AN ABSTRACT OF THE THESIS OF

Robert W. Lamb for the degree of Honors Baccalaureate of Science in Biology and Honors Baccalaureate of Arts in International Studies presented on August 25, 2008. Title: Marine Reserves in The Bahamas and Ecuador: A Scientific and Socioeconomic Perspective

Abstract approved: ____________________________________
Mark Hixon

Marine reserves are known to directly replenish overfished species. However, the community-wide effects of reserves are less clear. I examined the community of coral-reef fishes in a large, fully protected marine reserve in The Bahamas: the Exuma Cays Land and Sea Park. Visual-transect surveys provided estimates and comparisons of the density and size of all fishes on reefs located both inside and outside the reserve (n = 5 reefs each). Apex predators were larger and more abundant inside the reserve, resulting in much greater biomass there. Mid-trophic-level species had somewhat higher biomass outside of the reserve, where abundance of large predators was lower. Low-trophic-level species showed trends of higher biomass in the reserve. Although the community-wide effects of the reserve are complex, this general pattern is consistent with the existence of a trophic cascade through strong top-down effects of apex predators.

I also considered how subsistence-level fishing communities interact with protected marine life in a marine reserve in Ecuador: the Machalilla National Park. I examined the conflicting interests of park protection, fishing, and tourism. By analyzing these three categories, I summarized the needs and values of each group and how they interacted with each other and the environment.

Key Words: marine reserves, marine food webs, marine natural resource management

Corresponding email address: lambr@onid.orst.edu

Marine Reserves in The Bahamas and Ecuador: A Scientific and Socioeconomic Perspective

by

Robert W. Lamb

A THESIS

Submitted to

Oregon State University

University Honors College

In partial fulfillment of
the requirements for the
degrees of

Honors Baccalaureate of Science in Biology

Honors Baccalaureate of Arts in International Studies

Presented August 25, 2008
Commencement June 2009

Honors Baccalaureate of Science in Biology and Honors Baccalaureate of Arts in International Studies thesis of Robert W. Lamb presented on August 25, 2008

APPROVED:

Mark Hixon, Mentor, representing Zoology

Bruce Menge, Committee Member, representing Zoology

Darren Johnson, Committee Member, representing Zoology

Robert Mason, Chair, Biology Program

Joseph Hoff, Director, International Degree

Daniel Arp, Dean, University Honors College

I understand that my project will become part of the permanent collection of Oregon State University, University Honors College. My signature below authorizes release of my project to any reader upon request.

Robert W. Lamb, Author

Acknowledgements

I would like to thank Darren Johnson for the countless hours of effort through all of my moments of exasperation and elation, for his unending patience and diligence in helping me to comprehend statistical analyses and ecological concepts way beyond my education level, for taking me through the ropes of marine fieldwork in the Bahamas, and for doing all of it just because he was interested in helping me to succeed. I would like to thank my mentor, Mark Hixon, for taking an interest in my development as a marine ecologist starting when I came to his office freshman year looking for a job. Mark has helped me to become confident in my abilities as a scientist and has always provided the guidance and support I need. I would like to thank Bruce Menge for making time in his busy schedule to take an interest in my project and my development as a marine biologist: his input and teaching have been invaluable in developing high standards for my science ethics and writing. I would like to thank my family and friends for all their support, especially my mom, Janina, for instilling within me a love of nature and a passion for science, and my dad, Bob, for being an unceasing support in all of my endeavors. I would like to thank my fiancé Johana for being a constant reminder of the good in this world and for inspiring me to pursue my wildest dreams. Funding for this project has come from grants to R. Lamb from the Oregon State University URISC program, the Howard Hughes Medical Institute Undergraduate Fellowship, and the Gilman Congressional Scholarship Fund, as well as research grants to M. Hixon from the National Atmospheric and Oceanic Administration and the National Science Foundation.

This thesis is dedicated to the memory of my Grandpa, Carl Fuller

TABLE OF CONTENTS

LIST OF TABLE AND FIGURES

Table Page

Figure Page

Marine Reserves in The Bahamas and Ecuador: A Scientific and Socioeconomic Perspective

Chapter 1

Exuma Cays Land and Sea Park: impacts of a marine reserve on the community structure of coral reef fishes

Introduction

Trophic cascades are characterized by three or more trophic levels in a linear relationship of predator and prey marked by strong top-down controls (Paine, 1980). Trophic cascades may be revealed by removal of top-level predatory species and subsequent shifts in biomass dominance through descending levels of the food web (Power, 1990, Strauss, 1991), and have been observed in many different marine communities (Steneck, 1998, Daskalov, 2002, Graham et al., 2003, Frank et al. 2005). A top-down release from predation may lead to changes in the intensity of competition and predation at lower trophic levels, potentially restructuring communities and interactions therein (Carpenter et al. 1985, Carpenter and Kitchell, 1988). Most trophic cascades have been described in relatively simple systems with few trophic levels and low species diversity (Strong, 1992, Menge, 1995, see also Pinnegar et al., 2000 for review). Indeed, Strong (1992) suggests that the buffering effects of varied and differentiated consumptive relationships, as well as multiple prey refuges may prevent strong trophic cascades in more speciose systems. However, Pace et al. (1999) and Frank et al. (2005) highlighted distinct signatures of trophic cascades in moderately complex coastal food webs, leaving open the possibility for such a mechanism even in diverse, complex communities, such as assemblages of coral reef fishes.

As Pace et al. (1999) showed in their review, trophic cascades are becoming an indicative signature of human activities. Fishing effort is usually concentrated on species of the highest trophic levels (Jennings and Polunin, 1997, Steneck, 1998), though effort may be redirected down the food web as upper trophic level species decline in abundance (Pauly et al. 1998). In the Caribbean, the largest predators of the highest trophic levels are often those that are removed first (Jackson et al., 2001), such as the Nassau grouper *Epinephelus striatus* (Parrish, 1987), the most important species in Bahamian fisheries (Chiappone and Sealey, 2000). As these large piscivorous fish are removed, their prey populations may increase in abundance and size due to release from predation (Frank et al., 2005). Fishing intensity often does not decline with decreasing yields (Gordon, 1991), which only exacerbates this problem.

Marine reserves can provide spatial refuges from fishing for commercially important species, resulting in higher abundances and larger individuals inside the reserve compared to outside (Sluka et al., 1996, Friedlander and DeMartini, 2002, Halpern, 2003). This protection potentially has significant impacts on the structure of the local community, because the replenishment of populations of large, top-level target fishery species is known to affect the relative abundances of other species in coral reef fish communities (McClanahan and Nyawira, 1998). Marine reserves also provide a relatively pristine habitat less affected by the ‘shifting baseline syndrome’ found in fished areas (Pauly, 1995, Sheppard, 1995, Dayton et al., 2000), and thus provide a control with which to compare conditions in unprotected waters.

A large number of comparative studies inside vs. outside of marine reserves exist (Cote et al., 2001, Halpern, 2003), but most focus on single or small groups of commercially important species (e.g. Polunin and Roberts, 1993, Wantiez et. al, 1997, Chapman and Kramer, 1999), and few studies have encompassed entire fish communities. I examined the reef fish community as a whole on reefs inside and outside of a large, enforced marine reserve in The Bahamas, to see how species biomass changed in response to protection. The response of each species to the reserve may depend on the size of the species. For marine fishes, consumption of food types is limited by gape size, and because gape size scales directly with body size, body size is a large determinant of trophic level and ecological role. Body size can therefore be a direct proxy for trophic level. The relationship between species' responses to reserve protection and species' body size may reveal effects of fishing selectivity as well as the effects of trophic interactions among species, including trophic cascades. I hypothesized four general types of responses that could be observed (Fig. 1). First, species' responses may be independent of body size (Fig. 1, solid line) and species may be, on average more (or less) abundant within the reserve. This would indicate uniform fishing pressures upon all species rather than concentrated effort in higher trophic levels. It would also signify no indirect effect of the reserve on biomass distributions by trophic level. Second, average effects may be positive for species of all sizes, but larger species may be afforded greater protection within the reserve (Fig. 1, dashed line). Again, this pattern would indicate no indirect effect of the reserve on biomass distributions by trophic level. Third, large species may be more abundant and small species less abundant within the reserve (Fig. 1 dot-and-dashed line). This pattern would likely indicate a two-trophic level system where increased abundance of large fish within the reserve drives down the abundance of smaller fish (mainly by predation, but possibly due to competition). Finally, the relationship between species' size and effect of the reserve could alternate between positive and negative values indicating a true trophic cascade of three or more levels (Fig. 1, dotted line). On the far right of the graph, the largest species (and thus those of the highest trophic levels) would be positively affected by the marine reserve. The trendline may then change between positive and negative values of reserve effect depending on size, with the number of trophic levels indicated by the number of times that the line crosses zero (e.g., a three-level trophic cascade would cross the zero line twice to delineate a positive-negative-positive relationship between reserve effect and species' size; a four-level cascade would cross the zero line three times). Our data were collected and analyzed with these potential patterns in mind.

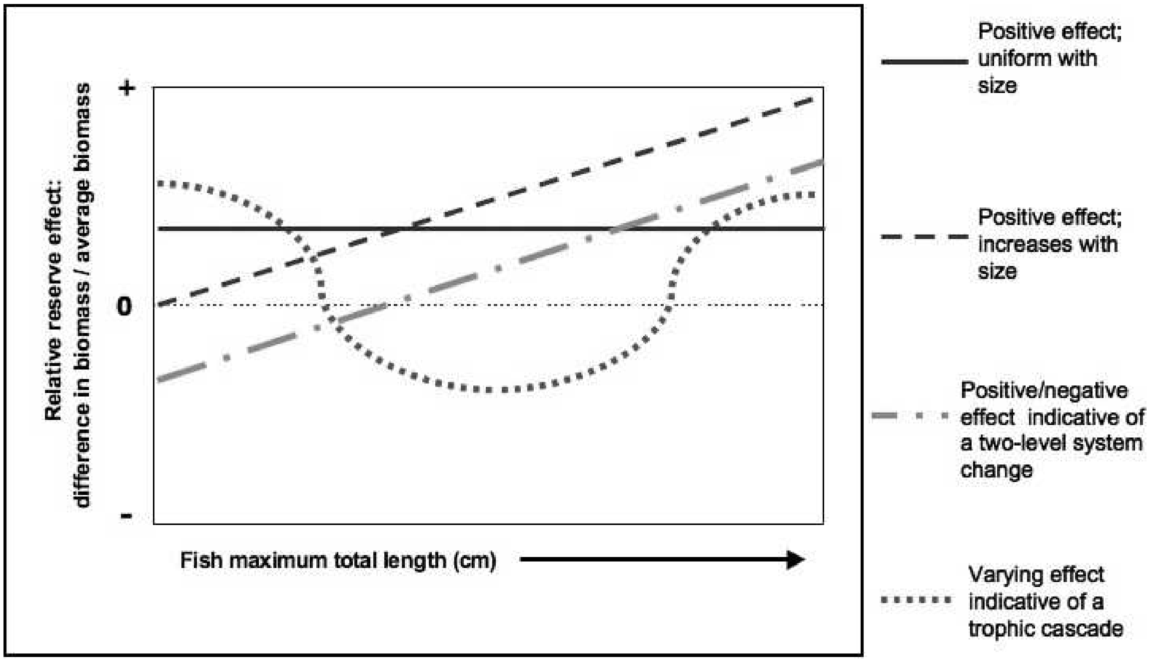

Fig. 1. Null models of the effects of fishing on the community structure of coral reef fishes.

Materials and Methods

Study Sites

The marine reserve studied was the Exuma Cays Land and Sea Park, established in 1958, and closed to all forms of fishing in 1986 (Chiappone and Sealey, 2000). Since then, no fishing or destructive activities have been allowed inside the park boundaries. The reserve encompasses an area of 442 km^2, and the no-take policy to protect marine life is effectively enforced by regular boat patrols within the reserve by park staff.

I surveyed fish communities on five reefs within the reserve and five reefs outside of the reserve. Within each treatment, three sites were located on the fore reef: deep, complex coral structures on the outward-facing reef slope. Two sites were located in back-reef areas: shallow-water habitats where small coral heads are interspersed with sandy habitat. Sites inside and out of the reserve were paired by habitat similarity to control for natural variation in fish communities occupying different habitats. Reef complexity and coral composition were measured to maximize habitat similarity. The five unprotected sites (three fore-reef and two back-reef) were centered around Lee Stocking Island, roughly 50 km to the south of the reserve.

Survey Methods

Fish communities were assessed using underwater visual census (UVC) methods. Six horizontal transects were performed at each of the five protected and five unprotected reefs (6 transects covered virtually all of the contiguous reef in most cases). Transects were 5 m wide by 25 m long and encompassed the entire water column from the seafloor to surface. Transects were haphazardly placed within the confines of the reef, and oriented so that the divers swam up current. Within each transect, a diver swam over the transect line identifying all fish within 2.5 m on either side. For each observation the diver identified the species and total length (TL) of the fish. Larger, more mobile species were identified on the first pass as the transect line was laid, then smaller, cryptic species on consecutive passes. Fish lengths were estimated in 1 cm intervals from 0-10 cm TL, and in 5 cm intervals >10 cm TL. Two divers highly trained in UVC methods performed all transects inside and outside of the reserve. Therefore, any observer bias would be equal across all transects, allowing for comparisons between sites. Measurements of substrate rugosity (estimated as vertical rise of substrate above the seafloor) and coral cover (scored on a 1-6 index scale) were taken every 5 m along each transect for habitat comparisons.

Effects of the Reserve on Species' Biomass

All fish lengths were converted to biomass using length-weight conversion equations for each individual species obtained at *www.fishbase.org*. The effect of the reserve on each species was calculated as the mean difference in biomass (g/transect) for each species between paired protected/unprotected fore reef sites, as well as for paired protected/unprotected back reef sites. To evaluate the strength of evidence for differences in biomass between reserve and non-reserve sites, these comparisons were evaluated with paired t-tests. Comparisons were deemed significant if the p-values of the t-test were <0.05.

To examine evidence for a community-wide trophic cascade, I examined whether the relative effect of the reserve varied systematically with species size. Body size was summarized by the maximum total length recorded for individual species. Maximum total length serves as a good proxy for trophic level in marine fish communities, because on the scale of communities, trophic level increases linearly with species size (Rice and Gislason, 1996, Jennings et al., 2002). For each species, the “relative reserve effect” was calculated as the average of the differences in biomass between reserve sites and their paired non-reserve site. The average difference was then divided by the average biomass for all sites in the study. Scaling the reserve effect to the overall biomass of each species allowed us to make meaningful comparisons among species of widely different body sizes. When relative reserve effect is positive, individuals are larger and/or more abundant inside the marine reserve than outside. When negative, individuals are larger and/or more abundant outside the marine reserve than inside. Scaling reserve effect to overall biomass places bounds on the values of relative reserve effect. The maximum effect would occur for a species seen only inside the marine reserve, yielding a scaled reserve effect value of +2, whereas the minimum effect would occur for a species only seen outside of the marine reserve, yielding a scaled reserve effect value of -2.

The relationship between relative reserve effect and species’ size was examined with a generalized additive model using R statistical computing software version 2.6.2 (R core development team 2007). Relative reserve effect was modeled as a smooth function of species’ size (framed by standard error lines) and cross-validation was used to determine the degrees of freedom for the optimal spline smoothing function. This approach provides a flexible way to find the best-fit description of general patterns in the relationship between species' size and relative reserve effect. The overall pattern of the relationship was interpreted in light of my hypothesized general patterns (see Fig. 1).

In a separate, but similar analysis, I compared reserve and non-reserve sites with respect to the relative biomass of fishes within several trophic categories. Each species was then assigned to one of five categories: piscivores (mainly consumes other fishes), mixed carnivores (consumes a combination of other fishes as well as marine invertebrates), omnivores (consumes a combination of algae, detritus, and marine animals), herbivores (only consumes algae), or planktivores (only consumes plankton from the water column), based on field observations and consumptive relationships based on gut contents summarized in *www.fishbase.org*. The average biomass per transect was then calculated for each trophic level and compared to the average total biomass per transect for sites outside and inside of the reserve. This comparison was designed to supplement the main analysis using body size as a proxy for trophic level.

Finally, habitat similarity was measured using the values of rugosity and coral cover obtained at points located at 5-m intervals along each transect. Rugosity was measured as the average height (cm) that the reef substrate rose above the seafloor. Coral cover was measured by an index that compared the relative amounts of hard coral vs. soft substrate (sandy bottom, seagrass, or coral rubble). The index ranged from 1 (if all five measurements in a transect were soft bottom) to 6 (if all five measurements in a transect were hard coral). Habitat similarity was analyzed on a protected/unprotected site-pair basis using paired two-sample t-tests for both rugosity and coral cover (each transect was treated as a replicate). Because significant differences were found between some sites for some habitat measures (see Results section) and because some of the fine-scale differences in habitat may have confounded the paired-site comparisons, I created site-specific equations for each species to adjust for the effects of difference of habitat on biomass. For each species, I used linear regression to estimate the relationship between biomass and rugosity score. Based on these relationships, an expected biomass value was generated for each species at each site. For further analysis, the biomass of each species at each site was expressed as residual biomass (i.e., the observed biomass – the expected biomass) to statistically account for the effects of slight differences in habitat measures on protected vs. unprotected comparisons of species' biomass. The main analyses were then repeated using residual biomass instead of observed biomass.

3. Results

Reserve Effect vs. Species' Maximum Length

The largest fish species (greater than ~70 cm TL) were virtually uniformly positively affected by the marine reserve. Most species of this size were only observed in transects inside of the protected sites (reserve effect ≈ +2). Mid-sized fishes (mid-level predators and omnivores), between 15 and 70 cm TL, were, on average, negatively affected by the marine reserve. Reserve effect for the smallest fishes (small planktivores and herbivores), species less than 15 cm TL, appeared to be increasing into positive values, although given the high variability in reserve effect among small fishes, the average effect is too small to be considered significant.

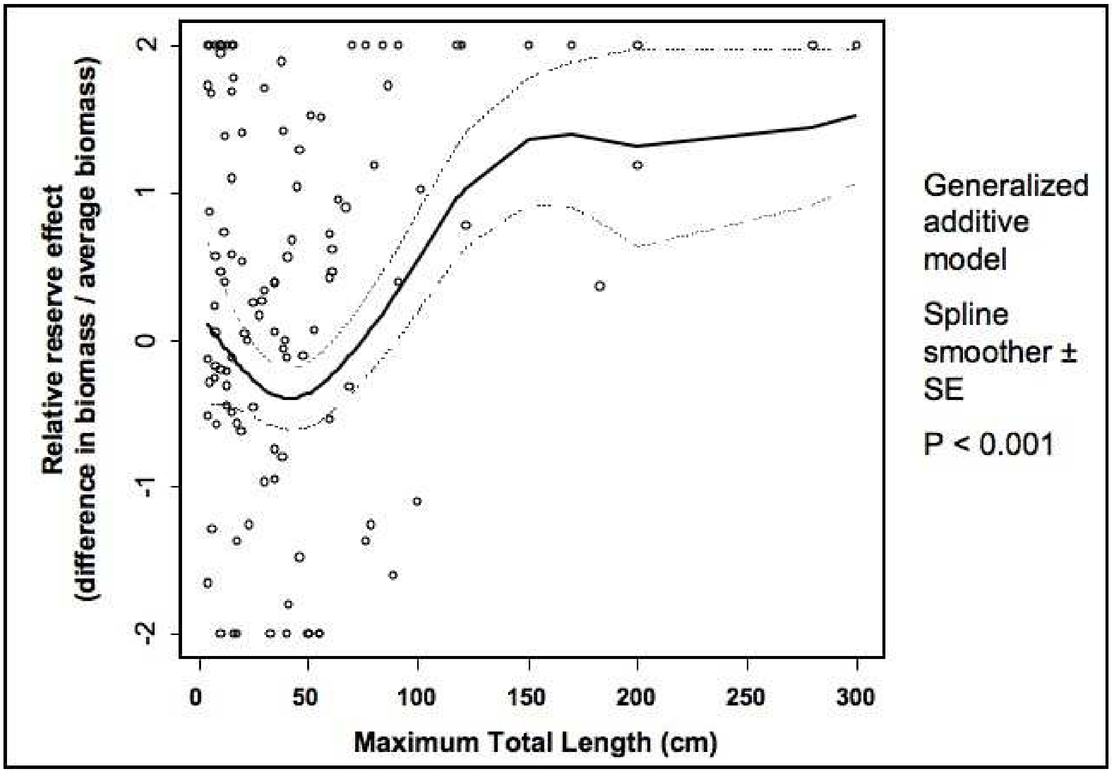

Fig. 2. Relative reserve effect vs. species size.

Reserve Effect by Species

When reserve effect was expressed on an absolute, rather than a relative scale (i.e., as the average difference in biomass per transect among protected and unprotected sites), the general pattern was similar to that observed for relative reserve effect. Species' responses to the reserve were variable, but in general, the largest fishes tended to be more abundant within the reserve, intermediate-sized species were less abundant, and the effect for the smallest species was variable, but tending toward an increase, on average (See Appendix A).

Biomass Distribution by Trophic Level

Piscivores ranged from 15 % of the total biomass in unprotected areas to 72 % of the total in protected areas (Fig. 3). All other categories (omnivores, herbivores, mixed carnivores, and planktivores; Fig. 3), decreased in proportion from unprotected to protected areas.

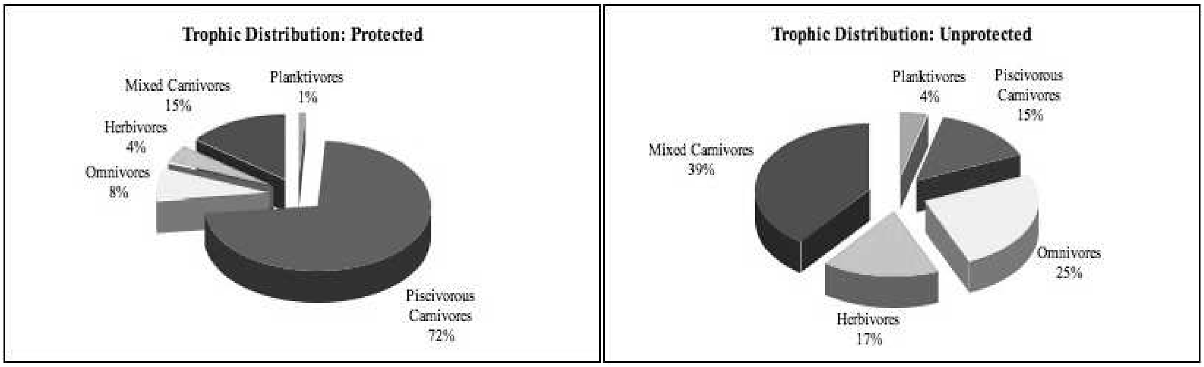

Fig. 3. Biomass distribution by trophic level for protected and unprotected sites.

Habitat comparisons

Average substrate rugosity (height in cm above the seafloor that the substrate rose) differed for some site pairings (1, 2, and 4; Table 1). The average difference in coral cover was not significant for any of the site pairings.

Site Pair	Reef Type	Mean Rugosity Difference (cm) ± Standard Error	Significant / not significant	Mean Coral Cover Difference ± Standard Error	Significant / not significant
1	Back Reef	30.8 ± 9.21	Significant	1.25 ± 1.31	Not significant
2	Back Reef	41.6 ± 19.2	Significant	1.31 ± 0.99	Not Significant
3	Fore Reef	23.7 ± 31.6	Not Significant	0.70 ± 1.46	Not Significant
4	Fore Reef	67 ± 20.2	Significant	0.19 ± 1.35	Not Significant
5	Fore Reef	26 ± 15.9	Not Significant	1.71 ± 1.09	Not Significant

Table 1. Habitat comparisons for site pairs based on rugosity and coral cover.

Because significant differences were found between some sites for some habitat measures, the main analyses were repeated after statistically accounting for slight differences in habitat features (i.e., by examining the residual biomass after accounting for effects of rugosity). However, repeating the analyses using residual biomass produced no qualitative differences in the results (data not shown). For ease of interpretation, I therefore presented analyses based on observed biomass data, rather than statistically adjusted data. Reserve effect was also compared between back reef and fore reef site pairings (see Appendix A), and differed in only four of the 114 species observed, suggesting no overall difference in the effect of reserves in fore reef and back reef habitats.

Discussion

Although a large amount of natural variation existed in reserve effect relative to species size (Fig. 2), the general pattern that emerged from the generalized additive model was partially consistent with the hypothesis of a trophic cascade. Under this hypothesis, large predators such as sharks, large grouper, barracuda, and large jacks inside the marine reserve were likely consuming small snapper, grouper, jacks, and grunts, decreasing their abundances. The lowered biomass of mid-sized species should reduce predation on their prey (species such as damselfish and butterflyfish) resulting in an increase in relative biomass of these smaller species. The lack of significant differences in reserve effect between fore reef and back reef sites (Appendix A) suggested that these changes were similar in habitats with different physical characteristics and varying intensities of fishing.

With the exception of *Sparisoma viridae* (stoplight parrotfish), all species of the largest size class were piscivores. These species are at the highest trophic levels of the Bahamian reef food web. The values of the absolute reserve effect was many orders of magnitude larger for this group than the other two size classes, which reflects the deliberate targeting of fishing towards these species. The average medium-sized fish species was negatively affected by the marine reserve, though there was more variation seen in this size class. The large variability in reserve effect observed in this size group is undoubtedly due in part to natural forces outside the scope of this study. However, by controlling for habitat similarity and recognizing the tendency of fishing to concentrate on larger-bodied species, we can infer that the average trend towards negative values of reserve effect in this size group was at least in part due to the indirect effects of fishing.

Greater abundances of large predatory species can also have non-lethal negative effects on smaller predatory fishes, such as the inhibitory effects of large groupers on small grouper shown by Stallings (2008), which could contribute to such changes in size and abundance in mid-trophic level species. In the smallest size class of fish species, the trend of the average reserve effect was moving into positive values, though the magnitude of the average effect was small relative to the variability in reserve effect, making it somewhat difficult to interpret this trend (Fig. 2). This result could indicate a diffusion of the effects of the trophic cascade in the lower levels of the food web. This pattern would be expected because of the wider species/biomass base and more varied ecological interactions that exist at lower trophic levels (Cohen et al., 2003).

The exception to the general pattern of high positive reserve effect correlating with large, piscivorous predatory species is the stoplight parrotfish *S. viridae*, an herbivore. As shown by Mumby et al. (2006), *S. viridae* populations in the ECLSP are more abundant than in surrounding waters because of increased fishing on this parrotfish outside the reserve. Further, this higher abundance occurred despite higher abundances of potential predators (e.g. *E. striatus*) inside the park.

In the middle and small size class groups of species, the differences in reserve effect were of a much lower magnitude than in the large size class. In a simple trophic cascade characterized by a single predatory species within a balanced, three-level, three species system, the absolute amount of biomass change should be amplified down through the other two levels following removal of the predator (Strong, 1992). However, this particular case is one of slow reestablishment of many top predatory species into an already altered system. Additionally, all fish species in the community were included, generating a different pattern of change than what would be expected from a trophic cascade of only three or four species.

By assigning species to individual trophic levels it becomes apparent that major shifts in the concentrations of biomass throughout the food web have occurred between unprotected and protected areas, such as the increase from 15% to 72% of the biomass concentrated in piscivores (Fig. 3). This result indicates that perhaps a relatively healthy, unfished reef like those found within the ECLSP would normally have about 70 % of the biomass concentrated in top-level predatory species. This pattern suggests that many supposedly undamaged reefs teeming with schools of small fish may actually be in an altered ecosystem state, whereas natural levels of high predation in truly pristine habitats keep prey fish populations low and hiding in the coral structure. The major reductions in biomass concentration in the trophic levels of mixed carnivores and herbivores indicate that the strongest effects of the increase in predation occurred at these levels of the food web. Jennings and Polunin (1997) surveyed a Fijian reef fish community and found that although the biomass of the largest piscivorous predators was inversely correlated with fishing intensity, this difference had no effect on non-target prey species. However, due to census limitations, this study did not encompass all reef fish species, only those of a few families. As in the study from Fiji, our assessment of biomass distribution by trophic level assigned species to rigid food web hierarchies rather than using fish size as an indicator of trophic level. However, this method does not incorporate the mixed diets of many reef fishes, or ontogenetic diet shifts undertaken by individual species, and so length was used as a proxy for trophic level for all other analyses.

The salient pattern from our study is one of significant alteration of the distribution of biomass at the top and intermediate sizes in the reef fish food web inside the marine reserve vs. outside. Our interpretation is that selective fishing focusing on large-bodied species of the highest trophic levels outside of the reserve is the direct cause of these changes, and that as a consequence, a trophic cascade is visible throughout the fish community. Further studies might incorporate actual fisheries data of the two areas in order to give more robustness to the inference of fishing on a selective basis as a source of these changes.

Chapter 2

Machalilla National Park: a case study for the interactions between people and marine reserves

Introduction

The Machalilla National Park lies on the central coast of Ecuador in the province of Manabi. Established in 1979, it is a fully protected land and sea reserve, with an area of 1,280 km^2 (Rieger, 2007). Aside from the world-famous Galapagos Islands, Machalilla is the only marine reserve in Ecuador. The marine section of the reserve covers a series of beaches that are sensitive to high tourism levels, as well as two major offshore islands: Isla de la Plata and Salango. The terrestrial portion of the park is comprised mostly of dry tropical forest, one of the most critically imperiled ecosystems on Earth (Janzen, 1988). While the dry tropical forest of the reserve faces large-scale logging and development as in other parts of the world, the marine portion has historically felt fewer threats to conservation. However, a growing market for fish and a booming tourism industry have led to an intricate conflict of interests in the Machalilla marine reserve, played out in the coastal town of Puerto Lopez.

Puerto Lopez lies in the province of Manabí on the Ruta del Sol scenic highway, which passes through some of Ecuador's most beautiful and popular coastline. With approximately 8,000 inhabitants, Puerto Lopez houses the headquarters of the Machalilla National Park (MNP). The economy of Puerto Lopez is founded on two major industries:

fishing and tourism. These businesses are the focal point of a conflict of interests that exemplifies the dissonance surrounding marine reserves in the area.

Several interested parties are all trying to stake their claims to the natural marine resources abounding in this park. Backed by various environmental groups from Ecuador and elsewhere, the park warden and rangers work for the continued prosperity of the local ecosystem and the preservation of marine life. The town's tour operators and the tourists they serve are also interested in the conservation of the region, but only as long as that conservation does not interfere with their daily operations. The local fishermen are, for the most part, fishing on a subsistence level: they catch enough to feed themselves and their families, and they sell whatever is left to local restaurants or to merchants who take the fish elsewhere (Pollnac and Poggie, 1991). Larger, more expensive catches are exported to other cities in Ecuador, as well as Asia and North America. While certainly open to and interested in the long-term sustainability of their fisheries, these men are much more concerned with their daily catches and the prices of gasoline and fishing gear. In essence, everyone wants their own piece of the pie, but few are willing or able to negotiate the issues of conservation and exploitation in order to preserve the fragile economy and the even more fragile ecosystem.

My first introduction to the MNP was through my internship supervisor, Andres Baquero. Andres is an Ecuadorian scientist who studied in the mountain capital of Quito before getting his master's degree in California. He had done fieldwork for several years in Puerto Lopez as director of *Equilibrio Azul*, the Ecuadorian NGO that employed me. I worked with Andres and *Equilibrio Azul* from the beginning of February to the end of April of 2006. Although foreigners have to pay 20 dollars for a five-day visitor's pass, I was given complete access to all park grounds in order to do my research. I was also informed that the previous park warden had been removed from office for stealing funds designated for infrastructure development, but the new director was keeping him on staff. Bureaucratic corruption in Ecuador is a common occurrence, as in many other third-world countries, and its effects must be taken into account when assessing the efficacy of park protection.

Over the next week, Andres introduced me to the duties I was to fulfill for the organization. It was immediately obvious that I would be on my own most of the time, so two things were of great importance: one, that I know my jobs inside and out since no one would be around to direct me, and two, that I establish a good rapport with the fishermen with whom I would be coming into contact each day. This second point was especially important for my main task: monitoring the illegal shark fishery out of Puerto Lopez. I learned very quickly that for an Ecuadorian fisherman to trust a nosy *gringo* with his illegal catch, a good deal of trust was required.

The Fishermen

In 2004, then-president Lucio Gutierrez, under pressure from international conservation organizations such as Sea Shepherd, signed a decree that banned all shark fishing in Ecuador (Lewis, 2005). By 2006, in response to pressures from the fishing community and in recognition of the inability to sufficiently enforce the law, the fishery was reopened with a legal limit set in hopes of at least regulating this activity. My exposure to this lack of enforcement commenced the very first morning.

By 6:30 a.m. every day, the main beach at Puerto Lopez is filled with local buyers and fish merchants with flatbed trucks ready to take their catches to far-off towns. Vendors offer a rice and milk drink called *morocho*, along with warm fresh-baked bread and coconut milk amidst fish cleaners who scale, gut, and filet while the ever-present frigate birds and pelicans look for stray morsels. The first fishing boats come in slowly, one by one, but after an hour or so, beach access is in short supply as each captain does his best to sell his catch to the merchants before someone else does. Men walk back and forth in the surf hauling huge plastic crates full of fish on their shoulders to unload the boats. They have to carry a length of bamboo in their free hand to bat away the mischievous frigates trying to steal a small fish or two.

The types of gear used by the subsistence fishermen in Puerto Lopez include long-lines, drift-nets hook and line, and small purse seines (Pollnac and Poggie, 1991). The daily haul is mostly made up of small groundfish species (e.g. Pleuronectids, Sciaenids, and Gadids), complemented by pelagic species such as mahi-mahi (*Coryphaena hippurus*) and black marlin (*Makaira indica*). Occasionally though, the unmistakable shape of a sharply angled tail or the classic, jutting dorsal fin that has come to strike fear into moviegoers everywhere juts over the lip of a crate: a shark. At this point the trust factor came into play. Although marine law enforcement is scarce in this part of the world, the local coast guard captain did occasionally stroll through the fish market, admonishing rule breakers and sometimes even doling out fines or confiscating catches. Thus the fishermen had become distrustful about prying eyes investigating landed sharks, and did their best to keep it all under the table. Only by communicating with these men that I was merely a student of biology researching fishing methods and by getting to know the fishermen personally was I brought into their confidence.

The species of sharks most often caught were thresher (*Alopius vulpinus*) and bigeye thresher (*A. superciliosus*) sharks, and scalloped hammerhead sharks (*Sphyrna lewini*). Upon spotting one of these, I talked with the fisherman or the merchant who had bought it about where it was caught and with what sort of gear. I was almost always told that the sharks were landed as bycatch (unintentional catch of non-target species). These claims could have been a result of President Guitierrez's 2005 decree that retaining sharks was legal as long as they were caught as bycatch, a move heralded by international conservationists as effectively annulling the 2004 ruling that banned shark fishing entirely (Lewis, 2005). Motivations were called into doubt, however, when a boat pulled into port with nothing but five three-meter long sharks onboard. The sharks were brought to another area of the beach where large cleaning stations had been set up. There I was allowed to look more closely at the specimen to tell the species, take body measurements, and determine the sex. The measurements I made provided data for Andres' report to the Ecuadorian government on illicit fishing activities, but I was more interested in what drove these killings. As I began to interact more closely with the fishermen, I learned that, surprisingly, shark meat is generally not a very high quality food product. Due to an excretory system that deposits high concentrations of urea in the tissues (Randall et al., 2002), the flesh has a distinct bitter taste, only removable by a long soak in fresh water. The real source of income provided by the shark fisheries in Ecuador is the shark fin export market to Asia where a bowl of shark fin soup, a sign of status and supposedly an aphrodisiac, can go for as much as 200 dollars (Raloff, 2002).

The vast majority of the Puerto Lopez fishing fleet is made up of *lanchas*, wooden or fiberglass boats about 15 feet long, with shallow drafts and no cabin. Usually occupied by three to five men, these small boats stay at sea for two to four days at a time, during which the fishermen have little protection against the sun, rain, or waves. Several fishing ports, including Puerto Lopez, are within the confines of the MNP, the boundaries of which encompass roughly 40% of Ecuador’s coastal subsistence fisheries (Rieger, 2007). As such, their inhabitants are given special permission to fish within the waters near town and offshore, but fishing is strictly prohibited in other areas of the mainland or around either of the two offshore islands. A 60 year-old fisherman named Pedro, related to me how this was becoming an ever-increasing problem. Pedro told me that just 15 years ago, the entire Puerto Lopez fishing fleet was able to sustain itself by fishing within the small, enclosed bay where the *lanchas* are now moored. But nowadays a boat has to travel 10 or15 miles offshore, risking high waves and burning costly gasoline. “Either that,” he followed, “or just fish along the shore inside the reserve, or on the steep seawalls surrounding one of the offshore islands.” I asked him if he knew that that was illegal, and he responded with a tired smile: “Yes, but we have to go where the fish are, and regardless, no one comes out there to stop us.”

My duties with *Equilibrio Azul* brought me to Isla de la Plata, the larger of the two offshore islands, commonly referred to as the “Poor-Man’s Galapagos.” About 10 miles from Puerto Lopez, Isla de la Plata houses much of the same dry brush habitat seen in the Galapagos, and provides nesting sites for seabirds such as frigate birds (*Fregata minor),* blue (*Sula nebouxii)* and red-footed (*S. sula)* boobies, and waved albatross (*Phoebastria irrorata)* (Cisneros-Heredia, 2005). Andres and I traveled there periodically to place mooring buoys, check underwater temperature gauges, and conduct underwater community surveys using SCUBA. We often saw fishermen covered in linens to ward of the sun's rays in *lanchas* casting their lines about 50 feet away from the island. Andres once shouted over to them, alerting them to the illegality of their activities, and they nodded and waved politely before continuing to fish. As we suited up for the dive, Andres grumbled something about cutting their anchor line, but it was frivolous talk as we both knew he would never do such a thing. His frustration mirrored one of the basic roots of the problem facing marine reserve management in developing countries the world over: how to convince a local resident to forego harvesting natural resources now in hopes of preserving them for the future when ceasing to fish now could signify not having food for tonight's dinner. Why would one boat captain decide to obey the laws and stay away from a protected area when he knows that three other boats will quickly take his place? Until small fishing communities like Puerto Lopez decide that their marine resources need to be preserved and are able to work together to provide support to the fishermen, conservation in these areas might be merely a high-minded ideal.

The Park

Although the MNP was started in 1979, its protection was severely limited until the intervention of the Parks in Peril program, an offshoot of the Nature Conservancy and USAID (Rieger, 2007). With the help of Parks in Peril, a visitor's center was established, programs were put in place for regulation of tourism and extraction, more staff was hired, and greater dialogue was initiated between the park authorities and the national government. However, today little funding is provided for park maintenance and control, or for assessing the quality of the marine habitat and the impacts of the local fishing fleet upon it. Most quantitative studies on the area are performed by freelance conservation groups such as *Equilibrio Azul* without governmental support. Fishermen's cooperatives, while used frequently in small-scale fishing communities such as Puerto Lopez, have a high rate of failure (Pollnac, 1985), and have not found success here. Thus, the only permanent protection for the marine ecosystem comes from what the park can provide.

Aside from the relatively meager enforcement of catch laws in the fishing port, the MNP staff have at their disposal a large boat for patrolling park waters. However, gasoline is usually in short supply, and the boat is frequently chartered for use by tourists. Rotating park rangers with a *lancha* are also permanently stationed at the visitor's center on Isla de la Plata. These rangers receive tourist groups and discourage fishing along the outskirts of the island. However, as Andres and I observed, their presence seems to do little to dissuade poaching in reserve waters. Because even very short periods of intense fishing can completely reverse the benefits gained from long-term conservation, this inconsistent pattern of park supervision might not be sufficient for maintaining the integrity of the marine ecosystem.

The Tourism Industry

Over the past few decades, many Puerto Lopez inhabitants have made the transition from the faltering fisheries to jobs in the booming tourism industry. This trend of exchanging extractive activities for ecotourism dollars is growing in coastal communities throughout the world, and can be quite lucrative (Hill, 2005). Indeed, the revenue and jobs provided by the tourism industry in a given area can be greater than that provided by all available fisheries. In the MNP, the draw for marine-oriented tourists is usually comprised of seasonal whale watching tours or the allure of tropical beaches. There are also a few small sport-fishing and SCUBA diving outfits in the area. These activities can provide major economic gains for the local people, strengthen conservation awareness and national identity, and provide meaningful customer satisfaction (Cubero et al., 2006).

With the added influx of people and money into the MNP comes the responsibility to monitor and regulate the impacts that the tourism industry has on the marine ecosystem. For instance, by trampling nests or collecting eggs, the large numbers of visitors to local beaches can be detrimental to the nesting habits of sea turtles (Jacobsen and Lopez, 1994) that lay their eggs in the area between December and March. Part of my duties with *Equilibrio Azul* was to monitor three different beaches within the MNP for turtle nests. One of these beaches, called La Playita, had 23 confirmed nests in only half a kilometer of coastline. La Playita is also a very popular beach for Ecuadorian visitors. This is especially true in February, during the four-day holiday of Carnaval, when a mass exodus of people descends from the highland cities in the Andes to the coast. Following my report on the unusually high concentration of nesting sites, the MNP closed the beach to all tourists for the holiday. This provides a heartening example of a concerted effort by an NGO and the park service to research the needs of the local habitat and to prioritize conservation.

The impacts of tourists in Puerto Lopez are not felt only by the surrounding natural environment. The constant stream of foreigners and the money they bring can significantly impact the local culture and way of life in rural towns (Huang and Stewart, 1996). Just south of Puerto Lopez lies the town of Montañita. Originally a similar fishing port, Montañita has transformed over the past few decades into a surfing mecca. The town is now populated by more foreigners than Ecuadorians during the busy season, and few remnants exist of the original fishing culture and traditions. The open-seas fishermen of Manabí as a group are very independent and fiercely defensive of their livelihoods. This comes as a result of the competitive nature of their profession and a dedication to the fishing culture and way of life (Pollnac and Poggie, 1991). The growth of tourism provides much needed revenues in the area, but can also undermine the integrity of fishing culture. Whether this change is considered positive or negative, it is a considerable adjustment for old-timers like Pedro.

Conclusion

The role of marine reserves in small coastal communities like Puerto Lopez is not always clear. Whether implemented as fishery management tools, for tourism or for wildlife conservation, they are a response to the need for preservation of an entire habitat. This goal implies that either the habitat is already in danger or that it is one of few remaining pristine areas of its kind and as such must be protected. In the case of the Machalilla National Park, the marine habitat is being protected with the hopes of preserving the national heritage while ensuring the economic prosperity of the region through both tourism and fishing. Unfortunately, these goals do not always point clearly in the same direction, leading to conflicts among the various interested parties.

Regardless of the impetus for the establishment of a marine reserve, such an effort shows recognition for the need to preserve the integrity of marine habitats. Habitat protection is a common goal for all groups involved, but it can only be achieved through cooperation, dialogue, and compromise. High priority must also be given to the integrity of the local culture and economy. With greater cooperation between the fishing and scientific communities, a broader wealth of knowledge about the oceans and the life within them can be obtained for more effective management solutions. When the government follows the recommendations made by such a collaborative effort and the parties involved align on a structure for regulatory enforcement, conservation endeavors like the Machalilla National Park can be shining examples of preserving the environment for generations to come.

Bibliography

Carpenter. S.R., Kitchell, J.F., Hodgson, J., R., 1985. Cascading trophic interactions and lake productivity. Bioscience. 35, 634-639.

Carpenter, S.R., Kitchell, J.F., 1988. Consumer control of lake productivity. Bioscience. 38, 764-769.

Chapman, M.R., Kramer, D.L., 1999. Gradients in coral reef fish density and size across the Barbados Marine Reserve boundary: effects of reserve protection and habitat characteristics. Mar. Ecol. Prog. Ser. 181, 81-96.

Chiappone, M., Sealey, K.M., 2000. Marine reserve design criteria and measures of success: lessons learned from the Exuma Cays Land and Sea Park, Bahamas. Bull. Mar. Sci. 66, 691-705.

Cisneros-Heredia, D.F., 2005. La avifauna de la Isla de la Plata, Parque Nacional Machalilla, Ecuador, con notas sobre nuevos registros. Cotinga. 24, 22-27.

Cohen, J.E., Jonsson, T., Carpenter, S.R., 2003. Ecological community description using the food web, species abundance, and body size. Proc. Nat. Acad. Sci. 100, 1781-1786.

Cubero, P., Banks, S., Zambrano, H., Herron, P., Chasqui, L., Martinez, C., Reck, G., 2006. Criteria to determine carrying capacity and LACs for ecotourism in the four MPAs under study, including a revision of experiences with ecotourism outside the Eastern Tropical Pacific. Kiel, Germany: INCOFISH.

Daskalov, G.M., 2002. Overfishing drives a trophic cascaded in the Black Sea. Mar. Ecol. Prog. Ser. 225, 53-63

Dayton, P.K., Sala, E., Tegner, M.J., Thrush, S., 2000. Marine reserves: parks, baselines, and fishery enhancement. Bull. Mar. Sci. 66, 617-634.

Frank, K.T., Petrie, B., Choi, J.S., Leggett, W.C., 2005. Trophic cascades in a formerly cod-dominated ecosystem. Science. 308**,** 1621-1623.

Friedlander A.M., DeMartini, E.E., 2002. Contrasts in density, size, and biomass of reef fishes between the northwestern and the main Hawaiian islands: the effects of fishing down apex predators. Mar. Ecol. Prog. Ser. 230, 253-264.

Gordon, H.S., 1991. The economic theory of a common-property resource: the fishery. Bull of Math. Biol. 53, 231-252.

Graham, N.A.J., Evans, R.D., Russ, G.R., 2003. The effects of marine reserve protection on the trophic relationships of reef fishes on the Great Barrier Reef. Env. Conserv. 30, 200-208.

Halpern, B., 2003. The impact of marine reserves; do reserves work and does reserve size matter? Ecol. Appl. 13, 117-137.

Hill, N.A.O., 2005. Livelihoods in an artisanal fishing community and the effect of ecotourism. Master's dissertation, Imperial College of London.

Huang, Y.H., Stewart, W.P., 1996. Rural tourism development: shifting basis of community solidarity. Journal of Travel Research. 34, 26-31.

Jackson, B.C., Kirby M.X., Berger, W.H., Bjorndal, K.A., Botsford, L.W., Bourque, B.J., Bradbury, R.H., Cooke, R., Erlandson, J., Estes, J.A., Hughes, T.P., Kidwell, S., Lange, C.B., Lenihan, H.S., Pandolfi, J.M., Peterson, C.H., Steneck, R.S., Tegner, M.J., Warner, R.R., 2001. Historical overfishing and the recent collapse of coastal ecosystems. Science. 293, 629-638.

Jacobsen, S. K., Lopez, A.F., 1994. Biological impacts of ecotourism: tourists and nesting turtles in Tortuguero National Park, Costa Rica. Wildlife Society Bulletin. 22, 414-419.

Janzen, D.H., 1988. Tropical dry forests: the most endangered major tropical ecosystem, in Wilson, E.O., Peter, F.M. (eds). Biodiversity. Washington, D.C., National Academies Press, pp. 130-137.

Jennings, S., Polunin, N.V.C., 1997. Impacts of predator depletion by fishing on the biomass and diversity of non-target reef fish communities. Coral Reefs. 16, 71-82.

Jennings, S., Pinnegar, J.K., Polunin, N.V.C., Boon, T.W., 2002. Weak cross-species relationships between body size and trophic level belie powerful size-based trophic structuring in fish. J. Anim. Ecol. 70, 934-944

Lewis, S., 2005. Shark finning banned in Eastern Pacific ocean. Environment News Service. http://www.ens-newswire.com/ens/jun2005/2005-06-29-03.asp

McClanahan, T.R., Nyawira, A.M., 1998. Changes in Kenyan coral reef community structure and function due to exploitation. Hydrobiologia. 166, 269-276.

Menge, B.A., 1995. Indirect effects in marine rocky intertidal interaction webs: patterns and importance. Ecol. Mon. 65, 21-74.

Mumby, P.J., Dahlgren, C.P., Harborne, A.R., Kappel, C.V., Micheli, F., Brumbaugh, D.R., Holmes, K.E., Mendes, J.M., Broad, K., Sanchirico, J.N., Buch, K., Box, S., Stoffle, R.W., Gill, A.B., 2006. Fishing, trophic cascades, and the process of grazing on coral reefs. Science. 311, 98-101.

Pace, M.L., Cole, J.J., Carpenter, S.S., Kitchell, J.F., 1999. Trophic cascades revealed in diverse ecosystems. T. Ecol. Evol. 14**,** 483-488.

Paine, R.T., 1980. Food webs: linkages, interaction strength, and community infrastructure. J. Anim. Ecol. 49, 667-685.

Parrish, J.D., 1987. The trophic biology of snappers and groupers, in Polovina, J.J, Ralston, S. (eds). Tropical snappers and groupers: biology and fisheries management. Boulder, Westview Press Inc, pp. 405-463.

Pauly, D., 1995. Anecdotes and the shifting baseline syndrome of fisheries. Trends Ecol. Evol. 10, 430.

Pauly, D., Chirstensen, V., Dalsgaard, J., Froese, R., Torres, F., 1998. Fishing down marine food webs. Science. 279, 860-863.

Pinnegar, J.K., Polunin, N.V.C., Francour, P, Badalamente, F., Chemello, R., Harmelin-Vivien, M.-L., Hereu, B., Milazzo, M., Zabala, M., D-anna, G., Pipitone, C., 2000. Trophic cascades in benthic marine ecosystems: lessons for fisheries and protected area management. Env. Conserv. 27, 179-200.

Pollnac, R. B., 1985. Social and cultural characteristics in small-scale fishery development. in: Putting people first: sociological variables in rural development. Cernea, M.M. ed. pp. 189-223. New York: Oxford University Press.

Pollnac, R.B., Poggie, J., 1991. Psychocultural adaptation and development policy for small-scale fishermen’s cooperatives in Ecuador. Human organization. 50: 43-49.

Polunin, N.V.C., Roberts, C.M., 1993. Greater biomass and value of target coral-reef fishes in two small Caribbean marine reserves. Mar Ecol. Prog. Ser. 100, 167-176.

Power, M.E. 1990. Effects of fish in river food webs. Science. 250, 811-814.

Rakitin, A., Kramer, D.L., 1996. Effect of a marine reserve on the distribution of coral reef fishes in Barbados. Mar. Ecol. Prog. Ser. 131, 97-113.

Raloff, J., 2002. Clipping the fin trade. Science News. 162, 232-234.

Randall, D., Burggren, W., French, K., 2002. Animal physiology: mechanisms and adaptations. New York, W.H. Freeman and Company, p. 614.

Rice, J., and Gislason, H., 1996. Patterns of change in the size spectra of numbers and diversity of the North Sea fish assemblage, as reflected in surveys and models. ICES J. Mar. Sci. 53, 1214-1225.

Rieger, J., 2007. Parks in peril: Machalilla National Park. Arlington, Nature Conservancy. http://www.parksinperil.org/wherewework/southamerica/ecuador/ protectedarea/machalilla.html

Sluka, R., Chiappone, M., Sullivan, K.M., Wright, R., 1997. The benefits of a marine fishery reserve for Nassau Grouper *Epinephelus striatus* in the central Bahamas. Proc. 8th Coral Reef Sym. 2, 1961-1964.

Sheppard, C., 1995. The shifting baseline syndrome. Mar. Poll. Bull. 30, 766-767.

Stallings, C.D., 2008. Indirect effects of an exploited predator on recruitment of coral-reef fishes. Ecology. 89, 2090-2095

Steneck, R.S., 1998. Human influences on coastal ecosystems: does overfishing create trophic cascades? T. Ecol. Evol. 13, 429-430.

Strauss, S.Y., 1991. Indirect effects in community ecology: their definition, study, and importance. Trends Ecol. Evol. 6, 206-210.

Strong, D.R., 1992. Are trophic cascades all wet? Differentiation and donor-control in speciose ecosystems. Ecology. 73, 747-754.

Wantiez, L., Thollot, P., Kulbicki, M., 1997. Effects of marine reserves on coral reef fish communities from five islands in New Caledonia. Coral Reefs. 16, 215-224.

Appendices

Appendix A.

Scientific Name	Max Length (cm)	Mean Reserve Effect (g/transect)	Standard Deviation	Difference in Reserve Effect: Fore vs. Back Reef
Carcharinus perezii	300	36884.90667	9466.802774	not significant
Ginglymostoma cirratum	280	3028.242465	1236.27481	not significant
Gymnothorax moringa	200	1.155284459	0.471642905	not significant
Sphyraena barracuda	200	1285.68825	802.9271364	not significant
Scomberomorus regalis	183	11.55845077	26.25820174	not significant
Dasyatis centroura	170	3365.75	1374.061684	not significant
Mycteroperca bonaci	150	2057.19512	561.5236997	not significant
Epinephelus striatus	122	270.4324937	213.2218673	not significant
Scarus coeruleus	120	56.18840935	14.50778491	not significant
Caranx latus	118	1801.08784	291.1516215	not significant
Mycteroperca tigris	101	131.8560575	75.59866097	not significant
Aulostomus maculatus	100	-26.74105811	9.861888832	not significant
Chaetodipterus faber	91	14.81883904	6.049765703	not significant
Diodon hystrix	91	39.34273058	63.66756611	not significant
Lutjanus griseus	89	-460.245972	110.1041083	significant
Ocyurus chrysurus	86.3	537.2606712	104.110122	significant
Mycteroperca interstitialis	84	60.70833333	15.82910387	not significant
Kyphosus sectator	80	1669.783655	1094.063647	not significant
Haemulon album	79	-121.0931711	67.71728157	not significant
Epinephelus guttatus	76	-35.13222029	16.69694113	not significant
Urolophus jamaicensis	76	22.41568641	6.019235954	not significant
Malacanthus plumieri	70	7.663403547	2.489835294	not significant
Caranx ruber	69	-61.0144992	110.409552	not significant
Lutjanus apodus	67.2	584.9822386	303.3238965	not significant
Sparisoma viride	64	597.7094354	281.3662131	significant
Holocentrus adscensionis	61	115.8884106	75.22486733	not significant
Scarus vetula	61	84.76761273	65.2446844	not significant
Balistes Vetula	60	32.9999445	34.71035465	not significant
Lutjanus synagris	60	-91.85292668	126.2497249	not significant
Pomocanthus arcuatus	60	69.52584429	66.13087378	not significant
Calamus calamus	56	605.3046583	302.1975105	not significant
Hemiramphus brasiliensis	55	-82.1340807	33.53109803	not significant
Lactophrys trigonus	55	-21.8500737	8.920255233	not significant
Haemulon plumierii	53	23.90405217	176.6285975	not significant
Halichoeres radiatus	51	6.482330531	3.034399483	not significant
Heteropriacanthus cruentatus	50.7	-14.95544625	3.869633789	not significant
diodon holocanthus	50	-8.7965	3.591156087	not significant
Lutjanus mahogoni	48	-38.10133586	164.4699117	not significant
Haemulon sciurus	46	-516.7100858	142.6045729	not significant

Sparisoma chrysopterum	46	25.4953125	16.14940933	not significant
Holocanthus ciliaris	45	125.4003166	70.19975284	not significant
Cephalopholis cruentatus	42.6	65.83549901	39.90831673	not significant
Cephalopholis fulvus	41	-92.8725	21.047187	not significant
Anisotremus virginicus	40.6	7.325160533	10.64443107	not significant
Bodianus rufus	40	-1.506932752	8.268218646	not significant
Synodus saurus	40	-0.229137241	0.093544887	not significant
Mulloidichthys martinicus	39.4	0.331201859	196.5467834	not significant
Acanthurus chirurgus	39	88.28658199	20.88514041	significant
Acanthurus coereulus	39	-8.000653802	42.87574858	not significant
Acanthurus bahianus	38.1	-25.71592047	15.11972455	not significant
Pterois volitans	38	22.41013085	9.676485623	not significant
Halichoeres bivittatus	35	-30.90343932	11.32286659	not significant
Holocentrus rufus	35	-220.3938086	94.97397633	not significant
Holocanthus tricolor	35	17.18167896	21.99391023	not significant
Scarus iserti	35	196.2476216	140.6285022	significant
Scarus taeniopterus	35	2.7983025	27.80833188	not significant
Haemulon melanurum	33	-0.977913617	0.384389514	not significant
Clepticus parrae	30	38.7557856	56.83204962	not significant
Haemulon flavolineatum	30	-292.8331571	170.0717915	not significant
Pseudupeneus maculatus	30	34.65788459	8.197487878	not significant
Serranus tigrinus	29	5.285914992	8.592272295	not significant
Sparisoma aurofrenatum	28	50.9173425	92.46817245	significant
Sparisoma atomarium	25	-2.519184458	3.631962112	not significant
Thalassoma bifasciatum	25	24.29762567	20.62997279	not significant
Abedufduf saxatilis	22.9	-74.69302034	29.17089362	significant
Serranus tabacarius	22	0	0.517647586	not significant
Microspathodon chrysurus	21	1.04572879	9.56213407	not significant
Chromis multilineata	20	4.494196494	1.194089551	not significant
Chaetodon ocellatus	20	27.7662553	22.66715411	not significant
Halichoeres garnoti	19.3	-107.6999362	67.88391825	not significant
Halichoeres maculipinna	18	-7.978316361	5.245173115	not significant
Neoniphon marianus	18	-5.105883488	2.054254828	not significant
Sargocentron vexillarium	18	-0.697857468	0.284899118	not significant
Chromis insolata	16	0.255306176	0.10422831	not significant
Cheatodon striatus	16	-1.021484356	0.417019242	not significant
Liopropoma rubrae	16	1.292457025	0.592446679	not significant
Hypoplectrus puella	15.2	19.45547634	4.480559374	not significant
Hypoplectrus spp	15.2	0.799393159	0.5949321	not significant
Chromis cyanea	15	134.3117959	78.38772395	not significant
Chaetodon sedentatus	15	0.008466462	0.003456419	not significant
Sargocentron coruscum	15	-0.089971028	0.606528755	not significant
Stegastes adustus	15	-2.795285607	3.569623983	significant
Apogon binotatus	13	-0.005366948	0.009742616	not significant

Halichoeres pictus	13	-5.264912855	11.23048552	not significant
Stegastes planifrons	13	-8.138334004	8.574756616	not significant
Hypoplectrus unicolor	12.7	2.022199642	0.825559547	not significant
Stegastes diencaeus	12.5	48.16190052	12.80715011	not significant
Stegastes variabilis	12.5	9.269119046	7.522044719	not significant
Canthigaster rostrata	12	7.384090257	3.733251362	not significant
Cheatodon aculeatus	10	22.22036733	2.804344953	not significant
Gramma melacra	10	1.482282999	0.6051395	not significant
Hemiemblemaria simulus	10	-0.076931121	0.025409715	not significant
Monacanthus tuckeri	10	4.152262224	1.165418344	not significant
Opistognathus aurifrons	10	4.69587975	1.80955798	significant
Stegastes leucostictus	10	-3.262896202	6.936438586	not significant
Stegastes partitus	10	34.81257104	21.38233622	not significant
Gnatholepis thompsoni	8.2	-2.321046217	2.132643533	not significant
Blueside spp	8	0.016060227	0.286715397	not significant
Coryphopterus glaucofraenum	8	9.368688675	4.440427817	not significant
Gramma loreto	8	-15.33149311	40.24907592	not significant
Malacoctenus gilli	7.6	0.012813165	0.005230953	not significant
Chaetodon capistratus	7.5	18.43405897	41.42818256	not significant
Malacoctenus triangulatus	7.5	-0.165198833	0.212979448	not significant
Malacoctenus boehlkei	6.4	-3.09705514	0.686385348	significant
Malacoctenus macropus	5.5	0.618972074	0.270961965	not significant
Acanthemblemaria maria	5.1	0.006646647	0.002713482	not significant
Coryphopterus dicrus	5	1.192001622	0.506048546	not significant
Elacatinus horsti	5	-0.002092368	0.00597944	not significant
Gobiosoma genie	4.5	-0.315490728	0.216925167	not significant
Coryphopterus personatus	4	114.9406862	18.03805404	not significant
Gobiosoma evelynae	4	-0.013527256	0.057234317	not significant
Priolepis hipoliti	4	-0.025955213	0.01283066	not significant
Lucayablennius zingaro	3.8	0.076931121	0.020392764	not significant

Appendix 1. Reserve effect (g/transect), max total length (cm), and difference in fore reef vs. patch reef habitats for all fish species observed.