spawning stock within the MPA to generate the observed increase in abundance, or that periodic recruitment from Puerto Rico populations has a greater impact than originally thought. Both interpretations suggest that there is sufficient recruitment to support the recovery of the MPA. If recruitment is indeed local, that abundance increases occurred throughout the MPA indicates that the process is of a scale larger than the MPA, and that larval spillover from the closed areas to the fished areas can be expected. The fished area being proportionally small compared to the closed areas would also facilitate this.

Despite the observed increase in smaller species, no increases were observed for the larger species, either within transects or roving surveys. The absence of any significant increase within the transect data is expected due to low sighting frequencies. There are several possible explanations for the lack of any observed increase within the roving surveys. One is that the spawning stocks of these more valuable and previously heavily exploited species are significantly lower than those of smaller species. Another possibility is that the nursery areas for these species are located in areas of different habitat or depth than those sampled within this study. Ontogenetic migration from nearshore nursery areas out to coral reef habitats (e.g., seagrass, mangrove, nearshore hardbottom) is known to occur for a number of reef fishes, including snappers and groupers (Cocheret de la Morinière 2002; Nagelkerken & van der Velde 2003; Appeldoorn et al. 2003; Cerveny 2006; Aguilar-Perera & Appeldoorn 2007; 2008) and this



has been well-documented for the more abundant species at Mona Island (Schärer-Umpierre 2009). The larger species are not as well studied, but ontogenetic migrations have been documented elsewhere for Nassau grouper (Dahlgren & Eggleston 2001) and red hind (Cerveny 2006).

A clear reserve effect was not immediately evident. For a fully functional reserve, the expectation would be that there would be a greater abundance and biomass of fishes in the control areas, with the difference most evident for the larger species under the greatest fishing pressure. This result would probably be most evident in the data from roving transects, since these targeted the larger species. In reality, the results were more complex. Statistical analysis of these data indicated that the increase of these species in the impacted (open) area was not significant, while the increase in abundance and biomass in C1 (SWNTZ) was significant, with *C. fulva*, *L. apodus*, *B. vetula*, *L. mahogoni*, *E. guttatus* and *M. venenosa* contributing to this change. In contrast, there was a significant decrease in the biomass and abundance within C2 (ENTZ). Thus, the positive response within the SWNTZ corresponded to expectations relative to the impacted area. On the other hand, the negative response within the ENTZ was completely unexpected. This illustrates the importance of having multiple control areas (Underwood 1994, Glasby & Underwood 1998); without these it would not have been possible to detect either the positive response of protection in C1 or the differential response in C2. If combined, the two areas would have canceled each other, resulting in a conclusion of no reserve effect.

Several processes could have contributed the differential response within the two controls. One is simply a function of time, with four years not being sufficient for a strong reserve effect to be established. Another could be due to the movement of fishes relative to the type, abundance and distribution of habitat within the two control areas. Differences in habitat types and availability are known to affect fish distributions and can override initial reserve effects (Monaco et al. 2007; Lopez-Rivera & Sabat 2009). The two control areas are known to differ in their respective seascapes. For example, the extent of the shelf in C1 is very narrow while within C2 it is broad. Thus, given equal levels of recruitment, densities within C1 should be higher due to the reduced area of available habitat. Further compounding this potential effect, C1 is characterized predominately by hardbottom habitats, while coral reef habitats are most abundant in C2 (Schärer-Umpierre 2009). Adding to this effect is the possibility that ontogenetic migration within C2 may not extend out fully to occupy all coral reef habitat if overall densities are low and sufficient nearshore adult habitat is available (Appeldoorn et al. 2003). Lastly, habitat patchiness and distribution patterns are known to affect both species abundance and

richness (Appeldoorn et al. 2003; Kendall et al., 2003; Pittman et al. 2007) and it is possible that this also could contribute to the observed differences.

While the above processes can contribute to significant differences between the two control areas, they cannot explain the actual observed decreases in abundance and biomass in C2. For this to have occurred there would either have to be a migration of fishes out of the area, or an increase in the rate of mortality relative to C1. Inspection of the data showed no evidence that fish movement, for example to known seasonal spawning aggregation sites, affected the results. In contrast, there is strong circumstantial evidence that illegal fishing primarily in C2 significantly affected the results. This area is the closest to the Puerto Rico coast and includes one of the two access points to Mona Island (the other is on the western side in the impacted area), both of which increase the opportunity for poaching. Additionally, enforcement at Mona Island is land-based and centered on the western side, with little oversight given to activities off the east coast. During the time period of this study, poaching was evident throughout the MPA, but the incidence was much higher within C2 (personal observations). Anecdotal conversations with fishermen also suggested that poaching was significantly greater within C2. Given generally low abundances of large species, only a slight increase in fishing pressure could result in a significant decline.

Enforcement and compliance are fundamental to the effectiveness of NTZs for both stock replenishment and enhanced fishing opportunities due to spillover (Roberts et al. 2001; Guidetti et al. 2008; Guidetti & Sala 2007). The variability in response between the two control areas observed in this study indicates the importance of documenting the extent of legal and illegal fishing activities within an MPA when tests for effectiveness are being planned. Such information can be obtained through the direct monitoring of fishing activities or through structured interviews with fishermen and other stakeholders (Valdes-Pizzini et al. 1997, Cinner et al. 2003), with the latter being more practical for remote locations.

Despite the advantages of using BACI design and PERMANOVA together they are rarely used to evaluate the efficiency of NTZs (Claudet et al 2006). Studies are often lacking in data before NTZ establishment, especially in the Caribbean region (Appeldoorn and Lindeman 2003). In the present study, the combination of BACI design with both permutational multivariate and univariate analysis of variance, were essential for understanding the complexity of the response to the NTZs at Mona Island. Without these it would not have been possible to elucidate the effects of overall recruitment in smaller species, nor separate the differential response between the two control areas. Having two control areas was critical for both

establishing broad site-specific differences and, more importantly, for establishing a positive reserve effect between C1 and the impacted area. Discriminant analysis was important for testing and to visualize the magnitude of the observed effects, thus allowing for a deeper knowledge of what has occurred since the Mona NTZ was established.

## **Conclusion**

The results of this study exemplify the problems of testing NTZ effectiveness at small isolated areas with limited recruitment but also point to ways in which these problems can be managed. One clear point is that where recruitment is limited, substantial time must be given for potential increases in abundance and biomass to be realized, and this may be a function of the degree to which spawning stocks have been reduced prior to enactment of an NTZ. Another obvious point is the importance of monitoring enforcement/compliance. In our study there was sufficient anecdotal information to suggest that the negative response in the ENTZ may be due to a proportionally high degree of illegal fishing, and without such information the understanding of NTZ impact would not have been possible. Future studies should plan to collect compliance data directly, although this can be challenging in remote locations. In the present study, the robust BACI design and the combination of multivariate and univariate statistics used were necessary to elucidate and interpret the results, and this approach is highly recommended. The small area of Mona Island made the analysis particularly susceptible to the effects of spatial variation in the abundance and distribution of different habitat types. Attempting to control for this by limiting assessments to coral reef habitat still did not account for seascape-scale effects, and the small size of Mona did not allow for a greater degree of stratification or the selection of areas with equal seascapes the latter were just not available. However, having two control areas at least allowed the potential effects of different habitat complexities to be analyzed separately. Lastly, due to its isolation, the only impacted area at Mona Island for comparison was located in close proximity to the NTZs. Due to potential spillover of juvenile and adult fishes into the impacted area, the response within the latter may not be independent of the response of the NTZ, making assessment of effectiveness more difficult. While a separate fished area along the Puerto Rico coast could have been included in the study in an attempt to control for this effect, this area would have been subject to a different fishing regime, presumably more intense due to its proximity to major population centers, as well as potentially greater recruitment from a broader area. In summary, while the isolation of small areas may seem beneficial for testing the impacts

of NTZs because they may control for large-scale variability, they are in fact subject to a unique set of limitations that require extra care be given to sampling design and statistical analyses.

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## Appendices

Appendix A. List of the fish species used by different methodologies with frequencies (%) for each time per location (n=36) and for each time (n=108), and their size groups. Size groups were defined by species of minimum and maximum length observed in the range 8-20 cm (S), 20-45 cm (M), 45-200 cm (L). I: Impact area; C1: Control 1, C2: Control 2.

Species	Location						Year		Size Group
	I-T0	I-T1	C1-T0	C1-T1	C2-T0	C2-T1	T0	T1	
<b>Transects</b>									
<i>Balistes vetula</i>	16,7	19,4	2,8	19,4	25,0	38,9	14,8	25,9	M
<i>Cephalopholis cruentata</i>	41,7	30,6	80,6	52,8	33,3	38,9	51,9	40,7	S
<i>Cephalopholis fulva</i>	88,9	91,7	47,2	72,2	83,3	94,4	73,1	86,1	S
<i>Epinephelus guttatus</i>	8,3	5,6	5,6	8,3	5,6	8,3	6,5	7,4	M
<i>Epinephelus striatus</i>	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	L
<i>Mycteroperca tigris</i>	0,0	2,8	0,0	2,8	0,0	2,8	0,0	2,8	L
<i>Mycteroperca venenosa</i>	5,6	0,0	0,0	8,3	2,8	5,6	2,8	4,6	L
<i>Lutjanus apodus</i>	5,6	25,0	38,9	50,0	13,9	25,0	19,4	33,3	M
<i>Lutjanus jocu</i>	0,0	2,8	0,0	0,0	2,8	0,0	0,9	0,9	L
<i>Lutjanus mahogani</i>	5,6	13,9	11,1	19,4	22,2	22,2	13,0	18,5	S
<b>Roving Seach</b>									
<i>Epinephelus guttatus</i>	19,4	19,4	8,3	19,4	2,8	13,9	10,2	17,6	M
<i>Epinephelus striatus</i>	2,8	2,8	0,0	0,0	2,8	0,0	1,9	0,9	L
<i>Mycteroperca tigris</i>	0,0	5,6	2,8	5,6	5,6	2,8	2,8	4,6	L
<i>Mycteroperca venenosa</i>	0,0	2,8	2,8	19,4	13,9	0,0	5,6	7,4	L
<i>Lutjanus jocu</i>	0,0	0,0	0,0	8,3	8,3	2,8	2,8	3,7	L

## Appendix B

Mean total **abundances** per year and per location ( $\pm$ SE) assessed in transects (n=216)

Groups considered	2005			2009		
	— I —	— C1 —	— C2 —	— I —	— C1 —	— C2 —
Total fish abundance	4.42 $\pm$ 0.41	3.28 $\pm$ 0.44	5.31 $\pm$ 0.68	7.25 $\pm$ 0.56	8.17 $\pm$ 1.38	9.25 $\pm$ 1.89

Mean total **abundances** per year and per location ( $\pm$ SE) assessed in roving surveys (n=216)

	2005			2009		
	— I —	— C1 —	— C2 —	— I —	— C1 —	— C2 —
Total fish abundance	0.28 $\pm$ 0.09	0.17 $\pm$ 0.09	0.36 $\pm$ 0.11	0.39 $\pm$ 0.12	0.78 $\pm$ 0.23	0.22 $\pm$ 0.09

## Appendix C

Mean total **biomass (gr)** per year and per location ( $\pm$ SE) assessed in transects (n=216)

	2005			2009		
	— I —	— C1 —	— C2 —	— I —	— C1 —	— C2 —
Total fish biomass	141 $\pm$ 22	213 $\pm$ 46	214 $\pm$ 40	230 $\pm$ 29	663 $\pm$ 203	283 $\pm$ 34

Mean total **biomass (gr)** per year and per location ( $\pm$ SE) assessed in roving surveys (n=216)

	2005			2009		
	— I —	— C1 —	— C2 —	— I —	— C1 —	— C2 —
Total fish biomass	162 $\pm$ 68	48 $\pm$ 27	724 $\pm$ 250	433 $\pm$ 297	1056 $\pm$ 453	137 $\pm$ 76