# Management Failures and Coral Decline Threatens Fish Functional Groups Recovery Patterns in the Luis Peña Channel No-take Natural Reserve, Culebra Island, Puerto Rico

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## ABSTRACT

Target fishery species have been traditionally used as indicators of compliance and management success in no-take marine protected areas (MPAs). However, this approach has the limitation of ignoring the effects that no-take MPAs may have on the functional role of fishes at the community and ecosystem levels. The first objective of this study was to document spatial and temporal variation patterns in the structure of coral reef fish communities at the functional group level within the Luis Peña Channel No-Take Natural Reserve (LPCNR) in Culebra Island, Puerto Rico. The second objective was to test the efficiency of fish functional groups as indicators of management success in the LPCNR. There was a rapid recovery of fish communities three years following the designation of the LPCNR in 1999. Fish communities at a control fished reef located outside the reserve boundaries also showed a rapid recovery. However, management failures have resulted in poor compliance and in a recent increase in illegal fishing activities. This has resulted in a fish decline trend within core areas of LPCNR during the period of 2002 to 2004. Control sites showed the opposite trend. Also, fish communities at the reserve boundary site collapsed as a combined result of increased fishing pressure by fishers displacement after LPCNR designation and by chronic environmental degradation from areas outside reserves boundaries (i.e., large volumes of sediment- and nutrient-loaded runoff, raw sewage discharges). Chronic environmental degradation between 1997 and 2003 has been associated to a major phase shift in the community structure of coral reef benthic communities from coral to algal dominance within LPCNR. In spite of that, LPCNR has been a successful tool restoring overexploited fish communities in Culebra Island. This suggests that even with very limited efforts no-take MPAs can be successful in restoring severely depleted fishery resources. However, management failures within and outside LPCNR need to be addressed and eliminated in order to keep community support, and to restore trust and compliance.

KEY WORDS: Fish functional groups, management failure, MPAs

# La A Pérdida de Corales y la Ausencia de Cumplimiento Amenazan los Patrones de Recuperación de los Grupos Funcionales de Peces en la Reserva Natural de No-Captura del Canal Luis Peña, Isla de Culebra, Puerto Rico

Las especies objeto de pesca se han utilizado tradicionalmente como indicadoras del éxito y del cumplimiento en las áreas marinas protegidas (AMPs) de no-captura. Sin embargo, ésto tiene la limitación de ignorar los efectos que las AMPs puedan tener en el rol funcional de los peces al nivel de la comunidad y del ecosistema. Más aún, ignora el rol funcional que puede tener la integridad de los habitáculos bénticos arrecifales en el mantenimiento de las comunidades de peces. El primer objetivo de este estudio fue el de documentar los patrones de espaciales y temporales de variación en la estructura de la comunidad béntica y de peces arrecifales al nivel de los grupos funcionales. En segundo lugar, se probó la eficiencia de los grupos funcionales de peces como indicadores del éxito y cumplimiento en la Reserva Natural de No-Captura del Canal Luis Peña (RNCLP), en la Isla de Culebra, PR. Las comunidades bénticas y de peces arrecifales se monitorearon desde el 1996 utilizando transectos fijos lineales y censos visuales estacionarios aleatorios, respectivamente. Se documentó una pérdida neta de 46% en la cobertura de corales, un incremento de 683% en la cobertura de macroalgas y un 279% en la cobertura de cianobacterias. Se demostró mediante pruebas ANOSIM que dichos patrones fueron significativos a través del tiempo y a través de las zonas de profundidad. Dicho cambio de fase se ha asociado con los pulsos frecuentes de escorrentías altamente sedimentadas y cargadas de nutrientes, así como con brotes de enfermedades de corales. Las comunidades de peces dentro de las áreas núcleo de los arrecifes de coral de la RNCLP mostraron valores promedio mayores de riqueza de especies, abundancia total, biomasa total, biomasa de herbívoros totales y raspadores, y de carnívoros totales, generalistas, piscívoros y planctívoros, que en aquellos arrecifes localizados en el borde o afuera de la RNCLP. Sin embargo, la biomasa de 36% de las especies de peces ha disminuído a través de dicho período de 7 años, con 19% de éstos habiendo disminuído >50%. Se ha observado también una disminución en H'n y J'n como resultado de la dominancia en la biomasa de algunos grupos funcionales (ej. herbívoros raspadores y no desnudadores). Se sugiere que dicha dominancia puede estar influenciada por la pérdida de corales y el cambio de fase hacia la dominancia de las algas. A pesar de que algunas especies depredadoras (ej. meros, pargos) han mostrado incrementos significativos en biomasa, ninguno de los grupos funcionales de depredadores han mostrado incrementos significativos luego de la designación de la RNCLP. Dichos grupos constituyen también el objeto principal de las actividades de pesca ilegal dentro de la reserva y reflejan la ausencia significativa de éxito y cumplimiento. Los efectos de las AMPs de no-captura son altamente variables dependiendo de la escala en los que se midan. El cumplimiento inicial causó un incremento rápido en la abundancia y biomasa de muchas especies, pero la recuperación de las comunidades de peces ha fallado al nivel de la mayoría de los grupos funcionales. Estos resultados sugieren que la degradación de los

arrecifes de coral, en combinación con la ausencia de cumplimiento, pueden prevenir la recuperación de los grupos funcionales de peces. Ésto podría tener implicaciones de manejo significativas en el mantenimiento de los procesos ecológicos al nivel del ecosistema en los arrecifes de coral.

PALABRAS CLAVES: Pérdida de corales, Culebra, áreas marinas protegidas (AMPs) de no-captura

#### INTRODUCTION

Fishing effects on marine ecosystems have been documented across multiple spatial and temporal scales (Jackson 1997, Jackson et al. 2001, Pauly et al. 2002). Fishing on coral reefs, often in combination with other human disturbances, such as eutrophication and disease outbreaks, has been shown to trigger long-term phase shifts in the community structure of both fish and epibenthic communities (Hughes 1994, Hawkins and Roberts 2004). It can also have profound effects at the ecosystem level (Jackson 2001), including an enormous loss of abundance and biomass of large animals, some of them undergoing extinction. Fishing can produce cascade effects affecting the abundance of marine fish populations (Pinnegar et al. 2000, Carr et al. 2002), age of maturity, size structure, sex ratio and genetic diversity of exploited species (Sobel and Dahlgren 2004). Fishing down the food web can indirectly affect marine biodiversity (Roberts 1995b, Bohnsack and Ault 1996), and as a result of bycatch, habitat degradation, by altering biological interactions (Carr et al. 2002), ecosystems structure and function and reducing the ability of reefs to recover from disturbance (Roberts 1995b, Sobel and Dahlgren 2004).

No-take marine protected areas (MPAs) have become a successful tool to help rebuild overexploited fish populations (Roberts 1994, 1995a, Roberts and Hawkins 1997, Roberts et al. 2001, Halpern 2002, Halpern and Warner 2002). Target fishery species have been traditionally used as indicators of compliance and management success in MPAs. However, this approach has the limitation of ignoring the effects that MPAs may have on the functional role of fishes at the community and ecosystem levels. Moreover, it ignores the functional role that coral reef benthic habitat integrity has on maintaining fish community Functional changes in fish communities accompany structural structure. changes at the ecosystem level, thus affecting major reef processes such as grazing, predation, competition, food web structure, energy flow, and interactions among species (Sobel and Dahlgren 2004), but also benthic processes such reef accretion and bioerosion (Roberts 1995b). Current large-scale reef crisis (i.e., Gardner 2002) requires an improved understanding of the ecological processes that underlie reef resilience (Bellwood et al. 2004). Such processes may include phase shifts in fish community structure and their relationship to modifications in their functional roles in coral reefs. The lowest fish biodiversity of the Caribbean, as compared to the Indo-Pacific region, suggests a relatively low functional redundancy and highlights the vulnerability of reef ecosystems to fish community declines. Therefore, we suggest expand traditional MPA effectiveness evaluation methods to document spatial and temporal patterns of variation in fish community structure at the functional

group level.

#### Why Use Fish Functional Groups?

Interactions among species make it difficult to predict how ecological communities will respond to environmental degradation (Davis et al. 1998) or to any source of anthropogenic stress, including fishing pressure. Many coral reef fish species are highly sensitive to overexploitation and may undergo rapid local extinction. This may have cascading negative consequences for the entire ecosystem (Hughes 1994, Carr et al., 2002). Unpredictability at the population level argues for whole-ecosystem approaches to biodiversity conservation (Ives and Cardinale 2004). The sensitivity of an individual species to anthropogenic stress depends not only on the direct impact of stress on that species, but also on the indirect effects on that species caused by changes in densities of other species (Ives 1995, Ives and Cardinale 2004). For instance, fishing pressure or environmental degradation may decrease the density of competitors and/or predators of a species, thereby causing a compensatory increase in the density of that species. This may lead to wide short-term fluctuations at the population level. Functional groups have shown higher short-term stability than populations of individual species (Tilman 1996, McGrady-Steed and Morin 2000). High biodiversity will result in high functional redundancy. Functional redundancy will buffer against such short-term variations at the functional group level. However, Caribbean coral reef fish functional groups sustain a lower functional redundancy in comparison to Indo-Pacific reefs as a result of its lower fish biodiversity (Bellwood et al. 2004). Therefore, coral reef fish functional groups may be more vulnerable in the Caribbean to the effects of any anthropogenic stressor, becoming more susceptible to rapid phase shifts in community structure and ecosystem functions as a result of human exploitation or impacts. Shifting ecosystem functions will need to be assessed under any ecosystem-based fisheries management model.

Ecosystem-based fisheries management will require expanding the focus of traditional target species-oriented fish monitoring efforts to a functionalgroup approach. Suggested alternatives to reduce or even reverse actual fishing trends include decreasing fishing efforts by 20 - 30% and a redistribution of remaining effort across trophic levels, from large top predators to small prey species (Pauly et al. 2003). However, such an alternative will require first building up a strong database of fishing impacts on fish functional groups (i.e., trophic guilds) to help parameterize ecosystem models. Effects of chronic environmental stress will also need to be incorporated to fish monitoring efforts with proper control sites (i.e., no-take MPAs, remote reefs, etc.). This could be effectively done integrating benthic and water quality monitoring programs to fish monitoring efforts. Ecosystem-based management will also require modeling based upon a system of metrics of community structure, including diversity indices based on species richness, evenness and dominance, ordination methods applied to species composition data, and aggregate indicators of ecosystem status such as biomass size spectra (Babcock and Pikitch 2004).

The first objective of this study was to document spatial and temporal variation patterns in the structure of coral reef fish communities at the func-

tional group level within the Luis Peña Channel No-Take Natural Reserve (LPCNR) in Culebra Island, Puerto Rico (PR). Second, we tested the efficiency of fish functional groups as indicators of management success in the LPCNR.

#### METHODS

#### **Study Sites**

Studies were carried out within the LPCNR, in Culebra Island, PR (Figure 1). Culebra is located at approximately 28 km off the northeastern coast of PR. The reserve was declared in 1999 and full descriptions of its marine communities, species inventories, ecological status assessments and threats from anthropogenic activities can be found elsewhere (Hernández-Delgado 2000, 2003a,b, 2004a,b, Hernández-Delgado and Sabat 2000, In press, Hernández-Delgado et al. 2000, Hernández-Delgado and Rosado-Matías 2003). Data was collected in 1996, 1998, 1999, 2002, 2003 and 2004 from Carlos Rosario Beach – CRO - (core area of LPCNR), and in 1999, 2002, 2003 and 2004 from Punta Melones – PME - (boundary area) and Punta Soldado – PSO - (control site outside). Sampling was conducted at two depth zones: I (<5 m), II (5-15 m). Data from year 1999 was collected prior to the LPCNR fishing prohibition in September 30, 1999.



**Figure 1.** Study sites within LPCNR. From north to south: 1) Carlos Rosario Beach, 2) Punta Melones, and 3) Punta Soldado (control site outside LPCNR).

## **Data Collection**

Fish community was sampled following a factorial design with time, sites, and depth zones as main factors. Data on fish species richness, abundance, and size estimates were collected at each site during the months of August and September of each year using the fish stationary visual census technique (Bohnsack and Bannerot, 1986). Size data (fish fork length) was used to calculate biomass following Bohnsack and Harper (1988) and Bohnsack (Unpub. data). Weight-length relationships were calculated by fitting a regression line to the equation:  $\log W = \log a + b \log L$ , which is equivalent to the equation W = aLb, where W is weight in grams, L is length in mm, and a and b are constants. Basic information of the fish community structure included species richness, abundance, species diversity index (H'n), evenness (J'n), biomass, and standing stock biomass. Also, provided was information about abundance and biomass at the family/subfamily level and at the trophic group level, including herbivore guilds (i.e., non-denuders, browsers, scrapers), carnivore guilds (i.e., generalist, piscivores, planktivores), omnivores, and detrivores. Also, it provided the same type of information on target fishery species guilds. Only species richness, abundance, H'n, J'n and biomass data of functional groups were analyzed during this study.

## **Statistical Analysis**

Spatio-temporal variation in community parameters at CRO was analyzed by means of one-way ANOVA using time and depth zones as main factors. No interaction analysis was carried out due to differences in the number of replicate samples per depth zone and per year. Two separate analyses were conducted for all years (1996-2004) and for the LPCNR designation year (1999) vs. 2004. A two-way ANOVA was used to test for spatio-temporal variation in community parameters among sites (MPA core, MPA boundary, control outside), year and depth zones. Post-hoc analysis was conducted using Tukey's comparison of means (Zar 1984). Data on species richness and abundance was  $\sqrt{-transformed}$ , while data on proportions was arcsin-( $\sqrt{-transformed}$ ).

Individual coral reef fish functional group community matrices were compiled and imported into PRIMER ecological statistics software package (Clarke and Warwick 2001) for multivariate analysis. Mean fish functional group biomass proportion values were square root-transformed in order to appropriately weight the less abundant categories. Mean data from each year and depth zone at CRO, and from each site, year and depth zone were classified with hierarchical clustering using the Bray-Curtis group average linkage method (Bray and Curtis 1957) and then ordinated using a non-metric multidimensional scaling (MDS) plot (Clarke and Warwick 2001). Spatio-temporal variation patterns in community structure were tested using PRIMER's multivariate equivalent of an ANOVA called ANOSIM, which means "analysis of similarities" (Clarke 1993, Clarke and Warwick 2001). Both, global and pairwise tests were carried out by means of ANOSIM. All tests were based on 5,000 permutations and had no built-in assumptions about the data distribution. The key fish functional groups responsible for spatial

variation in community structure between groups of years, sites, and depth zones were determined using PRIMER's SIMPER routine (Clarke and Warwick 2001).

### RESULTS

#### Spatio-temporal Variation in Fish Communities at CRO: 1996-2004

There was an overall increase in the mean value of most community parameters at CRO after the LPCNR designation in 1999 (Figure 2). Fish abundance, H'n, J'n, fishery target species density, as well as total biomass, herbivore, browser, scraper, total carnivore and piscivore biomass, and the percent biomass of fishery target species showed significant temporal increases at CRO following MPA designation (Table 1). However, post-hoc analysis revealed that most of the differences were documented between years 2002-2003 and years previous to the LPCNR designation in 1999. Fish species richness, total abundance, abundance of fishery target species, total biomass, and fishery target species standing stock biomass declined between 2002 and 2004. A similar trend was documented in the mean biomass values of total herbivores, browsers, scrapers, total carnivores, piscivores, planktivores and shallow-water omnivores (Figure 3). No significant differences were documented in many parameters when year 2004 was compared to years during the period of 1996 to 1999. Scraper herbivore and piscivore biomass were significantly higher in shallow-water habitats when data was pooled across years (Table 1).

## Spatio-temporal Variation in Fish Communities at CRO: 1999 vs. 2004

Total abundance, total biomass, total carnivore, generalist and piscivore biomass, and fishery target species standing stock biomass showed significantly higher mean values five years after the LPCNR designation (Figures 2 and 3, Table 1). Generalist carnivore biomass was significantly higher in deepwater habitats, while piscivore biomass was significantly higher in shallowwater habitats.

## Magnitude of Changes at CRO

The magnitude of change in total fish abundance during the first five years of the LPCNR no-take designation was dramatic, reaching up to 378% in shallow-water habitats and 235% in deeper waters (Table 2). Total biomass increased during the first three years a magnitude of 508% and 521%, respectively, but declining to only 188% and 206%, respectively, after five years. A similar pattern occurred with total herbivore, browser, and scraper biomass. Scraper herbivores constitute an important part of the Culebra Island reefassociated and showed a 521% and 354% increase in mean biomass in shallow and deeper habitats, respectively, during 2002. These plummeted to only 102% and 49% in 2004. A similar trend was documented for all carnivore groups, including piscivores. These showed a dramatic 1,392% and 1,105% increase in mean biomass after three years. After five years this increase was cut down nearly in half (Table 2).



**Figure 2.** Fish community parameter changes through time at Carlos Rosario Beach (LPCNR core area): A) Species richness, B) Abundance, C) H'n, D) J'n, E) Total biomass, F) Abundance fishery target species, G) Standing stock biomass fishery target species, and H) % Relative biomass fishery target species. Mean± one standard error.

| Parameters                                | All years | All years | 99 vs 04<br>(Time) <sup>b</sup> | 99 vs 04<br>(Denth) <sup>b</sup> |
|---|-----------|-----------|---------------------------------|----------------------------------|
| Species richness                          | 0.0601    | 0.4010    | 0 1127                          | 0.6594                           |
| Abundanaa                                 | 0.0031    | 0.4310    | 0.1127                          | 0.0534                           |
|   | 0.0024    | 0.5317    | 0.0329                          | 0.1565                           |
| Species diversity index (H'n)             | 0.0428    | 0.5890    | 0.3127                          | 0.2707                           |
| Species evenness (J'n)                    | 0.0127    | 0.3134    | 0.1541                          | 0.2112                           |
| Total biomass                             | 0.0015    | 0.4820    | 0.0185                          | 0.2019                           |
| Total herbivore biomass                   | 0.0060    | 0.8598    | 0.1411                          | 0.9892                           |
| Non-denuder herbivore                     | 0.1881    | 0.7256    | 0.3919                          | 0.9602                           |
| biomass                                   |           |           |                                 |                                  |
| Browser herbivore biomass                 | 0.0271    | 0.6345    | 0.3652                          | 0.8712                           |
| Scraper herbivore biomass                 | 0.0006    | 0.0472    | 0.1720                          | 0.5943                           |
| Total carnivore biomass                   | 0.0056    | 0.2644    | 0.0025                          | 0.0099                           |
| Generalist carnivore biomass              | 0.0792    | 0.0881    | 0.0130                          | 0.0175                           |
| Piscivore biomass                         | 0.0002    | 0.0032    | 0.0104                          | 0.0303                           |
| Planktivore biomass                       | 0.3005    | 0.0898    | 0.1067                          | 0.1070                           |
| Omnivore biomass                          | 0.2253    | 0.7878    | 0.7784                          | 0.8362                           |
| Fishery target species density            | 0.0062    | 0.3075    | 0.1492                          | 0.3611                           |
| Fishery target species standing           | 0.0009    | 0.3459    | 0.0196                          | 0.7116                           |
| stock biomass                             |           |           |                                 |                                  |
| Percent biomass fishery target<br>species | 0.0251    | 0.1186    | 0.0753                          | 0.4563                           |

**Table 1.** Significant changes documented in fish community parameters through time (1996-2004) and between 1999 and 2004. Figures are p values from ANOVA.

<sup>a</sup> D.F.= time (5,11), depth (1,11). <sup>b</sup> D.F.= time (1,3), depth (1,3).

| Table 2. | Magnitude of changes   | documented in fish | community parameters in |
|----------|------------------------|--------------------|-------------------------|
| Carlos R | osario Beach between 1 | 1999 and 2004.     |                         |

| Parameters                            | 1999 vs | 1999 vs | 1999 vs | 1999 vs |
|---------------------------------------|---------|---------|---------|---------|
|                                       | 2002    | 2002    | 2004    | 2004    |
|                                       | <5 m    | 5-15 m  | <5 m    | 5-15 m  |
| Species richness                      | 34%     | 37%     | 34%     | 53%     |
| Abundance                             | 235%    | -10%    | 378%    | 235%    |
| Species diversity index (H'n)         | -7%     | 26%     | -18%    | -6%     |
| Species evenness (J'n)                | -16%    | 15%     | -24%    | -18%    |
| Total biomass                         | 508%    | 521%    | 188%    | 206%    |
| Total herbivore biomass               | 404%    | 957%    | 70%     | 131%    |
| Non-denuder herbivore biomass         | 103%    | 24%     | 14%     | 112%    |
| Browser herbivore biomass             | 290%    | 2,384%  | 35%     | 306%    |
| Scraper herbivore biomass             | 521%    | 354%    | 102%    | 49%     |
| Total carnivore biomass               | 642%    | 313%    | 223%    | 226%    |
| Generalist carnivore biomass          | 442%    | 200%    | 209%    | 224%    |
| Piscivore biomass                     | 1,392%  | 1,105%  | 694%    | 750%    |
| Planktivore biomass                   | 28%     | 174%    | -36%    | -27%    |
| Omnivore biomass                      | 12%     | -44%    | -47%    | 292%    |
| Fishery target species density        | 355%    | 181%    | 122%    | 265%    |
| Fishery target species standing stock | 934%    | 581%    | 366%    | 413%    |

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**Figure 3.** Fish functional group biomass changes through time at Carlos Rosario Beach (LPCNR core area): A) Total herbivores, B) Non denuders, C) Browsers, D) Scrapers, E) Total carnivores, F) Generalists, G) Piscivores, H) Planktivores, and I) Omnivores. Mean± one standard error.

## Multivariable Analysis at CRO

There was a highly significant difference in fish community structure at the functional group level among years at CRO, particularly between year pairs 1996 and 2002, 1996 and 2003, and between 1999 and subsequent years following LPCNR designation (Table 3). No significant difference was documented between years 1996 and 2004. A low stress (0.07) MDS analysis revealed six different cluster patterns of years and depth zones at CRO when using the 20% dissimilarity cut-off level, with two of them grouping years 1996 and 1999, and years 2003 and 2004, respectively (Figure 4a). Years 1998 and 2002 grouped independently. These patterns suggest that fish communities were becoming significantly different, mostly three years after the LPCNR designation, but a reversal pattern has occurred during 2003 and 2004, leading to a stage close to where they were before the LPCNR designation. No significant patterns were documented between depth zones (Table 3), but a significant interaction effect was documented between years and depth zone as a result of the effect of the variable years.

| Factors       | Global R | Significance          |
|---------------|----------|-----------------------|
| Global test   |          |                       |
| Year          | 0.600    | 0.2%                  |
| Depth         | -0.013   | 42.9% NS <sup>2</sup> |
| Year x Depth  | 0.065    | 0.2%                  |
| Pairwise test |          |                       |
| 1996 vs. 1998 | 0.014    | 31.0% NS              |
| 1996 vs. 1999 | 0.056    | 15.8% NS              |
| 1996 vs. 2002 | 0.068    | 4.1%                  |
| 1996 vs. 2003 | 0.122    | 1.6%                  |
| 1996 vs. 2004 | -0.001   | 46.8% NS              |
| 1999 vs 2002  | 0 159    | 0.7%                  |
| 1999 vs. 2003 | 0.221    | 0.1%                  |
| 1999 vs. 2004 | 0.098    | 4.0%                  |

**Table 3.** ANOSIM analysis of spatio-temporal changes in fish community structure at Carlos Rosario Beach<sup>1</sup>.

<sup>1</sup>Based on 5000 permutations.

<sup>2</sup>NS= Non-significant (values <5% are considered significant).

## **Community Structure at CRO**

The annual percent contribution of total herbivore biomass increased from 51% in 1996 to 62% in 1999, but declined to 46% in 2003 (Table 4). However, it increased back to 59% in 2004. Non-denuders annual percent contribution increased from 10% in 1996 to 18% in 1998 and stabilized at 17% from 1999 to 2004. Browsers have shown fluctuations associated to the behavior of large acanthurid fish schools. However, they have remained largely unchanged through the study. Similarly, annual percent contribution of scraper herbivores has remained unchanged during the study. The annual percent contribution of total carnivore biomass declined from 44% in 1996 to 35% in 1999, but increased to 41% in 2002. However, it declined back to 38% in 2004. Percent contribution in generalist carnivores was declining during the two years previous to the LPCNR designation. Three years later there was an increase, followed by another decline in successive years. Percent contribution of generalist carnivores during 2003 and 2004 was even lower than that of 1999. Piscivore annual percent contribution was 10% in 1996 and declined to 6% in 1998, increasing back to 11% in 2003 and 2004. Planktivores have shown large fluctuations through time, while omnivores percent contribution has increased from a lowest 3% in 1999 to 13% in 2004.

| Functional group | 1996 | 1998 | 1999 | 2002 | 2003 | 2004 |
|------------------|------|------|------|------|------|------|
| Herbivores       |      |      |      |      |      |      |
| Non-denuders     | 10   | 18   | 17   | 17   | 17   | 17   |
| Browsers         | 20   | 17   | 23   | 9    | 11   | 22   |
| Scrapers         | 21   | 22   | 22   | 22   | 18   | 20   |
| Carnivores       |      |      |      |      |      |      |
| Generalists      | 21   | 17   | 18   | 20   | 17   | 16   |
| Piscivores       | 10   | 6    | 7    | 7    | 11   | 11   |
| Planktivores     | 13   | 15   | 10   | 14   | 9    | 11   |
| Omnivores        | 5    | 5    | 3    | 11   | 17   | 13   |

**Table 4**. Percent contribution of fish functional group biomass to community structure per year at Carlos Rosario Beach.

SIMPER indicator group analysis showed that changes in the biomass of different fish functional groups were significant causing temporal variation patterns in CRO depending on the temporal scale (Table 5). Planktivores caused the most significant change in community structure between 1996 and 1998, while non-denuders where the most important between 1996 and 2002, and 2002 and 2004, while piscivores did so between 1996 and 2003, and between 1996 and 2004, respectively. They were also the most significant factor influencing temporal variation in community structure between 1999 and 2003, and years 1999 and 2004. Overall, mean dissimilarity between 1999 and 2002 was 32%, but declined to only 21% between 1999 and 2004. This suggests that 2004 fish communities at CRO were more similar to 1999 fish communities than 2002 communities were.

## Spatio-temporal Variation in Fish Communities: MPA Core Zone, Boundary and Control Site

Overall, fish communities were significantly different at the LPCNR core zone (CRO) and in the control site (PSO) when compared to the boundary zone (PME), where fish communities have shown a dramatic decline since 1999 (Table 6). All community parameters were significantly different among sites, with the exception of total herbivore, browser and omnivore biomass, and fishery target species density (Table 7). Post-hoc analysis showed that both, CRO and PSO had significantly higher mean values in most parameters when compared to PME. All community parameters were also significantly different among years, with the exception of scraper herbivore, total carnivore, generalist, piscivore, and planktivore biomass. Post-hoc analysis showed that both,

CRO and PSO had significantly higher mean values in most parameters after the LPCNR designation. The opposite was observed at PME. No significant differences were documented between depth zones, with the exception of browser herbivores that showed a significantly higher biomass in shallower habitats. There were significant site x year interactions in all parameters, with the exception of non-denuder herbivore, piscivore, planktivore and omnivore biomass, and in fishery target species density. Site x depth interactions were non-significant, with the exception of percent biomass of fishery target species. All year x depth interactions were non-significant.

| Factors       | Group        | P Bio-<br>mass | P Biomass<br>Factor B | % contrib |
|---------------|--------------|----------------|-----------------------|-----------|
|               |              | Factor A       |                       |           |
| 1996 vs. 1998 | Planktivores | 0.03           | 0.11                  | 23.12%    |
| D=24.92%      | Non-denuders | 0.03           | 0.10                  | 19.09%    |
|               | Piscivores   | 0.01           | 0.06                  | 17.17%    |
| 1996 vs. 1999 | Non-denuders | 0.03           | 0.06                  | 23.57%    |
| D=12.42%      | Omnivores    | 0.05           | 0.08                  | 22.18%    |
|               | Planktivores | 0.03           | 0.05                  | 15.03%    |
| 1996 vs. 2002 | Browsers     | 0.02           | 0.32                  | 25.95%    |
| D=37.49%      | Piscivores   | 0.01           | 0.18                  | 20.02%    |
|               | Generalists  | 0.03           | 0.15                  | 14.16%    |
| 1996 vs. 2003 | Piscivores   | 0.01           | 0.13                  | 24.01%    |
| D=28.35%      | Planktivores | 0.03           | 0.16                  | 23.75%    |
|               | Non-denuders | 0.03           | 0.11                  | 15.80%    |
| 1996 vs. 2004 | Piscivores   | 0.01           | 0.11                  | 25.96%    |
| D=24.09%      | Generalists  | 0.03           | 0.13                  | 21.40%    |
|               | Non-denuders | 0.03           | 0.10                  | 17.54%    |
| 1999 vs. 2002 | Browsers     | 0.03           | 0.32                  | 27.04%    |
| D=33.76%      | Piscivores   | 0.01           | 0.18                  | 21.89%    |
|               | Scrapers     | 0.04           | 0.21                  | 18.58%    |
| 1999 vs. 2003 | Piscivores   | 0.01           | 0.13                  | 29.03%    |
| D=23.11%      | Planktivores | 0.05           | 0.16                  | 21.85%    |
|               | Generalists  | 0.04           | 0.10                  | 14.07%    |
| 1999 vs. 2004 | Piscivores   | 0.01           | 0.11                  | 29.47%    |
| D=20.94%      | Generalists  | 0.04           | 0.13                  | 20.65%    |
|               | Omnivores    | 0.08           | 0.13                  | 15.29%    |
| 2002 vs. 2004 | Browsers     | 0.32           | 0.06                  | 28.41%    |
| D=21.60%      | Scrapers     | 0.21           | 0.07                  | 19.11%    |
|               | Omnivores    | 0.08           | 0.13                  | 13.82%    |

**Table 5**. SIMPER test of indicator functional groups at Carlos Rosario Beach.

| Parameters <sup>a</sup> | Site | 99   | 66   | 02   | 02   | 03   | 03       | 04   | 04       |
|-------------------------|------|------|------|------|------|------|----------|------|----------|
|                         |      | -    | =    | -    | =    | -    | =        | -    | =        |
| Species richness        | CRO  | 18   | 16   | 24   | 22   | 26   | 27       | 24   | 24       |
|                         | PME  | 19   | 22   | 21   | 27   | 18   | 21       | 21   | 20       |
|                         | PSO  | 17   | 21   | 29   | 28   | 28   | <u>ω</u> | 30   | <u>ω</u> |
| Abundance               | CRO  | 97   | 163  | 327  | 145  | 1057 | 1495     | 465  | 541      |
|                         | PME  | 255  | 281  | 157  | 248  | 143  | 183      | 130  | 126      |
|                         | PSO  | 69   | 117  | 287  | 505  | 266  | 523      | 405  | 412      |
| Species diversity index | CRO  | 2.18 | 1.75 | 2.02 | 2.20 | 1.32 | 0.81     | 1.79 | 1.63     |
| (H'n)                   | PME  | 1.33 | 1.74 | 2.43 | 2.47 | 2.16 | 2.41     | 2.49 | 2.42     |
|                         | PSO  | 2.27 | 2.08 | 2.48 | 2.13 | 2.33 | 1.73     | 2.35 | 2.11     |
| Species evenness (J'n)  | CRO  | 0.76 | 0.62 | 0.64 | 0.71 | 0.41 | 0.25     | 0.58 | 0.51     |
|                         | PME  | 0.49 | 0.57 | 0.80 | 0.75 | 0.75 | 0.79     | 0.82 | 0.82     |
|                         | PSO  | 0.83 | 0.73 | 0.74 | 0.65 | 0.70 | 0.50     | 0.69 | 0.61     |
| Total biomass*          | CRO  | 2.61 | 2.78 | 15.9 | 17.3 | 10.9 | 7.31     | 7.51 | 8.54     |
|                         | PME  | 10.2 | 10.3 | 3.15 | 4.76 | 1.85 | 2.95     | 1.35 | 1.32     |
|                         | PSO  | 2.82 | 4.93 | 3.35 | 8.50 | 2.79 | 3.54     | 6.15 | 5.81     |
| Total herbivore bio-    | CRO  | 1.04 | 0.94 | 5.24 | 9.44 | 2.09 | 1.21     | 1.76 | 2.06     |
| mass*                   | PME  | 4.70 | 5.47 | 1.47 | 1.31 | 0.79 | 1.34     | 0.74 | 0.53     |
|                         | PSO  | 1.51 | 1.16 | 1.60 | 3.66 | 1.21 | 1.12     | 2.82 | 2.82     |
| Non-denuder herbivore   | CRO  | 58   | 49   | 118  | 54   | 110  | 68       | 66   | 92       |
| biomass                 | PME  | 51   | 57   | 100  | 139  | 88   | 234      | 70   | 150      |
|                         | PSO  | 155  | 208  | 342  | 319  | 191  | 218      | 259  | 202      |
| Browser herbivore       | CRO  | 420  | 286  | 1640 | 6739 | 292  | 179      | 568  | 1102     |
| biomass                 | PME  | 3553 | 3665 | 429  | 560  | 276  | 391      | 161  | 127      |
|                         | PSO  | 148  | 187  | 342  | 2544 | 227  | 374      | 1190 | 1857     |
| Scraper herbivore       | CRO  | 560  | 808  | 3480 | 2644 | 1690 | 966      | 1129 | 867      |
| biomass                 | PME  | 1098 | 1754 | 939  | 616  | 424  | 711      | 510  | 257      |
|                         | PSO  | 1183 | 763  | 917  | 794  | 791  | 525      | 1366 | 758      |
| Total carnivore bio-    | CRO  | 1.41 | 1.83 | 10.5 | 7.83 | 7.73 | 5.89     | 4.55 | 6.17     |
| mass*                   | PME  | 3.95 | 3.69 | 1.56 | 3.35 | 1.01 | 1.50     | 0.52 | 0.75     |
|                         | PSO  | 1.14 | 2.72 | 1.61 | 4.58 | 1.50 | 2.29     | 3.19 | 2.79     |

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| Generalist carnivore   | CRO | 515  | 1153 | 2793 | 3553 | 2696 | 1616 | 1593 | 3840 |  |
|------------------------|-----|------|------|------|------|------|------|------|------|--|
| biomass                | PME | 2783 | 2632 | 888  | 1753 | 741  | 1044 | 370  | 504  |  |
|                        | PSO | 669  | 1133 | 1172 | 2577 | 1144 | 1161 | 1836 | 2375 |  |
| Piscivore biomass      | CRO | 479  | 216  | 7148 | 2710 | 4326 | 2645 | 3803 | 1913 |  |
|                        | PME | 1123 | 1016 | 663  | 1580 | 247  | 435  | 107  | 240  |  |
|                        | PSO | 101  | 426  | 195  | 1704 | 253  | 892  | 992  | 312  |  |
| Planktivore biomass    | CRO | 417  | 541  | 534  | 1564 | 1616 | 1629 | 268  | 417  |  |
|                        | PME | 48   | 41   | 13   | 19   | 22   | 17   | 42   | 11   |  |
|                        | PSO | 342  | 1156 | 210  | 297  | 106  | 240  | 360  | 108  |  |
| Omnivore biomass       | CRO | 162  | 06   | 182  | 43   | 187  | 205  | 85   | 303  |  |
|                        | PME | 1550 | 1145 | 118  | 91   | 52   | 114  | 89   | 27   |  |
|                        | PSO | 185  | 1058 | 135  | 265  | 79   | 127  | 146  | 195  |  |
|                        |     |      |      |      |      |      |      |      |      |  |
| Fishery target species | CRO | 0.08 | 0.09 | 0.37 | 0.26 | 0.46 | 0.43 | 0.18 | 0.34 |  |
| density                | PME | 0.09 | 0.24 | 0.31 | 0.41 | 0.35 | 0.41 | 0.28 | 0.25 |  |
|                        | PSO | 0.09 | 0.14 | 0.50 | 0.45 | 0.47 | 0.21 | 0.74 | 0.57 |  |
| Fishery target spp.    | CRO | 7.15 | 7.09 | 73.9 | 47.4 | 46.1 | 26.8 | 33.3 | 35.8 |  |
| standing stock bio-    | PME | 20.6 | 20.1 | 13.5 | 20.4 | 7.1  | 11.3 | 4.5  | 5.0  |  |
| mass                   | PSO | 9.7  | 9.9  | 10.2 | 20.1 | 10.2 | 12.9 | 20.3 | 16.5 |  |
| Percent biomass fish-  | CRO | 50%  | 44%  | 75%  | 29%  | 74%  | 67%  | 71%  | 20%  |  |
| ery target species     | PME | 36%  | 38%  | %99  | 71%  | %99  | 67%  | 55%  | 64%  |  |
|                        | PSO | 56%  | 42%  | 49%  | 46%  | 63%  | 56%  | 57%  | 61%  |  |
| *Values x Kg.          |     |      |      |      |      |      |      |      |      |  |

Table 6 (cont.).

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| Parameters <sup>a</sup>                                 | Site        | Year       | Depth       | Site x   | Site        | Year       |
|---|-------------|------------|-------------|----------|-------------|------------|
|   | 0.110       |            |             | Year     | x           | X          |
|   |             |            |             |          | Depth       | Depth      |
| Species richness  | 0.0027      | 0.0020     | 0.1354      | 0.0295   | 0.2458      | 0.6791     |
| Abundance   | 0.0034      | 0.0027     | 0.0959      | 0.0027   | 0.5780      | 0.5278     |
| Species diversity index<br>(H'n)                        | 0.0034      | 0.0134     | 0.1201      | 0.0129   | 0.0811      | 0.6909     |
| Species evenness (J'n)                                  | 0.0038      | 0.0241     | 0.0581      | 0.0055   | 0.1488      | 0.6858     |
| Total biomass   | 0.0008      | 0.0130     | 0.0645      | 0.0005   | 0.1989      | 0.3638     |
| Total herbivore biomass                                 | 0.1360      | 0.0185     | 0.6211      | 0.0036   | 0.9562      | 0.5084     |
| Non-denuder herbivore                                   | 0.0005      | 0.0384     | 0.4242      | 0.5054   | 0.0665      | 0.5604     |
| Browser herbivore biomass                               | 0.3560      | 0.0043     | 0.0430      | 0.0007   | 0.2529      | 0.0982     |
| Scraper herbivore biomass                               | 0.0160      | 0.0511     | 0.0970      | 0.0112   | 0.4732      | 0.4542     |
| Total carnivore biomass                                 | 0.0015      | 0.0680     | 0.0616      | 0.0068   | 0.3009      | 0.7964     |
| Generalist carnivore bio-                               | 0.0286      | 0.1526     | 0.0314      | 0.0059   | 0.9770      | 0.3489     |
| Piscivore biomass                                       | 0.0070      | 0.0900     | 0.4018      | 0.0558   | 0.0987      | 0.5949     |
| Planktivore biomass                                     | 0.0000      | 0.1361     | 0.5157      | 0.0690   | 0.2589      | 0.1655     |
| Omnivore biomass  | 0.6140      | 0.0480     | 0.6808      | 0.1127   | 0.3344      | 0.7984     |
| Fishery target species den-<br>sity                     | 0.1578      | 0.0009     | 0.5429      | 0.1250   | 0.3038      | 0.2424     |
| Fishery target species standing stock biomass           | 0.0009      | 0.0108     | 0.5636      | 0.0018   | 0.2125      | 0.8538     |
| Percent biomass fishery                                 | 0.0000      | 0.0000     | 0.4043      | 0.0000   | 0.0375      | 0.0995     |
| <sup>a</sup> D.F.= time (2), year (3), de<br>error (6). | epth (1), s | ite x year | (6), site > | depth (2 | ), year x o | depth (3), |

**Table 7**. Significant spatio-temporal changes in fish community parametersthrough time (1999-2004). Figures are p values from ANOVA.

#### **Multivariable Analysis of Sites**

There was a highly significant difference in fish community structure at the functional group level among sites (Table 9). Fish communities at CRO were significantly different than both, PME and PSO. PME was significantly different than PSO. No significant differences were documented among years and between depth zones. However, a pairwise ANOSIM test documented significant differences between 1999 and 2002 when pooling all sites, and between 1999 and 2004. MDS analysis (stress=0.16) revealed seven different cluster patterns of sites, years and depth zones when using the 20% dissimilarity cut-off level, with a large group composed by PME and PSO, and a close group composed by CRO-1999 and CRO-II-2004 (Figure 4a). Clusters follow a gradient of change through time after the LPCNR designation, but also reflect a dramatic reversal in fish community structure at PME and the early signs of reversal at CRO.

#### Magnitude of Changes Within and Between Sites

There were dramatic within-site changes in community structure five years after the LPCNR designation (Table 8). Species richness increased by a factor of 41% and 61% at CRO and PSO, respectively, while fish abundance increased by a factor of 287% and 339%, respectively. However, abundance declined by 52% at PME. Total biomass increased by 198% at CRO and by 54% at PSO, but declined by 87% at PME. Browser herbivore biomass increased by 137% at CRO and by 810% at PSO, but declined by 96% at PME. Generalist carnivore biomass increased by 226% at CRO and by 130% at PSO, but plummeted by 84% at PME. Piscivores showed a similar decline at PME, but increased by 147% at PSO and by 722% at CRO. Fishery target species standing stock biomass increased by 392% at CRO and by 276% at PSO, but declined by 77% at PME.

Between-site differences in year 2004 were also significant for most parameters, particularly when CRO and PSO were compared to PME (Table 8). For example, CRO showed higher mean values when compared to PME in factors such as fish abundance (293%), total biomass (501%), and mean biomass of browsers (480%), scrapers (160%), total carnivores (744%), generalists (522%), piscivores (1547%), planktivores (1192%) and omnivores (234%), as well as in fishery target species standing stock biomass (631%). Differences were less pronounced between CRO and PSO, but CRO showed higher fish abundance (23%), total carnivore biomass (79%) and piscivore biomass (338%). However, CRO showed a slightly lower (6%) fishery target standing stock biomass than at the control PSO. PME showed dramatically lower mean values for most of the parameters when compared to PSO (Table 8), suggesting a fish community collapse.

| Parameters                                | CRO  | PME  | PSO  | CRO v<br>PME<br>2004 <sup>2</sup> | CRO v<br>PSO<br>2004 <sup>3</sup> | PME v<br>PSO<br>2004 <sup>4</sup> |
|---|------|------|------|-----------------------------------|-----------------------------------|-----------------------------------|
| Species richness                          | 41%  | 0%   | 61%  | 15%                               | -21%                              | -33%                              |
| Abundance                                 | 287% | -52% | 339% | 293%                              | 23%                               | -69%                              |
| Species diversity index<br>(H'n)          | -13% | 60%  | 3%   | -30%                              | -23%                              | 9%                                |
| Species evenness (J'n)                    | -21% | 55%  | -11% | -34%                              | -16%                              | 26%                               |
| Total biomass                             | 198% | -87% | 54%  | 501%                              | 34%                               | -78%                              |
| Total herbivore biomass                   | 93%  | -75% | 111% | 50%                               | -32%                              | -55%                              |
| Non-denuder herbivore                     | 48%  | 104% | 27%  | -28%                              | -66%                              | -52%                              |
| Browser herbivore bio-                    | 137% | -96% | 810% | 480%                              | -45%                              | -91%                              |
| Scraper herbivore bio-                    | 71%  | -73% | 9%   | 160%                              | -6%                               | -64%                              |
| Total carnivore biomass                   | 231% | -83% | 55%  | 744%                              | 79%                               | -79%                              |
| Generalist carnivore                      | 226% | -84% | 130% | 522%                              | 29%                               | -79%                              |
| Piscivore biomass                         | 722% | -84% | 147% | 1547%                             | 338%                              | -73%                              |
| Planktivore biomass                       | -28% | -49% | -69% | 1192%                             | 46%                               | -89%                              |
| Omnivore biomass                          | 54%  | -96% | -73% | 234%                              | 14%                               | -66%                              |
| Fishery target species                    | 206% | 61%  | 470% | -2%                               | -60%                              | -60%                              |
| Fishery target species                    | 392% | -77% | 276% | 631%                              | -6%                               | -87%                              |
| Percent biomass fishery<br>target species | 50%  | 61%  | 20%  | 18%                               | 19%                               | 0.8%                              |

 Table 8. Magnitude of changes documented in fish community parameters within and between sites between 1999 and 2004<sup>1</sup>.

<sup>1</sup>Annual means. <sup>2</sup>Relative magnitude of CRO compared to PME. <sup>3</sup>Relative magnitude of CRO compared to PSO. <sup>4</sup>Relative magnitude of PME compared to PSO.

| structure.           |          |                       |
|----------------------|----------|-----------------------|
| Factors              | Global R | Significance          |
| Global test          |          |                       |
| Site                 | 0.402    | 0.0%                  |
| Year                 | 0.079    | 11.9% NS <sup>2</sup> |
| Depth                | 0.004    | 40.0% NS              |
| Site x Year          | 0.403    | 0.9%                  |
| Site x Depth         | 0.382    | 0.0%                  |
| Year x Depth         | -0.073   | 77.4% NS              |
| Pairwise test – Site |          |                       |
| CRO vs. PME          | 0.640    | 0.1%                  |
| CRO vs. PSO          | 0.483    | 0.1%                  |
| PME vs. PSO          | 0.166    | 2.4%                  |
| Pairwise test - Year |          |                       |
| 1999 vs. 2002        | 0.280    | 2.6%                  |
| 1999 vs. 2003        | 0.200    | 7.4% NS               |
| 1999 vs. 2004        | 0.256    | 2.6%                  |
| 2002 vs. 2003        | -0.030   | 52.4% NS              |
| 2002 vs. 2004        | -0.189   | 99.4% NS              |
| 2003 vs. 2004        | -0.061   | 65.4 NS               |

 Table 9. ANOSIM analysis of spatio-temporal changes in fish community structure.

<sup>1</sup>Based on 5000 permutations.

<sup>2</sup>NS= Non-significant (values <5% are considered significant).

#### **Community Structure per Site, Year and Depth Zone**

Herbivores had a 38% biomass contribution at CRO, with 51% at PME and 49% at PSO, when data was pooled across time (Table 10). Carnivores had a 51% biomass contribution at CRO, with 35% at PME and 37% at PSO, when pooled across time. Omnivores showed little fluctuations among sites. Non-denuders were proportionally higher at PSO (23%) and PME (20%). Browsers, scrapers and generalists did not fluctuate much among sites. Piscivores (16%) and planktivores (19%) were proportionally higher at CRO. Herbivores percent contribution increased overall from 43% in 1999 to 50% in 2004. Non-denuders showed also a large increase from 14% to 20%. Carnivores did not fluctuate much overall through time, but piscivore percent contribution increased from 9% in 1999 to 14% in 2002. However, declined to 11% in 2004. There were not many differences between depth zones overall, but herbivores were proportionally more abundant in shallow water, while carnivores were more abundant in deep habitats.

SIMPER indicator group analysis showed that planktivores were the most significant functional group causing differences in fish community structure between CRO and PME, and between PSO and PME (Table 11). Piscivores were the most significant group explaining differences between CRO and PSO. CRO and PME showed the highest mean dissimilarity between sites (32%). Omnivores were the most significant group explaining differences between 1999 and subsequent years. Piscivores explained most of the differences between 2002 and 2004, while planktivores explained most of the variation between shallow and deep habitats.





**Figure 4.** Multi-dimensional scaling plots of fish community structure changes: A) Temporal variation patterns in Carlos Rosario Beach, B) Spatio-temporal variation patterns (reserve, boundary, control outside sites). Circles show groupings based on a 20% dissimilarity cut-off level.

| structure per sit | e, year ai | nd depth | zone. |    |    |    |    |    |    |
|-------------------|------------|----------|-------|----|----|----|----|----|----|
| Functional        | CRO        | PME      | PSO   | 99 | 02 | 03 | 04 | I  | II |
| group             |            |          |       |    |    |    |    |    |    |
| Herbivores        |            |          |       |    |    |    |    |    |    |
| Non-              | 12         | 20       | 23    | 14 | 17 | 20 | 20 | 18 | 18 |
| denuders          | 10         | 13       | 10    | 11 | 14 | 11 | 13 | 12 | 12 |
| Browsers          | 16         | 18       | 16    | 18 | 18 | 17 | 17 | 19 | 16 |
| Scrapers          |            |          |       |    |    |    |    |    |    |
| Carnivores        |            |          |       |    |    |    |    |    |    |
| Generalists       | 16         | 17       | 16    | 15 | 18 | 17 | 17 | 16 | 18 |
| Piscivores        | 16         | 12       | 8     | 9  | 14 | 12 | 11 | 11 | 13 |
| Planktivores      | 19         | 6        | 13    | 14 | 8  | 10 | 9  | 10 | 10 |
| Omnivores         | 11         | 14       | 14    | 19 | 11 | 13 | 13 | 14 | 13 |

**Table 10.** Percent contribution of fish functional group biomass to community structure per site, year and depth zone.

| Table 11.  | SIMPER | test of | indicator | functional | groups | for | sites, | year | and |
|------------|--------|---------|-----------|------------|--------|-----|--------|------|-----|
| deptb zone | es.    |         |           |            |        |     |        |      |     |

| Factors              | Group        | P Biomass | P Biomass | % contrib |
|----------------------|--------------|-----------|-----------|-----------|
|                      |              | Factor A  | Factor B  |           |
| CRO vs. PME          | Planktivores | 0.09      | <0.01     | 28.21%    |
| D=32.31%             |              |           |           |           |
| CRO vs. PSO          | Piscivores   | 0.09      | 0.02      | 22.76%    |
| D=25.53%             |              |           |           |           |
| PME vs. PSO          | Planktivores | <0.01     | 0.04      | 20.83%    |
| D=25.84%             |              |           |           |           |
| 1999 vs. 2002        | Omnivores    | 0.11      | 0.02      | 19.53%    |
| D=28.39%             |              |           |           |           |
| 1999 vs. 2003        | Omnivores    | 0.11      | 0.02      | 23.32%    |
| D=26.66%             |              |           |           |           |
| 1999 vs. 2004        | Omnivores    | 0.11      | 0.02      | 23.83%    |
| D=27.42%             |              |           |           |           |
| 2002 vs. 2004        | Piscivores   | 0.07      | 0.04      | 20.53%    |
| D=25.47%             |              |           |           |           |
| Depth I vs. Depth II | Planktivores | 0.03      | 0.05      | 19.78%    |

## DISCUSSION

## Effects of the LPCNR Designation on Fish Communities

Our study showed six important things:

- i) Fish communities were significantly overexploited by fishing activities before the LPCNR designation;
- There was a rapid increase in species richness, total abundance and biomass of most functional groups, including piscivores during the first three years after the LPCNR designation;
- iii) Since 2002 there has been a decline in biomass of fishery target species groups within the core areas at CRO;
- iv) In spite of that trend, core areas of the LPCNR supported higher biomass of most of the fishery target species groups in comparison to boundary areas;

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- v) Fish communities at the boundary area of PME suffered a severe decline between 1999 and 2004; and
- vi) There was a significant increase in biomass of most functional groups at the control site at PSO comparable to core areas within LPCNR.

Rapid recovery in fish communities within the LPCNR and control sites outside was outstanding and comparable to previous reports in the Caribbean (Helpern et al. 2002). For example, Roberts and Hawkins (1994) reported a total biomass slightly above 4.1 kg/count two years after an MPA designation in St. Lucia and a biomass of 1.8 kg/count at a control site outside. Roberts (1995a) reported a total biomass of 3.5 kg/count four years after an MPA designation in Saba and a biomass of 1.9 kg/count at a control site outside. Biomass increased to 4.5 kg/count within the MPA and to nearly 4.0 kg/count outside six years after the MPA designation. In our study, total biomass three years after the LPCNR designation increased from an annual mean of 2.7 kg/ count at the moment of designation to 16.6 kg/count within the core area of CRO. Biomass increased from 3.9 kg/count in 1999 to 5.9 kg/count in 2002 at a control site PSO. But five years after designation, total biomass declined at CRO to 8.0 kg/count, while biomass at PSO remained at 6.0 kg/count. The magnitude of the total biomass decline within the core area of the LPCNR was 52% only within two years, while at the same time biomass remained virtually unchanged at the control site subjected to fishing. A nearly similar pattern was documented within many of the individual functional groups. However, the most dramatic fish community collapse occurred at the boundary site of PME. Mean total biomass was 10.5 kg/count in 1999, but plummeted to 1.3 kg/count in 2004, a magnitude of 87%. These observations suggest that three factors might have affected fish communities:

- i) Illegal fishing activities within the LPCNR;
- ii) Environmental degradation in the boundary area at PME; and
- iii) A combination of both.

Artisanal fishing was eliminated and recreational fishing was significantly reduced after the designation of the LPCNR during the first three years. However, there has been a systematic increase in the presence of poachers within the LPCNR since year 2002. These include mostly off-island recreational spearfishers, and recreational and artisanal hook and line fishers (Hernández-Delgado 2004b). Also, there has been recent increase in illegal fishing activities, including shark long-lines, queen conch, topshell, and octopus poaching (Hernández-Delgado 2004b). Local residents have also documented for the first time several localized juvenile fish and invertebrate massive kills in rocky shores within and outside LPCNR, which might suggest the recent introduction of chemicals during fishing activities by off-island residents. But most of the fishing pressure documented at CRO has been recreational spearfishing from off-island private yacht operators (Hernández-Delgado Pers. obs.). Fishing can have rapid negative effects on the community structure of coral reef fishes (Roberts and Polunin 1993, Russ and Alcalá 1998) and benthic habitats (Hawkins and Roberts 2004). The effect of spearfishing pressure reflected on a decline in mean sizes of target fishery species such as red hind, Epinephelus

guttatus, graysby, Cephalopholis cruentatus, schoolmaster, Lutjanus apodus, dog snapper, Lutjanus jocu, and yellowtail snapper, Ocyurus chrysurus (data not shown). It has also reflected in catch and release data of E. guttatus at several sites within the LPCNR that has consistently showed a declining trend in mean abundance and size (López and Sabat Unpub. data). Moreover, fishery target species standing stock biomass at CRO increased from 7.1 g/m<sup>2</sup> at CRO in 1999 to 60.7 g/m<sup>2</sup> in 2002, a magnitude of 755%. These values were comparable to those reported by Polunin and Roberts (1993) but low to those reported by Roberts and Polunin (1994) from Hol-Chan. However, standing stock biomass at CRO declined to 34.5 g/m<sup>2</sup> in 2004, a magnitude decline of 43% within only two years. Meanwhile, standing stock biomass of fishery target species at PSO control site increased from 9.8 g/m<sup>2</sup> in 1999 to 36.8 g/m<sup>2</sup> in 2004, a magnitude of 276%. Recreational boats rarely frequent PSO, suggesting that recreational spearfishing pressure from private vacht operations is lower at this site in comparison to CRO. Rapid recovery at the control site outside the LPCNR may also suggest a possible combined effect of high recruitment and a possible fish spillover effect. If suitable habitats exist, mobile species will search for resources outside of the MPAs, leading to export of biomass to areas which are fished (Sánchez-Lizaso 2000).

On the other hand, PME has also shown a dramatic increase in fishing pressure immediately after the LPCNR designation due to a fishing effort displacement effect. Fishing has been mostly by hook and line from the shore and boat anglers, and by recreational spearfishers. But this site has also suffered severe environmental degradation resulting from sediment- and nutrient-loaded runoff from the urban area of Culebra. Nemeth and Nowlis (2001) showed that sediment-loaded runoff lead to coral decline in St. Thomas. Culebra Island has experienced extensive development during the last few years (Hernández-Delgado 2004a,b), exposing large areas of land to erosion without the required controls. Hernandez-Delgado and Sabat (in press) documented a 46% decline in coral cover, a 683% increase in macroalgal cover and a 279% increase in cyanobacterial cover within 1997 and 2003 at LPCNR. ANOSIM tests showed this trend to be highly significant through time and among depth zones. This phase shift was associated to the long-term cumulative effects of frequent highly sediment- and nutrient-loaded runoff pulses and coral disease outbreaks. Subsequently, Hernández-Delgado (unpub.data) has documented a close relationship between runoff pulses and disease outbreaks and mortality events in Acroporid corals. As a result, dead coral surfaces were rapidly occupied by algae. Thus, recent high coral mortality has resulted in a significant phase shift in benthic community structure from coral to algal dominance that could explain in part the rapid increase in non-denuder herbivore biomass (Pomacentridae). Most pomacentrids are highly territorial and can interfere with significant reef processes such as tissue regeneration in corals (Hernández-Delgado 2000) and bioerosion rates (Risk and Sammarco 1982). Similarly, Jones et al. (2004) documented a major decline in fish communities in Papua New Guinea following coral decline. Therefore, it is suggested that the observed phase shift in fish community structure at PME has been the combined result of fishing pressure and environmental degradation. This further suggests that management failures in combination with coral decline have con-

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### **Management Failures**

There has been an increasing concern for the ecological effects of noncompliance associated to management failures in MPAs (Kritzer 2004). Caribbean-wide surveys have shown that MPA effectiveness and compliance levels are directly related to the capacity of managing institutions (Appeldoorn and Lindeman 2003). Non-compliance usually results in illegal harvesting activities that can dissipate the potential benefits of management regulations (Gigliotti and Taylor 1990). Illegal fishing activities within the boundary and core zones of LPCNR have been the direct result of management failures by the PR Department of Natural and Environmental Resources (PRDNER), as well as by other co-enforcing agencies.

Several aspects regarding management failures can be mentioned:

- i) There was only a part-time management officer at LPCNR for the period of 2001 to 2003, and there has been none in Culebra since then;
- ii) Boundary buoys were placed in 2002 but vandalized or dislodged by strong currents in 2003 and not placed back for over a year;
- iii) There has never been continuous patrolling and law enforcement;
- iv) Sporadic patrolling has been conducted by local fishermen that have no legal authority;
- v) There is no management plan in place;
- vi) There is no educational and outreach program in place;
- vii) There is no coordination among enforcing agencies or between agencies and stakeholders;
- viii) Scientific information has not been translated into management action; and
- ix) Fishing pressure has shifted from artisanal to recreational and not much attention has been paid to recreational fishing effects.

Also, we identified combined natural resource management failures by public and private sectors outside the boundaries of LPCNR but that are negatively affecting the reserve. These included:

- i) Major land clearing activities on steep slopes;
- ii) Lack of compliance with erosion and sedimentation control regulations;
- iii) Lack of enforcement of these regulations by Municipal and State government agencies;
- iv) Illegal beach land clearing;
- v) Continuous illegal pumping of sediment-loaded waters from public project sites to coastal waters;
- vi) Construction and/or expansion of private and public dirt roads on steep slopes without any erosion control measure; and
- vii) Illegal raw sewage discharges to coastal waters.

Environmental degradation outside LPCNR boundaries has been identified as a major concern for the conservation of coral reef and seagrass benthic communities within LPCNR (Hernández-Delgado, 2004a,b). This study showed that fish communities at the PME boundary zone have been largely affected.

## CONCLUSIONS

There was a rapid recovery of fish communities three years following the designation of the LPCNR. Control fished reefs located outside the reserve boundaries also showed a rapid recovery in fish communities. However, management failures have resulted in poor compliance and in a recent increase in illegal fishing activities. This has resulted in a fish decline trend within core areas of LPCNR during the period of 2002 to 2004. Control sites showed the opposite trend. Also, fish communities at the reserve boundary site collapsed as a combined result of increased fishing pressure by fishers displacement after LPCNR designation and by chronic environmental degradation. In spite of that, LPCNR has been a successful tool restoring overexploited fish communities in Culebra Island. This suggests that even with very limited efforts notake MPAs can be successful in restoring severely depleted fishery resources.

MPA effectiveness can be limited by low institutional and community capacity for management (Jameson et al. 2002), leading to management failure. Management failure can result in declining community support and lack of compliance with management measures, including fishing prohibition (Coleman et al. 2004). User surveys have also shown that the lack of an educational and outreach program, combined with the lack of boundary buoys demarcation and the absence of enforcing personnel, prevented most off-island recreational navigators to know the exact location of the LPCNR and the existing fishing prohibition (Hernández-Delgado et al. Unpub. data). Management failures can also have profound effects on the success of a no-take MPA in achieving its goals and objectives (Coleman, et al. 2004). Those effects could be even more negative on the perception of the public. Furthermore, environmental degradation can magnify those effects. Therefore, there is a need to account for these variables through the development of a management plan that should involve local stakeholders, the academia, NGOs, etc.

Specific management recommendations include:

- Promote stronger coordination and collaboration among Federal, State, Municipal, academic, non-governmental agencies and community stakeholders;
- ii) Increase local public education and outreach;
- iii) Enforce existing LPCNR no fishing regulations and laws governing resource extraction;
- iv) Reduce the effects of fishing on the boundaries of the LPCNR;
- v) Build research and analytical capacity in the PRDNER;
- vi) Promote management-oriented research in the PRDNER;
- vii) Integrate a water quality monitoring component to existing coral reef epibenthic and fish communities monitoring programs;
- viii) Develop an ecosystem-based model for the design of a long-term ecological monitoring network;
- ix) Develop a management plan;
- x) Integrate stakeholders into a participatory management model;
- xi) Recognize and incorporate knowledge of the community;
- xii) Reduce or eliminate land-derived pollution from coastal development

- xiii) Enforce existing regulations and laws governing erosion and sedimentation controls; and
- xiv) Improve and maintain coastal water quality.

Management failures within and outside LPCNR need to be addressed and eliminated in order to keep community support, and to restore trust and compliance.

#### ACKNOWLDEGMENTS

This study was partly funded by the University of Puerto Rico(UPR) Sea Grant College Program, U.S. Coral Reef Initiative (NOAA/DNER), Caribbean Marine Research Center, Caribbean Fishery Management Council, and by UPR Institutional Funds for Research. Many thanks to the Culebra Island Fishers Association, Leonor Alicea, Joel Meléndez, Mary Ann Lucking (Coralations) and to many other volunteer assistants and collaborators.

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