

AN ABSTRACT OF THE DISSERTATION OF

Christopher D. Stallings for the degree of Doctor of Philosophy in Zoology presented on May 23, 2007.

Title: Indirect Effects of Fishing on Predators and their Prey

Abstract approved: _____
Mark A. Hixon

Predators are fundamentally important for regulating and driving prey population dynamics as well as structuring ecological communities. Over-exploitation of marine resources has caused dramatic depletions of predatory fish species and shifts in marine community composition, with attendant declines in productivity and diversity of marine ecosystems. Despite the important ramifications of these patterns for humankind, the specific ecological mechanisms and potential indirect effects underlying these trends have been largely unexplored.

I combined small-scale experiments and broad-scale observations to investigate how fishing can affect interactions among predators and subsequently be transferred to interactions between predators and their prey. Previous observations had indicated that small, unfished predators increase in abundance on reefs where large, fished predators are removed. To test the effects of such shifts in relative

abundance of different predatory fishes on community structure of lower trophic-level species, I manipulated the presence of fished and unfished predatory species on coral patch reefs in the Bahamas. This controlled field experiment demonstrated that different predatory fishes, which are often assumed to have similar effects on prey species, in fact had remarkably different effects on prey diversity and abundance. In a second field experiment, I found that increased abundance of a large, fished predatory species on coral reefs decreased the activity and growth of smaller, unfished predators. Although small, unfished predators had strong, negative effects on lower trophic-level prey on reefs with low abundances of larger, fished predators, these effects were reduced with increasing abundance of the fished species. Lastly, I used observational data from volunteer SCUBA-diver surveys to investigate how the structure of predatory fish communities on coral reefs across the greater Caribbean region has been affected by fishing. I used density of human populations as a proxy for fishing intensity. I found that, as human density increases, overall predator abundance and diversity decreases, and reef communities became dominated by only a few, small species.

This research indicates that the effects of fishing on larger predatory species can permeate throughout ecological communities, well beyond simple reductions in the abundance of fished species. In light of these community-wide effects, ecosystem-based approaches are necessary for successful management of fisheries and conservation of coral reefs.

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Indirect Effects of Fishing on Predators and their Prey

by

Christopher D. Stallings

A DISSERTATION

submitted to

Oregon State University

in partial fulfillment of

the requirements for the

degree of

Doctor of Philosophy

Presented May 23, 2007

Commencement June 2008

Doctor of Philosophy dissertation of Christopher D. Stallings presented on May 23,
2007.

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Chair of the Department of Zoology

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

Christopher D. Stallings, Author

ACKNOWLEDGMENTS

I first thank my advisor, Mark Hixon for his guidance, encouragement, advice on experimental design, financial support, assistance in the field, and thorough edits of my papers and talks. Mark has taught me much about how to succeed, and perhaps more importantly, what to do when I do not succeed, in both professional and personal aspects of my life. For that, my gratitude will continue well past the life of this thesis.

I also thank my graduate committee (in alphabetical order) for their advice and time. Scott Heppell served as my graduate representative, a lucky “draw” for me considering his extensive knowledge and experience working with groupers in the Caribbean. Bruce Menge provided valuable feedback on experimental design and taught me much on community ecology. Paul Murtaugh served as my statistics minor advisor, provided assistance with experimental design, and thankfully did not ask any questions about such topics as methods of moments during my prelims. Al Stoner, who has worked in the Bahamas for years, was a wonderful source of local information and was very enjoyable to discuss my research with during my visits to his office in Newport. Although not officially a committee member, I also thank Sally Hacker, who participated in my prelims and provided advice on my research on several occasions.

The Hixon lab (in chronological order) was a wonderful group to work with, and I thank them for their professional assistance and for their friendship. Karen McLeod (aka Big Sis) was instrumental in helping me to get settled in Corvallis and at OSU, and has truly been the dear friend and confidant that her nickname implies. Mark Christie (aka Bart) has a great sense of humor and was always a joy to have

discussions with, even when about nothing. Darren Johnson (aka John Soda) is an amazing source of random song and movie lines, was a pleasure to spend extended periods of time with in the field, and was great to have discussions with about current and potential future research ideas. Mark Albins (still seeking a nickname) knows what the Mason jar was really designed for, which this southern boy appreciates, and has a wonderful proficiency for philosophical discussions. Jenn Noell, our honorary all-star lab member, spent many hours with me both on the R.V. Nuwanda and underwater, and was a constant source of positive energy in the field. Lastly, although my time in the Hixon lab did not overlap with Glen Almany and Michael Webster, both provided important information for my research.

Many people in the Zoology Department, at OSU, and in the Corvallis community have provided support in many ways. From the Zoology office, I sincerely thank Tara Bevandich, Sarah Cain, Mary Crafts, Traci Durrell-Khalife, and Torri Schrock whose tireless efforts keep the whole show running. I especially thank Joe Beatty for his support of graduate students in the department and because he knows how to tend a grill. Bruce McCune taught one of the best classes I have ever taken and has provided excellent feedback on my broad-scale research. I also thank my cohort (aka the dictators), Betsy Bancroft, Barbara Han, and Laura Petes for their friendship and for staying so close through the years. Michael Bogan was an excellent housemate, may be a bigger music snob than me, and can probably be found naked in the desert somewhere. Rocky Parker (aka Potpourri Ali) made for a wonderful neighbor and I will miss him shaking his empty unicorn glass at me. Brock McLeod has been a dear friend, whose support and advice for all things very important in my

life cannot be overstated. Jerod Sapp and Evan Kristof helped me solve all my computer problems, and were part of a group I fondly refer to as my “knucklehead friends” that included Doug DeGross, Dave Paoletti, Tiffany Garcia, and Jessica Hewitt – thanks for keeping me “sane!”

I lovingly thank my family: Dan and Edna Reaves, Stan and Lillie Mae Stroud, Derek and Kristi Stallings, Jim and Susan Dail, Gloria Briya, Margaret White, Pat and David Britton, Joey Stallings, Jamie Stallings, Cady Dail, and Daniel Dail.

I also lovingly thank my fiancé (aka pre-wife) MJ Briya, whose support and encouragement have gotten me through the challenges of graduate school. MJ is truly my best friend and I adore her bright outlook on life and fun nature.

I am very grateful for logistical support provided by the Caribbean Marine Research Center and specifically from Craig Dahlgren, Kevin Buch, and Brenda Gadd. Financial support was generously provided by a Thompson Fellowship to me, and National Science Foundation and National Undersea Research Program grants to Mark Hixon.

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Indirect Effects of Fishing on Predators and their Prey

Chapter 1: General Introduction

Globally, marine fisheries are in trouble. The United Nations Food and Agriculture Organization reports that 75 percent of the world's marine fish stocks are fully exploited, overexploited, severely depleted, or recovering from depletion (FAO 2006). An increasing human population exacerbates the problem as the demand for seafood continues to increase. In addition to reducing the biomass of fished species, fishing can also indirectly affect marine communities by altering food web structure and function (Pauly et al. 1998, Jackson et al. 2001, Gislason 2003).

Fishing effort often targets higher trophic-level, predatory species (Myers and Worm 2003). Removal of these fishes may reduce the intensity of interactions between fished and unfished species, resulting in increased abundances of unfished predators (Pimm and Hyman 1987, Greenstreet and Rogers 2000). Such a shift in abundance of top trophic-level species may have strong "top-down" effects on abundances of other fishes and community structure, and could potentially have negative impacts on coastal ecosystems (Hughes 1994, Jackson et al. 2001, Carr et al. 2002, Cury et al. 2003).

In this dissertation, I use small-scale field experiments in the Bahamas to test the effects of fishing on interactions both among predatory coral-reef fishes and between these predators and their prey. Coral-reef fish communities are excellent systems to conduct such studies because species can be directly observed and experimentally manipulated *in situ* (Sale 1991). Additionally, I use broad-scale census data to examine the effects of fishing on the structure of predatory fish communities throughout the greater Caribbean region.

In Chapter 2, *Predator identity and recruitment of coral-reef fishes: an indirect effect of fishing?*, I manipulated the presence of Nassau grouper (*Epinephelus striatus*; fished large predator) and coney grouper (*Cephalopholis fulva*; unfished small predator) on isolated coral patch reefs in the Bahamas. Throughout the greater Caribbean, intense fishing has depleted populations of Nassau grouper, while populations of coney grouper have proliferated. The goal of this study was to elucidate the relative effects of the different groupers on recruitment of other coral-reef fishes in order to understand how overfishing Nassau grouper may indirectly affect coral-reef fish communities.

In Chapter 3, *Indirect effects of an exploited grouper on recruitment of coral-reef fishes*, I conducted another field experiment in which I translocated

young-of-year coney or graysby (*C. cruentata*) groupers, both small unfished predators, to isolated patch reefs. I also manipulated the abundance of Nassau grouper on these reefs to reflect a gradient a fishing intensity. I measured the effects of Nassau grouper abundance on coney and graysby grouper persistence, behavior, and growth in addition to their indirect effects of recruitment of other coral-reef fishes.

In Chapter 4, *Human population density and declines of predatory fishes in the Caribbean*, I examined the structure of predatory fish communities as a function of potential fishing intensity across the greater Caribbean. I used a fisheries-independent, publicly-accessible database of volunteer SCUBA-diver surveys from 23 continental and insular nations from the Caribbean region. To investigate potential factors driving the structure of the predatory fish communities, I incorporated latitude and density of human populations in the analyses.

The common theme in these studies is that fishing can have substantial effects on reef-fish communities well beyond reductions in the abundance of fished species. Field experiments and broad-scale comparisons indicate that the structure of predatory fish communities on corals reefs has been greatly altered at both local and regional scales. Fishing-induced changes in predator communities

can affect the ways in which predators interact with each other, which in turn can have important effects on both predator behavior and demographic processes. Altered predator communities can also translate to substantial effects on lower trophic-level species. Overall, this research demonstrates that fishing can have important indirect effects on marine communities, and strongly supports the current move towards more holistic approaches to management and conservation of marine ecosystems.

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Chapter 2:

**Predator identity and recruitment of coral-reef fishes:
an indirect effect of fishing?**

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Abstract. Food and interaction web studies are often simplified by aggregating different species of predator, especially those that are closely related, into guilds. Such aggregation requires the assumption that predators are functionally redundant or at least have similar effects on community structure. However, few studies have rigorously tested this assumption, particularly with exploited species of apex marine predators. Moreover, fishing can strongly alter the relative abundances of apex predators, further highlighting the need to examine the “top-down” effects of different predators on lower trophic-level species within marine communities.

Throughout the greater Caribbean, intense fishing has depleted populations of Nassau grouper (*Epinephelus striatus*), while populations of the unfished coney grouper (*Cephalopholis fulva*) have proliferated. In this study, I experimentally tested the effects of these different grouper species on recruitment of other coral-reef fishes to spatially isolated reefs. Fish recruitment to reefs occupied by Nassau grouper was similar to that on grouper-free control reefs, and both treatments accumulated higher recruit abundance and diversity than reefs occupied by coney grouper. Thus, even closely related species of top predator can have substantially different effects on lower trophic levels. Shifts in dominance of predatory species may therefore lead to dramatic changes in abundance and diversity of entire communities. These findings underscore the importance of addressing both the direct and indirect effects of fishing on marine communities.

INTRODUCTION

Overexploitation has caused dramatic depletions of predatory fish species and shifts in marine community composition, leading to declines in diversity of marine ecosystems (NRC 1999, Jackson et al. 2001, Pauly et al. 2003, Myers and Worm 2003). Large-bodied predators have been particularly vulnerable to fishing practices (Jennings et al. 1999) and are commonly replaced with smaller, often non-targeted predators (Pauly et al. 1998, Ward and Myers 2005). In addition to the loss of ecosystem services provided by large predators (e.g., food resources, aesthetic values, ecotourism), a shift to smaller predators may have “top-down” effects on abundances of other fishes and community structure, and could potentially have unanticipated impacts (Hughes 1994, Jackson et al. 2001, Carr et al. 2002).

Predation is an important process for regulating prey populations (Murdoch and Oaten 1975, Hixon et al. 2002) and structuring ecological communities (Hairston et al. 1960, Paine 1966, Menge and Sutherland 1976, 1987). Although much experimental work has been conducted on the role predatory marine fishes have on lower trophic-level species (reviews by Hixon 1991, Hixon and Webster 2002, Hixon and Jones 2005), the approach has typically been to manipulate either predator presence or density, without regard to predator identity beyond particular piscivorous guilds. Grouping predators in this way requires the assumption that

higher trophic-level species are functionally redundant. Although this assumption simplifies investigations, it cannot provide insight into how a shift from particular large predatory species to smaller predators affects populations and communities.

In this study, I experimentally tested the relative effects of a large-bodied, intensively fished piscivore (*Epinephelus striatus*, Nassau grouper) and a smaller, generally unfished piscivore (*Cephalopholis fulva*, coney grouper) on recruitment of coral-reef fishes. It is well documented that coney grouper biomass increases in areas where fishing reduces Nassau grouper biomass, probably due to modified predation and/or competition between the species (Sluka et al. 1996, Chiappone et al. 2000). The field experiment demonstrated how these different predators differentially affect recruitment of other reef fishes, thereby providing insight on the importance of indirect effects on reef-fish food webs, especially due to differential fishing of predatory fishes.

METHODS

Study site

I conducted this study using SCUBA on a matrix of isolated coral patch reefs located on a shallow sand and seagrass flat (3–5 m deep) near the Caribbean Marine Research Center, Lee Stocking Island, Bahamas. The reefs had been translocated to their present locations by Hixon and Carr (1997) approximately 10

years before the current study, and were standardized for size (mean area = 6.6 m²; SD = 1.0), structural complexity, and distance between reefs (200 m). The nearest naturally occurring reef was located > 1.0 km from the edge of the matrix.

Study species

Nassau grouper are large (TL_{max} = 122 cm) members of the Family Serranidae distributed throughout the greater Caribbean region (Heemstra and Randall 1993). Postlarvae settle to macroalgal flats, move onto patch reefs at approximately 15 cm TL (Eggleston 1995, Dahlgren and Eggleston 2000), and finally to fore-reefs at sizes between 30 and 40 cm TL (C.P. Dahlgren and M.A. Hixon, unpublished data). Diets of Nassau grouper consist of both benthic invertebrates (crabs and other crustaceans) and fishes, the latter becoming more prevalent as individuals grow larger than 20 cm TL (Randall 1967, Eggleston et al. 1998). Coney grouper are smaller serranids (TL_{max} = 41 cm), also distributed throughout the greater Caribbean region (Heemstra and Randall 1993). Postlarvae settle to a range of habitats, including patch reefs, in both back- and fore-reef habitats. Coney ontogenetic movement is not as structured as that of Nassau grouper, although larger individuals tend to occur in fore-reef habitats (pers. obs.). Diets of coney grouper also consist of benthic invertebrates and fishes (Randall 1967). Field observations suggested that coney may be voraciously piscivorous at a much smaller size than Nassau grouper. Individuals as small as 5 cm TL

actively hunt and consume other fishes (pers. obs.). Although subtle differences in the diets of these groupers have been detected (Randall 1967), no work has previously examined either the magnitudes or relative effects of these groupers on communities of coral-reef fishes.

Experimental design

To investigate the relative effects of Nassau and coney groupers on recruitment of other coral-reef fishes, I manipulated their presence on 18 of the translocated patch reefs. I assigned 6 reefs to each of three treatments: Nassau grouper only, coney grouper only, or no grouper (control). The grouper treatments were established to reflect natural, pre-manipulation abundances (Nassau grouper = 2 fish per reef; coney grouper = 1 fish per reef). Coney grouper (mean TL = 15.5 cm, SD = 3.4) were added to reefs as needed. Previous efforts had shown that Nassau grouper cannot be effectively added to reefs because of strong homing behavior, but they can be removed (M.A. Hixon, unpublished data). I therefore randomly selected reefs from those that had at least two Nassau grouper present (21 of the 32 reefs). Although this logistical constraint reduced the number of reefs possible for the Nassau grouper treatment, I did not detect any spatial patterns of Nassau grouper abundance or distribution across the entire matrix (i.e., they were randomly distributed). I selectively removed Nassau grouper from the reefs as needed so that the two remaining individuals were of two size classes.

The larger size class (mean TL = 25.3 cm, SD = 1.2) included fish that reportedly have increased proportions of fish in their diets (Eggleston et al. 1998). The smaller of the two Nassau grouper were individuals that had probably recently moved onto the patch reefs (mean TL = 16.5 cm, SD = 1.2), and were of similar size to the coney grouper ($t_{10} = 0.679$, $P = 0.512$). These two size classes were chosen to maximize the potential to detect impacts of Nassau grouper on fish recruitment, if such impacts in fact existed.

Prior to all grouper manipulations, I standardized the fish communities on the experimental reefs by removing all resident piscivores with diets consisting of $\geq 10\%$ fishes (Randall 1967). I also removed all territorial damselfish (Pomacentridae), which can be strong interference competitors with coral-reef fish recruits (Almany 2003, Carr et al. 2002). The reefs were dominated by grunts (Haemulidae) and gobies (Gobiidae), which were randomly distributed at low abundances. I did not remove these invertivores because I assumed their effects on recruitment of other fishes would be negligible. All fish manipulations were maintained as a “press” manipulation for the duration of the experiment. Removals were conducted using the fish anesthetic quinaldine and hand nets. Fish removed from the experimental reefs were released unharmed on reefs sufficiently distant to inhibit homing. Removed Nassau grouper were placed on natural reefs

located ~ 3 km from the experimental reefs, on the opposite side of a tidal cut that served as an effective barrier to homing.

The experiment ran for 52 days between June and August 2004, when recruitment of coral-reef fishes tends to be highest in the Bahamas (Thorrold et al. 1994). Once the treatments were established, I conducted recruit censuses on each experimental reef every four days. I counted both newly settled and previously recruited fish of all species to allow calculation of cumulative recruitment to each reef. I assumed that the supply of recruits (i.e., via settlement to the reefs) was even across treatments and did not vary spatially across the reef matrix, as indicated by previous studies of the same matrix of reefs (Almany 2003, 2004ab).

Statistical analysis

I compared cumulative fish recruitment among the grouper treatments at both the community and species levels. At the community level, I compared temporal changes in cumulative fish recruit community structure among treatments using Canonical Discriminant Analysis (CDA; SPSS 10.0). All species that accounted for at least 1% of the total observations were included in the ordination, and the data were $\ln(x + 1)$ transformed to approximate normality and stabilize variability (Zar 1999). Agreement between the CDA and a Principal Components Analysis (S-Plus 6.2) indicated that the experimental treatment was the dominant

signal in the data (Tabachnick and Fidell 2001). I displayed the effects of the CDA using the treatment by census matrix, where each treatment at each census was assigned with a unique code (3 treatments x 14 censuses = 42 codes). I used the CDA only as a tool to display changes in time, not for inferential statistics.

I measured treatment effects on final recruit species diversity using four indices: (1) richness (S , the total number of species), (2) the Shannon-Wiener Index of composite diversity ($H' = \sum (p_i \ln p_i)$), (3) evenness ($J = H' / \ln S$), and (4) rarefied richness (Gotelli and Entsminger 2001) to adjust for differences in recruit abundances among treatments. I compared diversity between treatments using two-sample t -tests with Bonferroni corrections for multiple comparisons ($\alpha = 0.05/3 = 0.017$).

I compared temporal changes in cumulative fish recruit abundance of common species ($\geq 1\%$ total observations) using a linear mixed effects model (LMEM; Pinheiro and Bates 2000, S-Plus 6.2 LME). Excluding the mean and error terms, the model was:

$$\text{Abundance} = \text{Treatment} + \text{Time} + \text{Treatment} * \text{Time} + \text{Reef}(\text{Treatment}) + \gamma$$

with Treatment and Time as fixed factors. Reef was included in the model as a blocking factor to accommodate within reef temporal structure of the repeated-measures data. The gamma term (γ) was specified as first-order autocorrelation to correct the temporal structure of the cumulative recruit abundance response (i.e., correlation between time $t + 1$ and time t). The interaction term describes the trajectory of each grouper treatment over time, and is the appropriate test of treatment effects (Hedeker and Gibbons 2006). Because each reef was unique to each treatment, the treatment term was tested over the blocking factor, and all other terms were tested over the error.

RESULTS

Recruit community structure

A total of 35 species of coral-reef fishes recruited to the experimental reefs, of which 27 were rare (each $< 1\%$ of total abundance). The abundances of four rare labrids of the genus *Halichoeres* (*H. garnoti*, *H. maculipinna*, *H. pictus*, and *H. radiatus*) were combined into a single response group, which was included with the eight most common individual species in the CDA. For simplicity, I hereafter refer to this combined group as another “species.” These nine common species comprised 97% of the total observations.

The communities of fish recruits were indistinguishable among treatments at the beginning of the experiment. Within about a week, however, the community structure on Nassau-grouper and control reefs was distinct from coney-grouper reefs. The total abundance of recruits accounted for the most variation in community structure (canonical discriminant 1 = 77.7 %) and corresponded with greater recruitment to both Nassau-grouper and control reefs (Fig. 1). Final recruit abundance (day 52) of the nine common species was 2.7 times higher on both Nassau-grouper reefs ($t_{10} = 5.27$, $P = 0.0002$) and control reefs ($t_{10} = 6.05$, $P < 0.0001$) than on coney-grouper reefs. Higher relative abundances of more cryptic species (e.g., gobies) on coney-grouper reefs accounted for the second largest portion of variation (canonical discriminant 2 = 8.6%).

Recruit species diversity

The species diversity of recruits at the end of the experiment was higher on reefs occupied by Nassau grouper and on control reefs than on reefs occupied by coney grouper (Fig. 2A-C). Although the differences between treatments were not significant for species richness (S) or evenness (J), the Shannon-Wiener Index of composite diversity (H') was higher on both Nassau grouper reefs [$H' = 1.99$ (0.028); $t_{10} = 3.06$, $P = 0.006$] and on control reefs [$H' = 1.94$ (0.038); $t_{10} = 2.48$, $P = 0.016$] than on coney grouper reefs [$H' = 1.68$ (0.096)]. Rarefied species richness did not differ between treatments (Fig. 2D).

Recruit species-level comparisons

Cumulative recruitment of four species was higher on Nassau-grouper and control reefs than on coney-grouper reefs (Table 2.1, Table 2.2, Table 2.3). Because cumulative recruitment between the Nassau grouper and control treatments did not differ, I report only comparisons between the two grouper treatments. The four species were among the most abundant to recruit to the experimental reefs (> 10 % total observations), and included *Stegastes leucostictus* (beaugregory damselfish, Pomacentridae; $t_{154} = -7.32$, $P < 0.001$), *Malacoctenus macropus* (rosy blenny, Labrisomidae; $t_{154} = -5.37$, $P < 0.001$), *Scarus iserti* (striped parrotfish, Scaridae; $t_{154} = -4.09$, $P = 0.001$), and *Sparisoma viride* (stoplight parrotfish, Scaridae; $t_{154} = -5.60$, $P < 0.001$) (Figure 3). Cumulative recruitment of two gobiids, *Coryphopterus glaucofraenum* (bridled goby) and *Gnatholepis thompsoni* (goldspot goby), was also high, but no differences were detected between treatments for these cryptic species. Cumulative recruitment of three other common species, *Thalassoma bifasciatum* (bluehead wrasse, Labridae), *Stegastes partitus* (bicolor damselfish, Pomacentridae), and the *Halichoeres* species group (Labridae), was lower than the other six species, and no differences were detected among treatments.

DISCUSSION

The goal of this study was to examine how different predatory species affect recruitment of lower trophic-level species. Predator identity was clearly an important factor, with two species of grouper having remarkably different effects on populations and communities of recruiting coral-reef fishes. Coney grouper had very strong, direct, negative effects on recruitment of other fishes, resulting in local communities with low diversity and abundance compared to grouper-free control reefs. Nassau grouper did not have any detectable direct effects on recruitment of other fishes, resulting in local communities indistinguishable from control reefs lacking predators.

Although not directly tested in the field experiment, predation by coney grouper was the likely mechanism that reduced recruitment of other fishes. Settling fishes do not avoid reefs occupied by coney grouper (Almany 2003) and coney grouper can be voraciously piscivorous on settlement-sized fishes in both the field (pers. obs.) and in laboratory aquaria (D.W. Johnson, unpublished data). No differences in rarefied richness between treatments (Fig. 2D) indicated that predation by coney grouper was generally not selective on any particular species. Reduced species richness at the end of the experiment on coney-grouper reefs was therefore due to their strong negative effect on overall recruit abundance.

Neither of the two size classes of Nassau grouper used in this experiment negatively affected recruitment. Although Nassau grouper larger than 30 cm consume increasing proportions of fish compared to the size classes examined here (Randall 1967, Eggleston et al. 1998), Nassau grouper of such size are unlikely to target small fish recruits (~ 1.5 cm TL). Indeed, in a separate experiment that included a greater range of Nassau grouper sizes and abundances, I did not detect a negative effect of groupers larger than 30 cm TL on recruitment (C.D. Stallings, unpublished data). The effects of predation by large Nassau grouper on juvenile and adult coral-reef fishes remain untested, but it seems unlikely that they would have an effect on those populations equivalent to that of coney grouper on recruits. Newly settled fish are more vulnerable to predation than juveniles and adults (Hixon 1991, Sogard 1997, Hixon and Webster 2002, Almany and Webster 2006), possibly because older fish have lived in the reef environment long enough to acquire predator avoidance behaviors (Almany 2004).

Differential predation by individual species of piscivore found in this study reveals complexity in the food web that may be oversimplified by grouping predators. Although aggregating species simplifies experiments and discussions of food and interaction webs, the current study highlights potential shortcomings of assuming that predators can be categorized into functionally similar groups (e.g., guilds), even with species from the same family. Arguments have been made

against grouping species because it does not allow detection of important species-level effects in food webs (May 1983, Paine 1988, Polis and Strong 1996). Recent experiments involving multiple predators have found predator identity to be more important than predator diversity (e.g., Schmitz and Suttle 2001, Chalcraft and Resetarits 2003, Bruno and O'Connor 2005, Straub and Snyder 2006). Although I did not manipulate predator diversity *per se*, results from this experiment indicate that different species of predator, typically assumed to function in similar ways, can in fact have substantially different effects on their prey.

Nassau grouper have been intensely fished throughout their range and are now ecologically extinct throughout much of the greater Caribbean region (Dahlgren 2004). Observational studies have indicated that the biomass of smaller groupers, including coney, increases in areas where the biomass of Nassau grouper is reduced (Sluka et al. 1996, Chiappone et al. 2000), possibly due to moderated interactions between these species. Shifts in biomass from large to small predators have been reported in other intensely fished marine ecosystems (e.g., Pauly et al. 1998, Jackson et al. 2001, Ward and Myers 2005). Such shifts in abundance or biomass can have cascading effects on lower trophic-level species (Dulvy et al. 2004). If smaller predators tend to be voraciously piscivorous on new recruits, one would expect deleterious effects on fish diversity and community structure as these mid-level predators increase in abundance, with important implications for

ecosystem functioning, stability, and services (McCann 2000, Loreau et al. 2001, Solan et al. 2006 and contributions within). For example, multiple species from several families in the current study were negatively affected by intense predation, and these fishes perform different ecological functions. Two of the species negatively affected were herbivorous parrotfishes, which graze on algae and therefore serve an important function for the restoration and maintenance of coral reef health (Hughes 1994, Pandolfi et al. 2003, Mumby et al. 2006). In the absence of healthy coral reefs, which serve as foundation species to the entire ecosystem, the community composition may move between alternate stable states (Knowlton 1992, 2004).

Figure 4 is a model interaction web depicting the relative effects of fishing on Nassau and coney groupers and the experimentally tested effects of these predators on recruitment of coral-reef fishes. This model not only indicates directions for future research, such as elucidating the details of biotic interactions between grouper species, but also describes a potential indirect effect of fishing on both predators and lower trophic levels. Fishing clearly has a direct negative effect on Nassau grouper biomass, but also has an indirect positive effect on coney grouper biomass, and consequently, an indirect negative effect on recruitment of other fishes (Fig. 4). Although not included in the conceptual model, the direct

negative effect of coney grouper on recruitment may have additional indirect negative effects on coral reef health (see previous paragraph).

In light of these considerations, it is imperative to understand the effects of fishing on marine ecosystems beyond the obvious reductions in biomass of fished species. Holistic approaches to management and conservation efforts, such as ecosystem-based fisheries management and marine reserves, may be strengthened by understanding and addressing both direct and indirect effects of fishing (Browman and Stergiou 2004 and contributions within, Pikitch et al. 2004, USCOP 2004).

ACKNOWLEDGMENTS

I thank J. Noell, N.R. Ehlers, M.R. Christie, M.A. Hixon, and D.W. Johnson for their assistance in the field. Various aspects of this study benefited from discussions with M.J. Briya, C.P. Dahlgren, S.D. Hacker, and C. Syms. This paper is a chapter from my dissertation, which benefited from comments by my doctoral committee -- M.A. Hixon (chair), S.A. Heppell, B.A. Menge, P.A. Murtaugh, and A.W. Stoner -- and by D.W. Johnson, S.R. Thorrold, and two anonymous reviewers. Financial support was provided by a Thompson Fellowship to the author, and NSF grants OCE-00-93976 and OCE-05-50709, as well as grants from the National Undersea Research Program, courtesy of the Caribbean Marine Research Center, to M.A. Hixon. This article is dedicated to the memory of Edna Reaves.

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Table 2.1. Multiple comparisons of recruit abundances across the nine most common fish species using linear mixed-effects models (LMEM). Comparisons are between control reefs versus *Epinephelus striatus* reefs.

Species	% Total	intercept	se	coef	se	<i>t</i>	<i>P</i> [†]
<i>Stegastes leucostictus</i>	23	0.57	0.98	-0.25	0.18	-1.36	0.175
<i>Coryphopterus glaucofraenum</i>	21	1.30	1.95	0.17	0.32	0.53	0.594
<i>Malacoctenus macropus</i>	13	-0.43	0.99	0.09	0.16	0.56	0.579
<i>Gnatholepis thompsoni</i>	11	1.01	1.53	-0.25	0.25	-1.02	0.312
<i>Scarus iserti</i>	11	0.40	1.46	0.18	0.20	0.90	0.368
<i>Sparisoma viride</i>	10	0.23	0.75	0.08	0.10	0.80	0.425
<i>Thalassoma bifasciatum</i>	4	3.75	1.17	-0.04	0.11	-0.39	0.700
<i>Stegastes partitus</i>	3	-0.28	0.39	-0.10	0.06	-1.55	0.122
<i>Halichoeres spp.</i>	1	1.05	0.74	-0.09	0.06	-1.51	0.134
TOTAL	97	7.14	4.56	-0.14	0.65	-0.21	0.834

† alpha = 0.05/3 = 0.0167
df = 154 for each comparison

Table 2.2. Multiple comparisons of recruit abundances across the nine most common fish species using linear mixed-effects models (LMEM). Comparisons are between control reefs versus *Cephalopholis fulva* reefs.

Species	% Total	intercept	se	coef	se	<i>t</i>	<i>P</i> †
<i>Stegastes leucostictus</i>	23	0.43	1.10	-1.28	0.15	-8.51	<0.001
<i>Coryphopterus glaucofraenum</i>	21	-1.44	2.91	0.01	0.29	-0.01	0.988
<i>Malacoctenus macropus</i>	13	-0.93	1.02	-0.73	0.09	-7.83	<0.001
<i>Gnatholepis thompsoni</i>	11	-3.29	2.57	-0.38	0.25	-1.49	0.138
<i>Scarus iserti</i>	11	1.48	1.22	-0.50	0.13	-3.90	0.001
<i>Sparisoma viride</i>	10	0.70	0.77	-0.47	0.10	-4.67	<0.001
<i>Thalassoma bifasciatum</i>	4	2.89	1.49	-0.16	0.06	-2.67	0.009
<i>Stegastes partitus</i>	3	0.04	0.48	-0.07	0.06	-1.14	0.254
<i>Halichoeres</i> spp.	1	1.33	0.75	-0.12	0.07	-1.78	0.078
TOTAL	97	-0.98	6.78	-3.62	0.43	-8.40	<0.001

† alpha = 0.05/3 = 0.0167
df = 154 for each comparison

Table 2.3. Multiple comparisons of recruit abundances across the nine most common fish species using linear mixed-effects models (LMEM). Comparisons are between *Epinephelus striatus* reefs versus *Cephalopholis fulva* reefs.

Species	% Total	intercept	se	coef	se	<i>t</i>	<i>P</i> †
<i>Stegastes leucostictus</i>	23	1.62	0.98	-1.03	0.14	-7.32	<0.001
<i>Coryphopterus glaucofraenum</i>	21	-2.35	2.52	-0.18	0.32	-0.57	0.569
<i>Malacoctenus macropus</i>	13	0.68	0.77	-0.82	0.15	-5.37	<0.001
<i>Gnatholepis thompsoni</i>	11	-0.60	2.83	-0.12	0.11	-1.08	0.282
<i>Scarus iserti</i>	11	1.55	1.26	-0.67	0.16	-4.09	0.001
<i>Sparisoma viride</i>	10	0.61	0.62	-0.52	0.09	-5.60	<0.001
<i>Thalassoma bifasciatum</i>	4	6.23	1.22	-0.13	0.11	-1.19	0.235
<i>Stegastes partitus</i>	3	0.18	0.39	0.03	0.05	0.55	0.583
<i>Halichoeres</i> spp.	1	3.20	0.78	-0.03	0.06	-0.52	0.605
TOTAL	97	11.25	5.91	-3.47	0.56	-6.18	<0.001

† alpha = 0.05/3 = 0.0167
df = 154 for each comparison

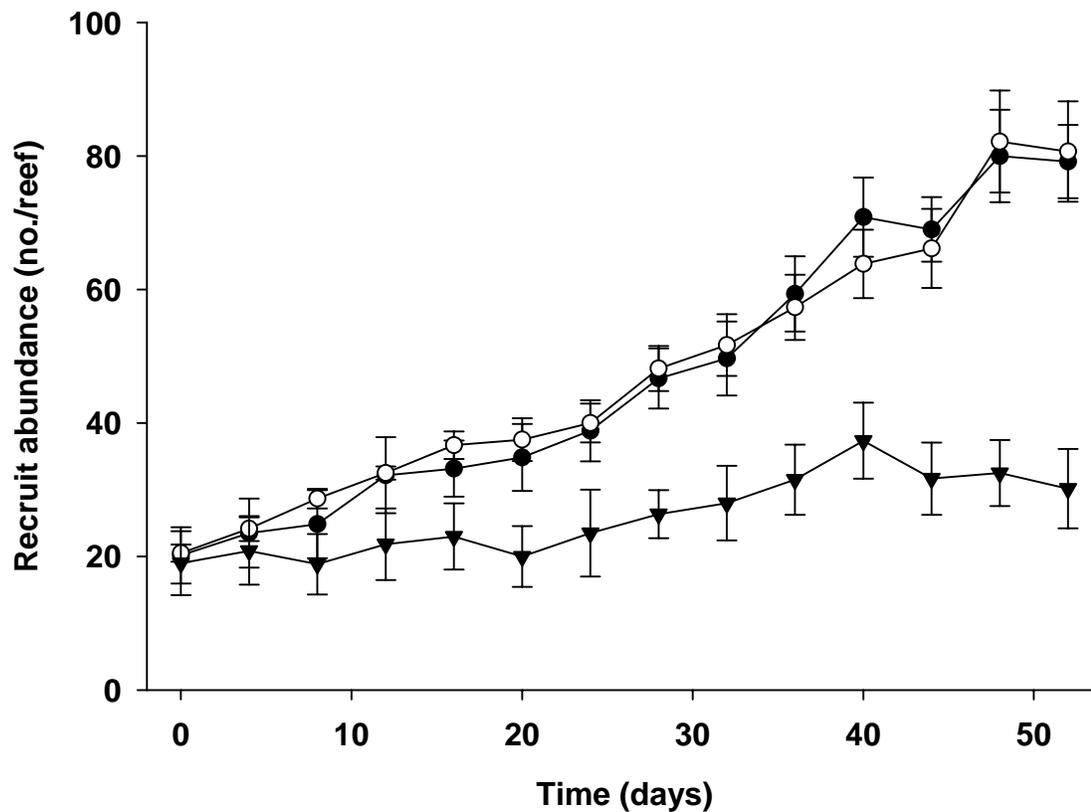


Figure 2.1. Temporal changes in fish communities on reefs occupied by different species of grouper. To simplify interpretation, total abundance (mean \pm SE) of fish recruits is displayed instead of scores on the first canonical discriminant, but the patterns were qualitatively identical. ● Control reefs; ○ Nassau grouper reefs; ▼ Coney grouper reefs.

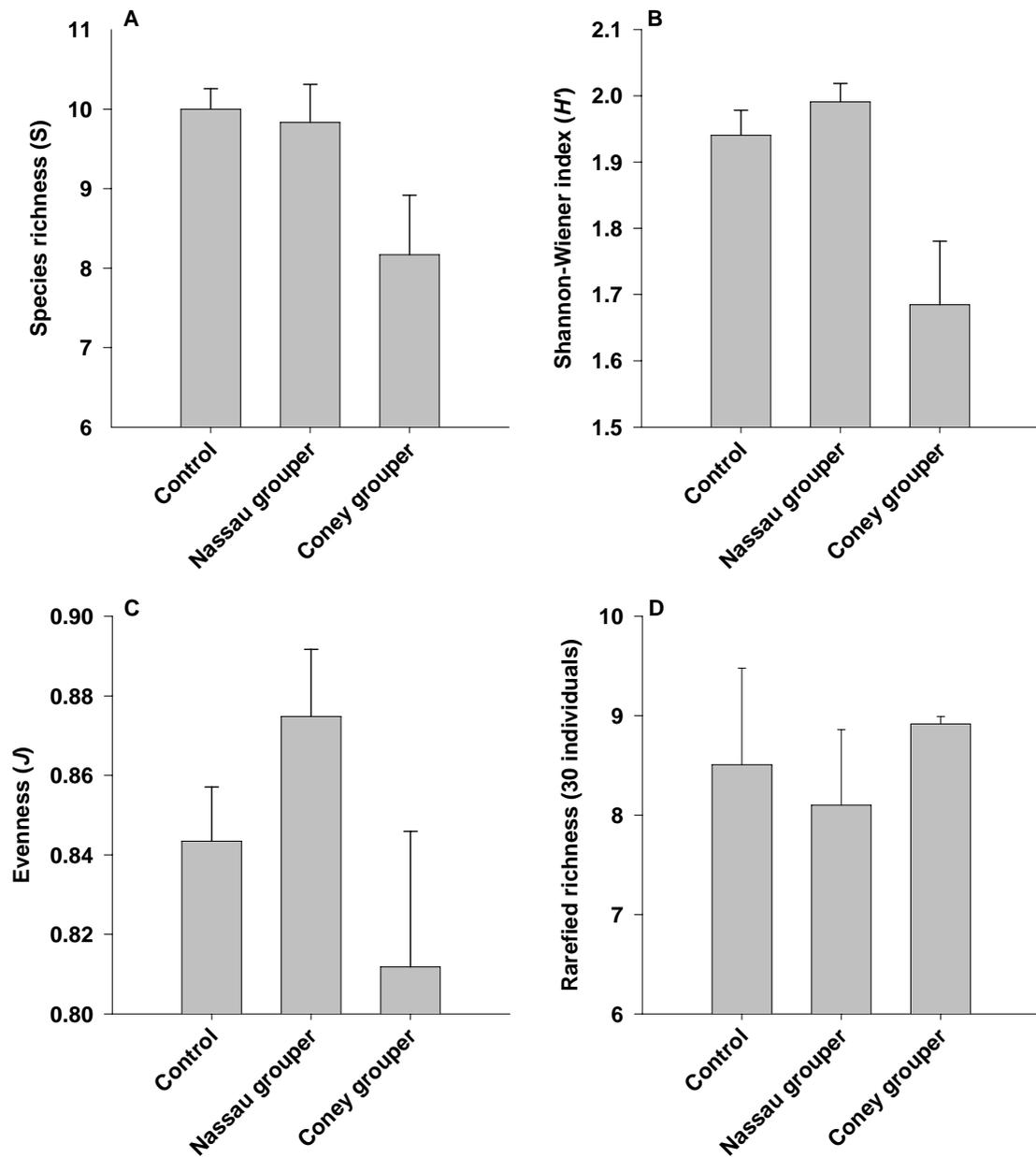


Figure 2.2. Recruit diversity (mean + SE) among treatments at the end of the experiment: A) species richness, B) evenness, C) Shannon-Wiener composite diversity index, and D) rarefied richness at 30 individuals.

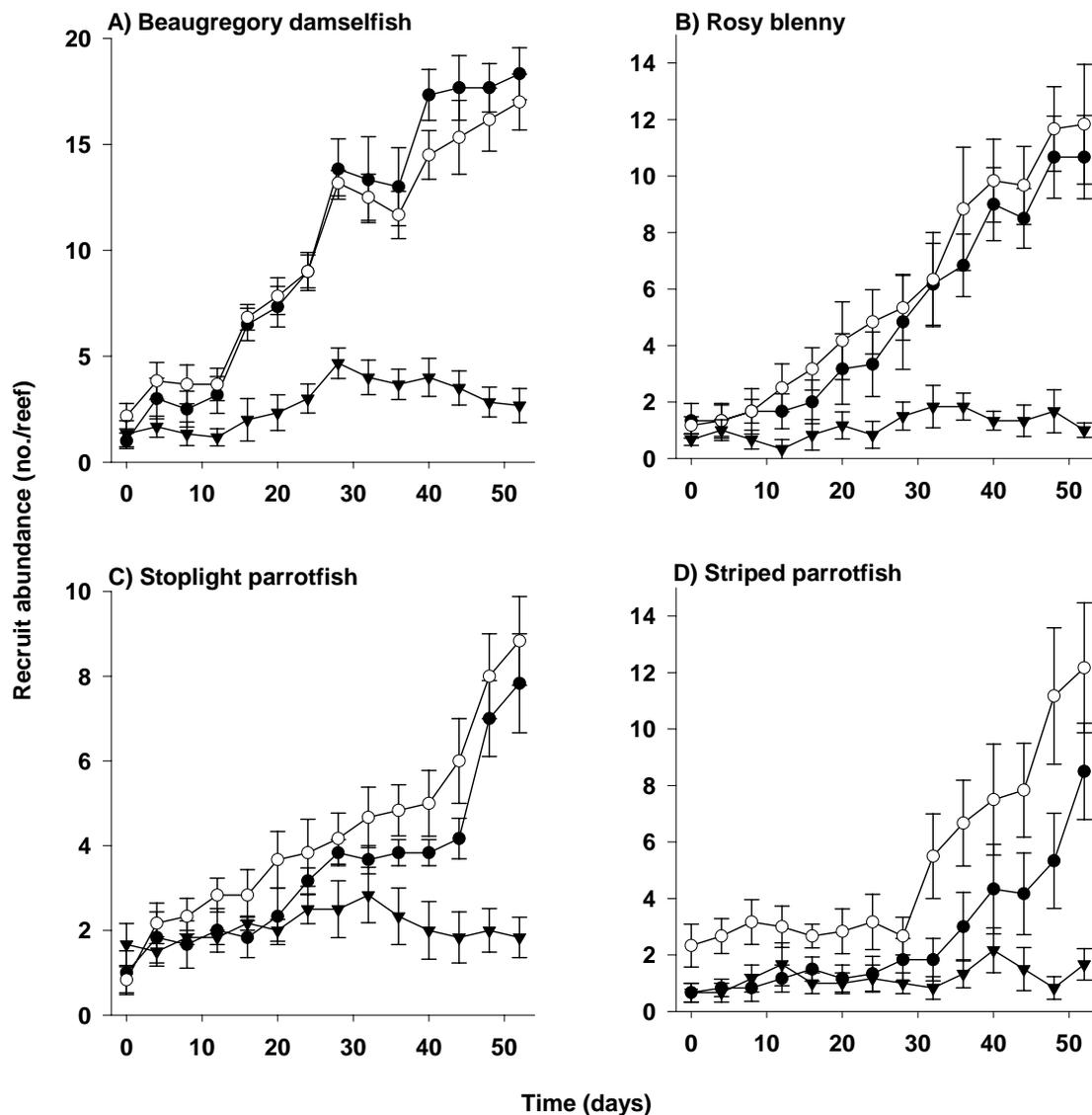


Figure 2.3. Temporal changes in cumulative recruit abundance (mean \pm SE) of four common species. A) *Stegastes leucostictus* (beaugregory damselfish), B) *Malacoctenus macropus* (rosy blenny), C) *Sparisoma viride* (stoplight parrotfish), and D) *Scarus iserti* (striped parrotfish). ● Control reefs; ○ Nassau grouper reefs; ▼ Coney grouper reefs.

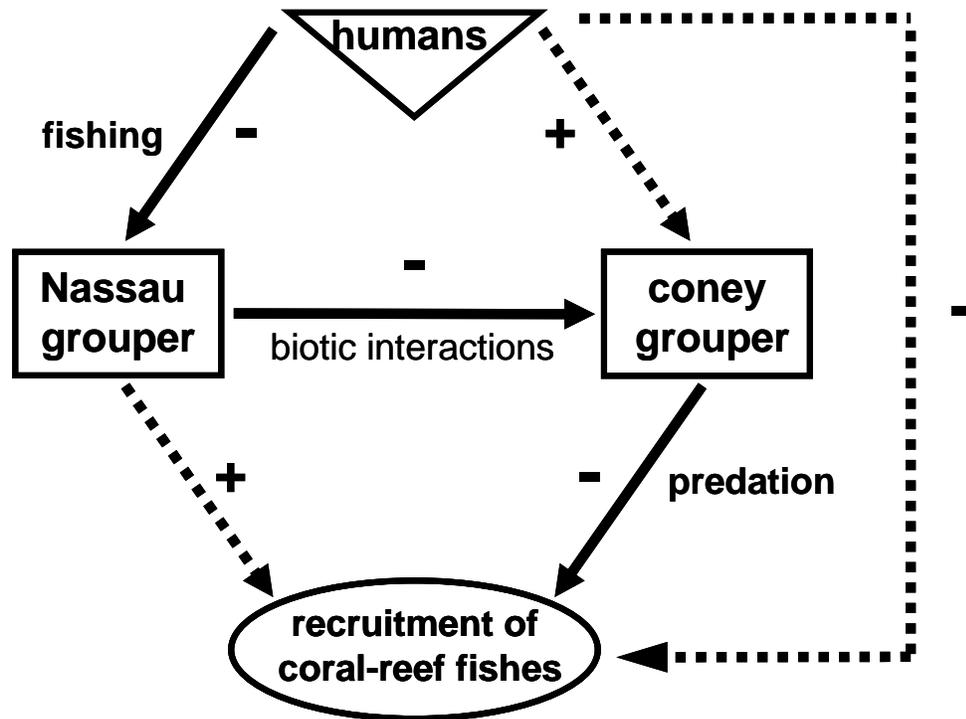


Figure 2.4. Model interaction web of direct effects (solid arrows) and indirect effects (dashed arrows) of fishing on predatory groupers and recruitment of coral-reef fishes in a Bahamian food web.

Chapter 3:

Indirect effects of an exploited grouper on recruitment of coral-reef fishes

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Ecology (in review)

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Abstract. Indirect interactions are common in ecological communities, and may be especially strong when populations of top predators are reduced by human activities. I examined interactions among fished and unfished predatory groupers and how these interactions affected recruitment of other coral-reef fishes. Previous observational studies indicated that reefs with lower abundances of fished groupers are inhabited by higher abundances of unfished groupers, and field experiments demonstrated that these different predatory fishes had dramatically different effects on lower trophic-level species. Here I examined experimentally how two unfished groupers--coney (*Cephalopholis fulva*) and graysby (*C. cruentata*)--were affected by variation in the densities of the fished Nassau grouper (*Epinephelus striatus*) on 20 isolated patch reefs in the Bahamas. With increasing Nassau grouper abundance, persistence of the unfished groupers remained high, but their activity levels and growth decreased. Although *Cephalopholis* groupers can be voracious predators on coral-reef fish recruits, recruitment of other reef fishes increased with increasing Nassau grouper abundance. These results indicate that Nassau grouper indirectly increased recruitment through nonlethal changes in the behavior of unfished groupers. Incorporating the complexity of such indirect effects into fisheries management may improve the sustainability of fished populations as well as strengthen marine conservation efforts.

INTRODUCTION

Indirect effects of predators on the structure of ecological communities have long been recognized (e.g., Hairston et al. 1960, Paine 1966), and have more recently been shown to be both ubiquitous and often strong (Menge 1995, Werner and Peacor 2003). Indirect interactions are transmitted to receiving species when an initiating species changes the abundance (density-mediated) or induces trait plasticity (trait-mediated, including behavior) of a transmitting species (Kerfoot and Sih 1987, Abrams 1995). Although often studied across distinct trophic levels (e.g., predators – herbivores – primary producers), indirect interactions can also be transmitted to lower trophic-level prey through interactions between top and intermediate predators (Schmitz et al. 2004).

Fishing commonly targets and removes large, top predatory fishes (Myers and Worm 2005). As fished species are removed, smaller, non-targeted predators may increase in biomass. For example, fishing in the Bahamas has reduced the biomass of Nassau grouper (*Epinephelus striatus*; Serranidae) while the smaller, usually non-targeted coney (*Cephalopholis fulva*; Serranidae) and graysby (*C. cruentata*; Serranidae) groupers have increased in abundance (Sluka et al. 1996, Chiappone et al. 2000). It has been demonstrated that Nassau grouper do not directly affect recruitment of coral-reef fishes on patch reefs, but that coney grouper can strongly reduce recruit abundance and diversity (Stallings in revision).

Intense fishing for Nassau grouper may therefore have positive, indirect effects on coney and graysby grouper biomass, and thus negative, indirect effects on recruitment of other fishes, but additional work was needed to elucidate patterns and mechanisms.

In this study, I experimentally tested how the abundance of Nassau grouper affected the persistence, behavior, and growth of coney and graysby groupers, as well as recruitment of other coral-reef fishes. Manipulated abundances of Nassau grouper used in the field experiment simulated a gradient of fishing intensity, which provided insight on the effects of fishing and the mechanisms that mediated indirect effects on other coral-reef fishes.

METHODS

Study site

I conducted this study using SCUBA on a matrix of isolated coral patch reefs located on a shallow sand and seagrass flat (3–5 m deep) near the Caribbean Marine Research Center, Lee Stocking Island, Bahamas. The matrix of reefs was constructed by moving coral heads approximately 10 years before the current study (Hixon and Carr 1997), and were standardized for size (mean area = 6.6 m²; SD = 1.0), structural complexity, and distance between reefs (200 m). The nearest unmanipulated reef was located > 1.0 km from the edge of the matrix.

Experimental design

I manipulated the abundance of Nassau grouper on 20 of these patch reefs using methods described in Stallings (in revision). Each reef was assigned to one of six levels of Nassau grouper abundance. This was a regression-based experimental design where the number of Nassau grouper (with number of replicate reefs) was 0 (4), 1 (4), 2 (2), 3 (4), 4 (2), and 5 (4); a range that was within the natural abundances found on the patch reefs prior to manipulation (mean = 1.84, SD = 2.29, max = 7). The sizes of Nassau grouper did not differ by treatment (mean total length, TL = 24.9 cm; $F_4 = 0.76$, $P = 0.56$). I then added one coney or graysby grouper young-of-year (YOY) to each of the 20 patch reefs (coney mean TL = 6.2 cm; graysby mean TL = 6.6 cm; $t_{18} = 1.15$, $P = 0.27$). I used both coney and graysby groupers to broaden the scope of inference to multiple intermediate predatory species, and assigned these species evenly across the Nassau grouper treatments.

Prior to all grouper manipulations, I standardized the fish communities on the experimental reefs by removing all potential strongly interacting species (i.e., predators and competitors). All fish manipulations were maintained for the duration of the experiment (press experiment). Removals were conducted using the fish anesthetic quinaldine and hand nets. Fish removed from the experimental

reefs were released unharmed on reefs located greater than 3 km from the study site, and they did not return.

The experiment ran for 63 days between June and August 2005, when recruitment of coral-reef fishes tends to be highest in the Bahamas (Thorrold et al. 1994). Once the treatments were established, I conducted surveys on each experimental reef every seven days. During each survey, I checked for the presence of the YOY grouper on each reef and monitored its activity level. Activity levels of the YOY grouper during the initial five minutes of the survey were assigned to one of four categories: 1) hiding in reef holes the entire time, 2) hiding > 50% of time, 3) hiding < 50% of time, 4) exposed (outside reef holes) the entire time. I also measured the total lengths of the YOY groupers at the beginning (day 0), middle (ca. day 28), and conclusion (ca. day 63) of the experiment. Lastly, I conducted recruitment censuses of all coral-reef fishes during each survey, with the exception of two occasions (days 21 and 35) due to logistical constraints.

Statistical analyses

I analyzed persistence, behavior, and growth of the YOY groupers, each as a function of Nassau grouper abundance, using linear regression (S-Plus 6.2). I measured persistence as the number of days the YOY grouper remained on the

reef. I calculated the mean behavior score for each YOY grouper across all surveys. Because the four behavioral categories represented a near continuum of activity level, and the responses were averaged across all observations, the data were considered to be continuous (Sokal and Rolf 1995). I calculated growth rates (mm/day) of the YOY grouper by dividing the change in total length by the time between measurements.

I analyzed the indirect effects of Nassau grouper abundance on coral-reef fish recruitment at both the community and species levels. At the community level, I compared temporal changes in cumulative fish recruitment among treatments using Canonical Discriminant Analysis (CDA; SPSS 10.0). All species that accounted for at least 1% of the total observations were included in the ordination, and the data were $\ln(x + 1)$ transformed to approximate normality and stabilize variability (Sokal and Rolf 1995). Agreement between the CDA and a Principal Components Analysis (S-Plus 6.2) indicated that the experimental treatment, rather than natural variation, was the dominant signal in the data (Tabachnick and Fidell 2001). I displayed the effects of the CDA using the treatment-by-census matrix, where each treatment at each census was assigned with a unique code (6 treatments x 8 censuses = 48 codes). I used the CDA only as a tool to display changes in time, not for inferential statistics.

At the species level, I analyzed the change in abundance (final – initial) for each of the common species ($\geq 1\%$ total observations) as a function of Nassau grouper abundance using linear regression (S-Plus 6.2). Ten species were deemed common, and I used Bonferroni corrections for multiple comparisons ($\alpha = 0.05/10 = 0.005$).

RESULTS

Persistence, behavior, and growth of small grouper

Persistence of young-of-the-year (YOY) groupers was high across all tested Nassau grouper abundances. The only losses occurred during the final week of the experiment (between days 56 and 63), and included one YOY coney grouper each on reefs with 0 and 1 Nassau grouper. The other 18 YOY grouper (one per reef) persisted for the duration of the entire experiment.

The behavior of the YOY groupers was affected by the number of Nassau grouper present on the reefs. Both coney and graysby groupers spent more time hiding as the abundance of Nassau grouper increased ($r^2 = 0.745$, $P < 0.001$) (Fig. 1). Both species exhibited a similar decline in activity with increased Nassau grouper abundance (i.e., regression slopes were parallel; ANCOVA interaction $P = 0.656$), although graysby grouper had a lower overall activity mean (i.e., lower y-intercept).

Growth of the YOY groupers was also affected by the number of Nassau grouper present on the reefs. The growth rates of both coney and graysby groupers decreased with increasing abundances of Nassau groupers ($r^2 = 0.386$, $P = 0.003$) (Fig. 2). Again, the slopes were not different between coney and graysby groupers (ANCOVA interaction $P = 0.524$).

Communities of reef-fish recruits

A total of 36 species of coral-reef fishes recruited to the experimental reefs, of which, 26 were rare (each < 1% of total abundance). I combined the abundances of four rare wrasses (Family Labridae) of the genus *Halichoeres* (*H. garnoti*, *H. maculipinna*, *H. pictus*, and *H. radiatus*) and all grunts (*Haemulon* spp., Family Haemulidae, mostly *H. plumieri*) into separate response groups. I included these two groups with the eight most common individual species in the CDA. For simplicity, I will hereafter refer to these combined groups as “species.” These ten common species comprised 99.24% of the total observations.

The recruit communities were indistinguishable among Nassau grouper treatments at the beginning of the experiment. After about two weeks, however, the recruit communities on reefs with three or more Nassau grouper became and remained different from those with zero and one Nassau grouper (Fig. 3). Communities of fish recruits on reefs with two Nassau grouper initially changed in

similar ways to those on reefs with ≥ 3 Nassau grouper, but became indistinguishable from reefs with 0-1 Nassau grouper after about six weeks. The total abundance of recruits accounted for the most variation in community structure (canonical discriminant 1 = 68.7 %) and corresponded with greater recruitment to reefs with higher abundances of Nassau grouper.

Species-level comparisons among reef-fish recruits

Recruitment of the most abundant, conspicuous species increased with increasing abundance of Nassau grouper, especially the four most common species (> 10 % total observations): *Scarus iserti* (striped parrotfish, Scaridae), *Sparisoma viride* (stoplight parrotfish, Scaridae), *Malacoctenus macropus* (rosy blenny, Labrisomidae), and *Stegastes leucostictus* (beaugregory damselfish, Pomacentridae) (Table 1). Recruitment of two relatively common labrids (> 5 % total observations), *Thalassoma bifasciatum* (bluehead wrasse) and the *Halichoeres* species group, also increased with higher abundances of Nassau grouper. The remaining species were not affected by the number of Nassau grouper present and included two relatively common, but cryptic gobies (Gobiidae)--*Coryphopterus glaucofraenum* (bridled goby) and *Gnatholepis thompsoni* (goldspot goby)--and the relatively rare *Haemulon* species group and *Stegastes partitus* (bicolor damselfish, Pomacentridae).

DISCUSSION

The goal of this study was to examine the interactions between a large-bodied, intensively fished piscivore and small-bodied, typically unfished piscivores, as well as the resulting effects on recruitment of other coral-reef fishes. Increased abundance of Nassau grouper reduced the activity of the smaller coney and graysby (*Cephalopholis*) groupers, with attendant decreases in growth of the small groupers and increased recruitment of other coral-reef fishes.

Persistence of young-of-the-year (YOY) coney and graysby groupers was high, regardless of Nassau grouper abundance. This result was surprising because Nassau grouper aggressively chase (per obs.) and occasionally eat small *Cephalopholis* groupers (Randall 1967; C.D. Stallings unpublished data from laboratory aquaria). Nonetheless, increased Nassau grouper abundance strongly reduced the activity of YOY groupers. While the exact mechanism that drove the change in behavior remains unclear (e.g., aggressive interactions vs. avoidance behavior), coney and graysby groupers spent more time hiding, and therefore less time feeding, with increased abundance of Nassau grouper.

Cephalopholis groupers have strong, direct negative effects on recruitment of coral-reef fishes, almost certainly due to intense predation, while Nassau grouper eat mostly invertebrates until they reach a large size and so do not have

detectable direct effects on coral-reef fish recruits (Stallings in revision). The decreased foraging efforts of YOY groupers on reefs with higher abundances of Nassau grouper likely led to the observed increase in recruitment of lower trophic-level species. The effects of Nassau grouper on recruitment of other fishes were therefore indirect, positive, and entirely trait-mediated.

Understanding both how predators interact with one another and the ensuing effects on prey species can provide insight into both the factors that structure communities (Sih et al. 1998) and the potential consequences of removing top predators. Although further investigations are needed to determine whether the patterns found here scale-up in time and space, chronic anti-predator behaviors can persist and can have important effects on other species (Beckerman et al. 1997, Schmitz et al. 2003). Indeed, although interactions between predators can vary ontogenetically with changes in relative sizes (Rudolf 2006), smaller predators such as *Cephalopholis* groupers may never attain sizes large enough to entirely avoid predation by larger reef fishes. The apparent voracity of *Cephalopholis* groupers on recruits of other reef fishes (Stallings in revision) and possibly that of other small predators may have resulted from selection for individuals that are successful at attaining food while remaining highly vigilant, a necessary trade-off for coexistence if larger predatory fishes commonly prey upon them (Polis and Holt 1992, Holt and Polis 1997).

Large predatory fishes are often targeted by fishing activities, and as a consequence, many of the world's populations of these fishes have been greatly reduced (Pauly et al. 1998, Jackson et al. 2001, Myers and Worm 2005). In this context, fishermen act as predators that may themselves initiate indirect effects on other species. As indicated by this study, in response to a release of predation by or competition with larger predators, smaller predatory fishes can increase in biomass (a density-mediated effect) and forage more actively (a trait-mediated effect), thereby potentially having important indirect effects on prey species. Such indirect effects add complexity to management and conservation efforts. In the current study, recruitment of five fishes from four families decreased as the small groupers became more active (Table 1). The ecological functions of these five fishes are likely very different, with notable roles performed by parrotfishes for the maintenance and recovery of coral reefs (Hughes 1994, Pandolfi et al. 2003, Mumby et al. 2006). Preservation of these ecological functions may keep these systems from alternating between desirable and undesirable stable states (Knowlton 1992, 2004). Fishing for large predators such as Nassau grouper can therefore have effects that cascade through the food web (Duffy 2002, Dulvy et al. 2004, Frank et al. 2005, Myers et al. 2007) and affect ecological stability (McCann 2000).

The effects of extractive activities can be both complex (Walters and Kitchell 2001) and unpredictable (Hughes 1994, Jackson et al. 2001, Carr et al. 2002). Future management and conservation efforts may have to account for both the direct and the indirect effects of resource use in order to be successful. Trait-mediated indirect interactions can be as strong as or stronger than direct consumptive (Preisser et al. 2005) and density-mediated indirect ones (Menge 1995, Dill et al. 2003, Werner and Peacor 2003). Accounting for such effects is therefore nontrivial, and not doing so can result in failure of fisheries (Hutchings 1996). Although logistically challenging, increased research on large bodied predators is necessary to improve our understanding of the more pervasive effects of predator removal on community dynamics. Such efforts can then better direct more holistic approaches to management (Francis et al. 2007).

ACKNOWLEDGMENTS

I am very grateful to J. Noell, J. Schellinger, and D.W. Johnson for their assistance in the field, and to M.H. Carr and M.A. Hixon for use of the translocated reefs. I thank the participants in the “Coney-for-Kalik” program for helping me locate and catch enough small groupers to conduct this study. This paper is a chapter from my dissertation, which benefited from comments by my doctoral committee -- M.A. Hixon (chair), S.A. Heppell, B.A. Menge, P.A. Murtaugh, and A.W. Stoner - - and by M. Albins, D.W. Johnson, and XX anonymous reviewers. Financial support was provided by a Thompson Fellowship to the author, and NSF grants OCE-00-93976 and OCE-05-50709, as well as grants from the National Undersea Research Program, courtesy of the Caribbean Marine Research Center, to M.A. Hixon.

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Table 3.1. Regression statistics of change in the abundance of coral-reef fish recruits between the first and last censuses, for the 10 most common species (99.24 % of total observations) across six levels of Nassau grouper abundance ($n = 20$ reefs).

Species	% Total observations	r^2	Intercept	se	Coefficient	se	t	P
<i>Scarus iserti</i>	25.78	0.60	-0.67	1.81	3.49	0.63	5.53	< 0.001
<i>Sparisoma viride</i>	16.77	0.62	-0.94	1.12	2.24	0.39	5.75	< 0.001
<i>Malacoctenus macropus</i>	12.79	0.74	-0.70	0.75	1.95	0.26	7.49	< 0.001
<i>Stegastes leucostictus</i>	12.27	0.61	-0.60	0.74	1.43	0.26	5.56	< 0.001
<i>Coryphopterus glaucofraenum</i>	11.95	0.08	1.53	0.91	0.41	0.32	1.31	0.205
<i>Thalassoma bifasciatum</i>	7.42	0.35	-1.00	0.70	0.80	0.24	3.28	0.004
<i>Halichoeres</i> spp.	5.75	0.25	-0.69	0.43	0.39	0.15	2.61	0.017
<i>Gnatholepis thompsoni</i>	4.02	0.01	0.63	0.66	0.11	0.23	0.47	0.647
<i>Haemulon</i> spp.	1.35	0.14	-0.04	0.25	0.16	0.09	1.82	0.084
<i>Stegastes partitus</i>	1.14	0.06	0.05	0.21	0.08	0.07	1.14	0.268

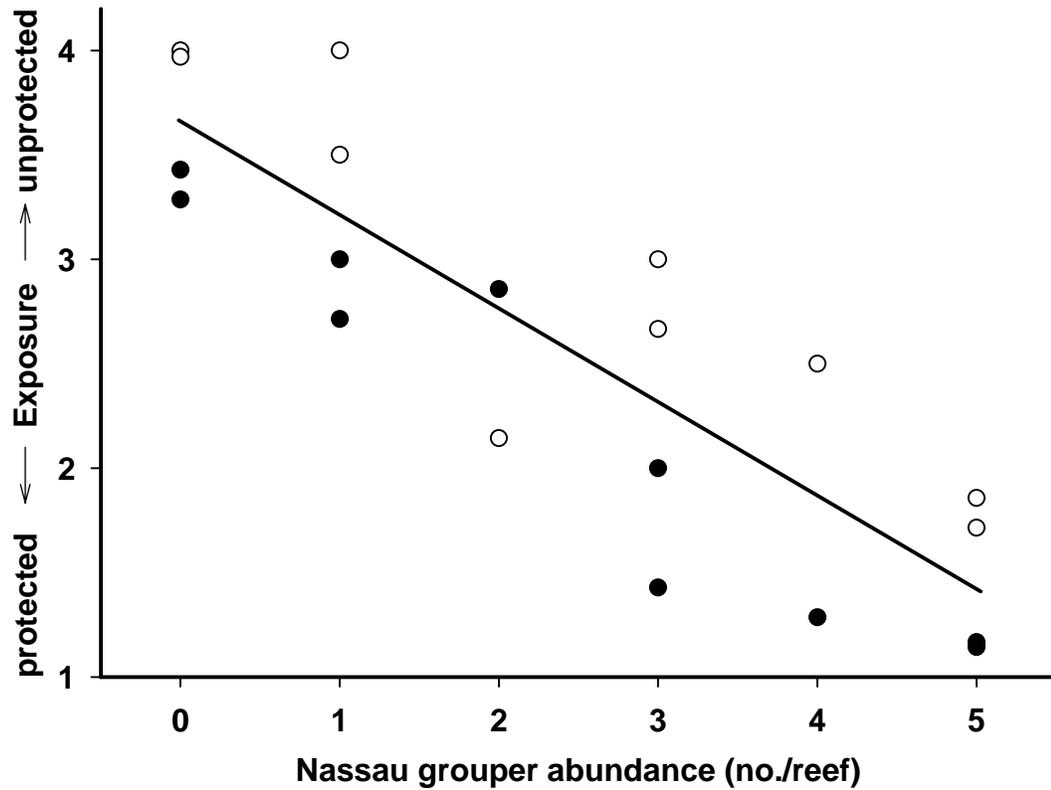


Figure 3.1. Behavior (ranging from protected inside to exposed outside reef holes) of *Cephalopholis* groupers across six levels of Nassau grouper abundance. Data are averaged across surveys for each individual fish and the regression is for the combined data for *C. fulva* (open circles) and *C. cruentata* (closed circles).

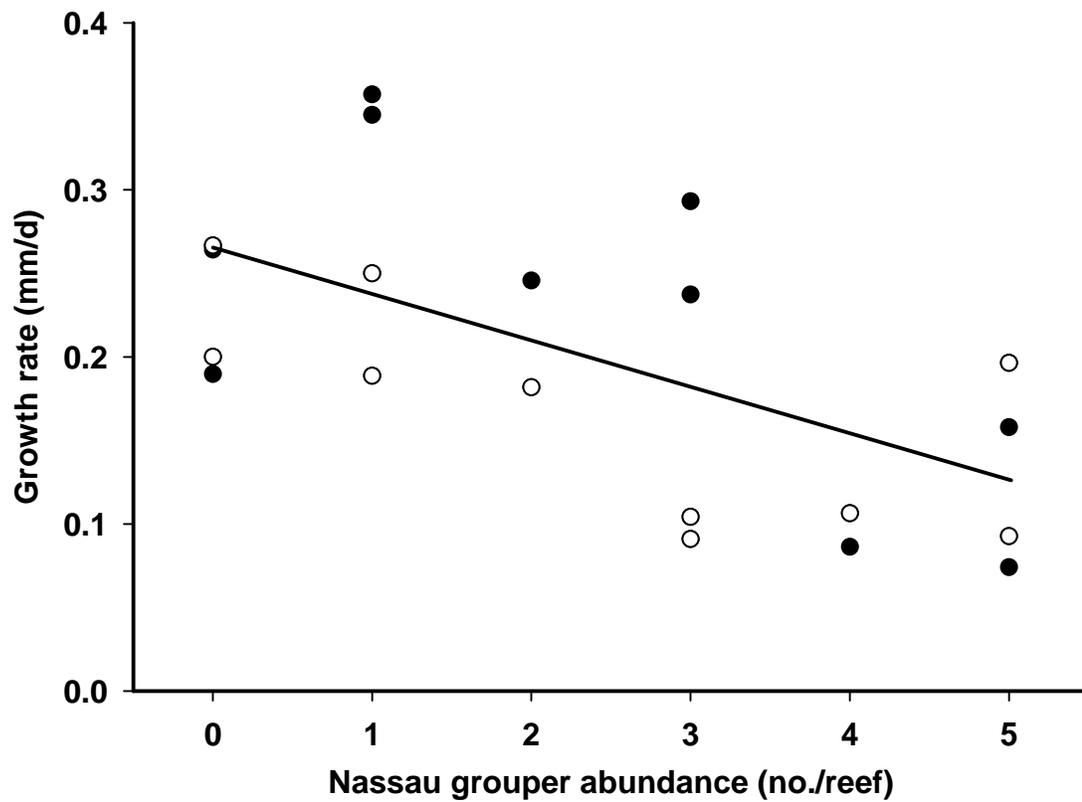


Figure 3.2. Growth rates of *Cephalopholis* groupers across six levels of Nassau grouper abundance. Regression is for the combined data for *C. fulva* (open circles) and *C. cruentata* (closed circles).

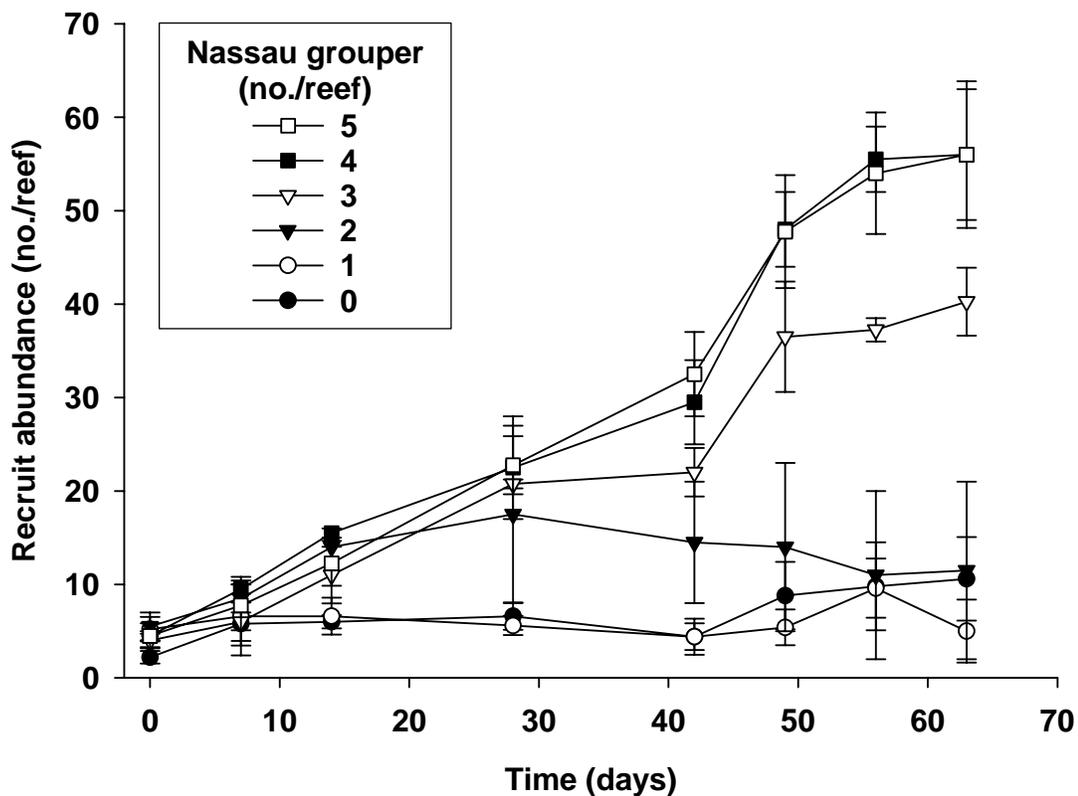


Figure 3.3. Temporal changes in abundance of fish recruits on reefs occupied by different abundances of Nassau grouper. To simplify interpretation, total abundance (mean \pm SE) of fish recruits is displayed instead of scores on the first canonical discriminant, but the patterns were qualitatively identical. Recruit censuses were not conducted on days 21 and 35 due to logistical constraints.

Chapter 4:

Human population density and declines of predatory fishes in the Caribbean

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Nature (in review)

Nature Publishing Group

Abstract: Artisanal fishing in developing nations, like industrial and recreational counterparts in developed nations, typically targets large-bodied, top trophic-level fishes. However, few data have been available to assess the impacts of such extraction on predatory fish populations and the ecological communities to which they belong. This difficulty was overcome by examining human population density as a surrogate of fishing intensity, and predatory fish distribution data from volunteer SCUBA-diver surveys across the greater Caribbean region. Comparing among regions, as human population density increases, abundances of large-bodied fishes decline, and fish communities become dominated by a few smaller-bodied species.

INTRODUCTION

Recent high-profile studies have indicated substantial impacts of commercial and recreational fisheries on populations and communities of predatory fishes worldwide (Pauly et al. 1998, Myers and Worm 2003, Coleman et al. 2004, Myers and Worm 2005, Worm et al. 2005, Essington et al. 2006, Sibert et al. 2006, Worm et al. 2006). These studies have based their conclusions on extensive databases of fisheries landings statistics, primarily from developed nations. The effects of artisanal (subsistence or small-scale commercial) fisheries on piscivores in developing nations have not received as much attention because there is a general lack of landings statistics (Russ 1991, Polunin et al. 1996, Sale 2002, Sadovy 2005).

Here, I use a publicly accessible, fisheries-independent database (REEF 2006) to provide a broad-scale, comprehensive analysis of human impacts on predatory reef-fish communities across the greater Caribbean region. I demonstrate that the composition of these communities varies substantially and that overall abundance and diversity of predatory reef-fishes decrease over a gradient of human population density. These findings fill a fundamentally important gap in our knowledge of the ecosystem effects of artisanal fisheries in developing nations.

METHODS

I queried predator presence/absence data from locations across the greater Caribbean region (Fig 4.1) using the Reef Environmental Education Foundation's (REEF) online database on February 16, 2006 (www.reef.org). The data included coral-reef habitats located in 23 continental and insular nations and consisted of 29,917 surveys conducted between 1996 and 2006. Within each of the 23 nations, I chose survey locations with a minimum of 10 surveys (Table 4.1). The data were collected by volunteer SCUBA divers using the Roving Diver Technique (RDT) where divers swim freely around a survey site and record all species that can be positively identified (Schmitt and Sullivan 1996). The RDT was specifically designed for volunteer data and is effective at rapid assessment of both fish distribution and abundance (Schmitt et al. 2002). Although the data from the REEF database were also available in a four-categorical, \log_{10} abundance format, I used presence data because they serve as an appropriate proxy for abundance at large spatial scales (McCune and Grace 2002), are more readily interpreted than the categorical data, and reveal stronger relations than the categorical data relative to population size (Appendix A).

I included all predators (trophic level ≥ 4 ; Froese and Pauly 2007) that met two fundamental criteria. First, their natural distributions included each of the 23

nations included in the study (Allen 1985, Heemstra and Randall 1993, Humann and DeLoach 2002, Froese and Pauly 2007). Secondly, because the data were collected by “amateur” scientists, I included only conspicuous species. Although cryptic species (e.g., moray eels, Muraenidae; lizardfishes, Synodontidae) were recorded by the divers, it was not clear how accurate the RDT was at estimating their presence. Twenty taxa of predatory fishes met the above criteria and included eight species of grouper (Family Serranidae), eight species of snapper (Lutjanidae), one species each of trumpetfish (Aulostomidae) and barracuda (Sphyraenidae), and jacks (Carangidae) and requiem sharks (Carcharhinidae) summarized at the family levels (Table 4.2). The 20 taxa included a range in maximum attainable total lengths from 40 cm to over 300 cm.

The predator presence/absence data had extremely low Whitaker’s beta diversity ($\beta = 0.1$) and low values of the coefficient of variation for both taxa ($CV = 77.1$) and sample units ($CV = 26.2$), and therefore did not require transformation. I removed two sample unit outliers, due to low total predator sightings across all species, using Sorensen’s distance measure of 2.0 standard units greater than the overall average among all sample units.

I ordinated the matrix of sample units by taxa presence using non-metric multidimensional scaling (NMS) (Kruskal 1964, Mather 1976). To investigate the

influence of human activities on the structure of the ordination, I constructed an environmental matrix with human population density (people per square kilometer) (United Nations 2005) across the 23 nations. I also included latitude data in the environmental matrix to investigate any biogeographical influences. The ordinations of sample units in species space are presented graphically, with overlays of the environmental data. I simplified the presentation by displaying national centroids and by grouping nations from the Lesser Antilles into ‘Windward’ (i.e., Barbados, Grenada, St. Lucia, St. Vincent and the Grenadines) and ‘Leeward’ (i.e., Anguilla, Antigua, Dominica, Saba, St. Eustatius, St. Kitts, St. Martin) islands. The resulting ordination displayed 14 regions across the greater Caribbean region. I ran all NMS ordinations in PC-ORD 5.14 using the ‘Autopilot Mode’ with Sorensen distance measure and random starting configurations (McCune and Mefford 1999).

I conducted linear regressions between human population densities and several metrics of the predator presence data per sample unit: 1) mean and median presence across all taxa as a metric of overall predator abundance, 2) richness (S , the total number of species), Shannon-Wiener Index of composite diversity ($H' = \sum (p_i \ln p_i)$), and evenness ($J = H' / \ln S$), and 3) skewness and kurtosis of the predator presence data. These analyses were used in combination with the ordinations to

arrive at a clearer understanding of the structure of predatory fish communities across the Caribbean.

Groupers and snappers are among the most speciose families of predatory reef-fishes in the Caribbean, with a range of maximum total lengths for the species included here from $< 0.5\text{m}$ to $> 1.5\text{m}$ (Froese and Pauly 2007). I therefore conducted additional NMS ordinations on both families to investigate their within-family associations with the survey locations relative to maximum sizes of each species. The first axes of both ordinations were strongly correlated with human population densities. The NMS scores along the first axis therefore served as an index of human population density in multivariate space for both ordinations. I analyzed how the sizes of the associated species changed across the index of human population densities using linear regressions of the NMS scores versus the maximum attainable lengths and masses of each species (Froese and Pauly 2007).

RESULTS

The NMS ordination converged on a stable, 2-dimensional solution (final stress = 16.53, final instability = 0.00048, iterations = 74) (Fig. 4.2). The first axis accounted for the majority of variation in the NMS ($r^2 = 0.695$), and was strongly correlated with both human population density ($r = 0.732$) and latitude ($r = 0.686$). The structure of the ordination was driven by strong associations of sharks

(Carcharhinidae), jacks (Carangidae), and large species of groupers (Serranidae) and snappers (Lutjanidae) with regions of low human population density (high latitude). The pattern was also driven by moderate associations of trumpetfish (Aulostomidae) and smaller species of groupers and snappers with regions of high human population density (low latitude) (Fig. 4.2). The second axis accounted for less variation ($r^2 = 0.155$) and was driven by regional differences in which particular taxa of large or small predators predominated.

Mean and median sighting frequencies decreased 2.2 – 4.0 % ($r^2 = 0.38$, $P < 0.0001$) and 4.1 – 7.1 % ($r^2 = 0.41$, $P < 0.0001$), respectively, per incremental increase of 100 humans per km². The predator communities exhibited lower richness ($r^2 = 0.19$, $P < 0.0001$), Shannon-Wiener composite diversity ($r^2 = 0.53$, $P < 0.0001$), and evenness ($r^2 = 0.40$, $P < 0.0001$) with increasing density of humans. In addition, the distributions of the predator presence data displayed higher skewness ($r^2 = 0.33$, $P < 0.0001$) and kurtosis ($r^2 = 0.17$, $P = 0.0001$) with increasing human density, indicating that fewer taxa accounted for increased proportions of predatory fish sightings. At the taxon level, 15 of the 20 predators were sighted less frequently with increasing human population density (Table 4.2). The remaining five predatory taxa were sighted either evenly or at increasing frequencies with increasing human population density, and included the smallest species of grouper (*Cephalopholis cruentata* and *C. fulva*) and snapper (*Lutjanus*

mahogoni and *L. synagris*), as well as the non-targeted trumpetfish (*Aulostomus maculatus*).

The grouper (final stress = 11.18, final instability = 0.00045, iterations = 59) and snapper (final stress = 11.21, final instability = 0.00045, iterations = 59) NMS ordinations each converged on stable, 3-dimensional solutions. The first axis of the grouper ordination accounted for the majority of variation ($r^2 = 0.546$; cumulative $r^2 = 0.915$) and was strongly correlated with human population density ($r = 0.754$). The first axis of the snapper ordination also accounted for the majority of variation ($r^2 = 0.587$; cumulative $r^2 = 0.940$) and was correlated with human population density ($r = 0.568$). The linear regressions within both families indicated strong decreases in both maximum length and maximum mass of the species associations with regions along the index from low to high human population densities (Fig 4.3).

DISCUSSION

The analyses presented here illustrate substantial differences in predatory reef-fish communities across the greater Caribbean region. Understanding the factors that drive these differences is ecologically interesting, but may also be extremely important to conservation and management efforts if the patterns are driven by anthropogenic impacts.

Human population densities tend to increase towards lower latitudes in the Caribbean region ($r = -0.576$). Although the structure of predatory fish communities within the region may vary along environmental gradients correlated with latitude per se, anthropogenic impacts better describe the patterns from the ordination for two reasons. First, although all taxa included in the analysis are naturally distributed across all locations in the study region, most fishes, particularly the larger-bodied ones, were rare or completely absent in surveys conducted in areas of high human population density. These patterns were evident in both the compressed, multivariate space (i.e., all large-bodied predators grouped on the left/negative side of axis 1, Fig. 4.2) and in the presence data of individual taxa (Table 4.2). In addition, historical data further illustrate that large groupers, snappers, and sharks were once abundant throughout the Caribbean, including reefs located in the Greater and Lesser Antilles where several of the species examined here are now ecologically or locally extinct (Dampier 1729, Jackson 2001, Levin and Grimes 2002).

Second, comparisons between inhabited and uninhabited islands within otherwise densely populated regions highlight potential human-induced impacts (Friedlander and DeMartini 2002, Miller and Gerstner 2002). For example, Isla de Mona and Navassa Island are uninhabited, relatively isolated nature reserves near the densely populated islands of Puerto Rico and Jamaica, respectively. The

similarities between the predator communities at these locales and those at other locations of low human density can be detected in both the ordinated space (italicized locations, Fig. 4.2) and in the presence/absence data for each taxon. Sighting frequencies of large-bodied predators, such as sharks, jacks, barracuda, and large groupers and snappers, were two to three times higher on reefs adjacent to the uninhabited islands relative to nearby inhabited ones. The more extensive presence of these predators within regions where they are otherwise rare or completely absent indicates that anthropogenic effects, not latitudinal gradients, limit the presence of these large-bodied fishes.

Fishing tends to target large-bodied fishes, and increased numbers of fishermen per unit area should therefore result in increased removal of larger species (Hawkins and Roberts 2004, Newton et al. 2007). Indeed, large predators were increasingly rare with increasing human population densities both in the taxon regressions and the grouper and snapper ordinations. Artisanal fishing tends to target multiple species, however, including smaller, lower trophic-level fishes (e.g., haemulids, scarids) that may serve as food items for large predators (Munro 1996). The large-bodied predators may therefore experience both direct top-down (via fishing mortality) and indirect bottom-up (via decreased prey) effects of fishing, leading to the observed shifts in sizes among predators.

Large-bodied fishes are typically longer lived and mature more slowly than smaller ones, and many form spawning aggregations, all of which increase their vulnerability to overfishing (Roberts 1997, Huntsman et al. 1999, Jennings et al. 1999, Sala et al. 2001, Levin and Grimes 2002). Removal of large-bodied predators may have allowed small-bodied predators to increase in abundance due to release from competition or predation. Different sized predators may also perform different functional roles and can have drastically different impacts on the diversity and abundance of prey species (Hixon and Carr 1997, Stallings in revision). Furthermore, loss of functional roles can lead to decreased ecological stability (McCann 2000), and management of human impacts on entire functional groups of predatory species may be more important than on specific taxa (Hughes et al. 2005). Continued efforts at both broad (Mumby et al. 2006, Newman et al. 2006) and fine spatial scales are necessary to better understand potential cascading and indirect effects of human impacts on marine ecosystems (Hughes et al. 2003, Pandolfi et al. 2005, Myers et al. 2007).

ACKNOWLEDGMENTS

I thank M. Briya, S. Heppell, M. Hixon, D. Johnson, B. McCune, B. Menge, P. Murtaugh, and A. Stoner for comments and discussion, the REEF volunteer divers for collecting data, and C. Pattengill-Semmens for assistance with REEF data acquisition and organization. This work was funded by NSF grants OCE-00-93976 and OCE-05-50709 to M. Hixon.

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Table 4.1. Fourteen regions from which REEF survey data are summarized, including human population density.

Country/region	Code	survey locations	total surveys	people/km ²
Belize	BZ	6	1691	12
Bahamas	BA	15	7083	21
Turks and Caicos	TC	10	2581	47
Mexican Caribbean	MC	5	3881	53
Honduras	HD	4	2124	62
Cuba	CU	3	567	102
Leeward Islands	LI	7	1468	131
British Virgin Islands	BV	3	1836	147
Cayman Islands	CI	4	3443	168
Dominican Republic	DR	4	202	183
Jamaica	JA	5	312	248
US Virgin Islands	UV	3	2049	308
Windward Islands	WI	7	1751	356
Puerto Rico	PR	7	929	430

Table 4.2. Predatory reef-fish taxa included in the analyses, including published maximum total lengths and calculated maximum masses. Regression statistics are for each taxon against human population density.

Family	Taxa	Common name	Maximum TL (cm)	Maximum calculated mass (kg)	Intercept	se	Coef	se	<i>t</i>	<i>P</i>
Aulostomidae	<i>Aulostomus maculatus</i>	trumpetfish	100	2.2	0.53	0.03	0.00041	0.0001	2.71	0.0082
Carangidae	<i>Caranx</i> spp.	jacks	69*	5.7*	0.32	0.03	-0.00082	0.0001	-6.4	0.0000
Carcharhinidae	<i>Carcharhinus</i> spp.	requiem sharks	300*	731.7*	0.32	0.03	-0.00082	0.0001	-6.4	0.0000
Lutjanidae	<i>Lutjanus cyanopterus</i>	cupera snapper	160	84.4	0.05	0.01	-0.00013	0.0000	-3.9	0.0002
	<i>L. jocu</i>	dog snapper	128	56.3	0.10	0.01	-0.00015	0.0001	-2.2	0.0309
	<i>L. analis</i>	mutton snapper	94	12.7	0.17	0.02	-0.00022	0.0001	-2.3	0.0260
	<i>L. griseus</i>	gray snapper	89	10.2	0.15	0.02	-0.00022	0.0001	-2.8	0.0072
	<i>Ocyurus chrysurus</i>	yellowtail snapper	86	10.0	0.80	0.03	-0.00062	0.0001	-5.1	0.0000
	<i>L. apodus</i>	schoolmaster	67	5.7	0.62	0.03	-0.00073	0.0002	-4.7	0.0000
	<i>L. synagris</i>	lane snapper	60	4.4	0.05	0.01	0.00011	0.0001	1.98	0.0513
	<i>L. mahogoni</i>	mahogany snapper	48	1.6	0.37	0.03	0.00022	0.0002	1.41	0.1632
Serranidae	<i>Mycteroperca bonaci</i>	black grouper	148	55.8	0.17	0.02	-0.00049	0.0001	-5.5	0.0000
	<i>Epinephelus striatus</i>	Nassau grouper	122	35.5	0.47	0.04	-0.00129	0.0002	-7.6	0.0000
	<i>M. tigris</i>	tiger grouper	101	16.9	0.32	0.03	-0.00082	0.0001	-6.4	0.0000
	<i>M. venenosa</i>	yellowmouth grouper	100	12.2	0.08	0.01	-0.00018	0.0001	-3.2	0.0023
	<i>E. guttatus</i>	red hind	76	5.7	0.26	0.02	-0.00005	0.0001	-0.4	0.6733
	<i>E. adscensionis</i>	rock hind	61	3.5	0.10	0.01	-0.00015	0.0001	-2.1	0.0355
	<i>Cephalopholis cruentata</i>	graysby	43	1.3	0.50	0.03	0.00033	0.0001	2.29	0.0248
	<i>C. fulva</i>	coney	41	1.1	0.52	0.04	0.00006	0.0002	0.3	0.7670
Sphyraenidae	<i>Sphyraena barracuda</i>	barracuda	200	139.8	0.49	0.03	-0.00071	0.0001	-5.1	0.0000

* Size data for sharks and jacks are for Caribbean reef shark (*Carcharhinus perezi*) and bar jack (*Caranx ruber*), respectively, which were among the smallest species in their families and were therefore conservative estimates.

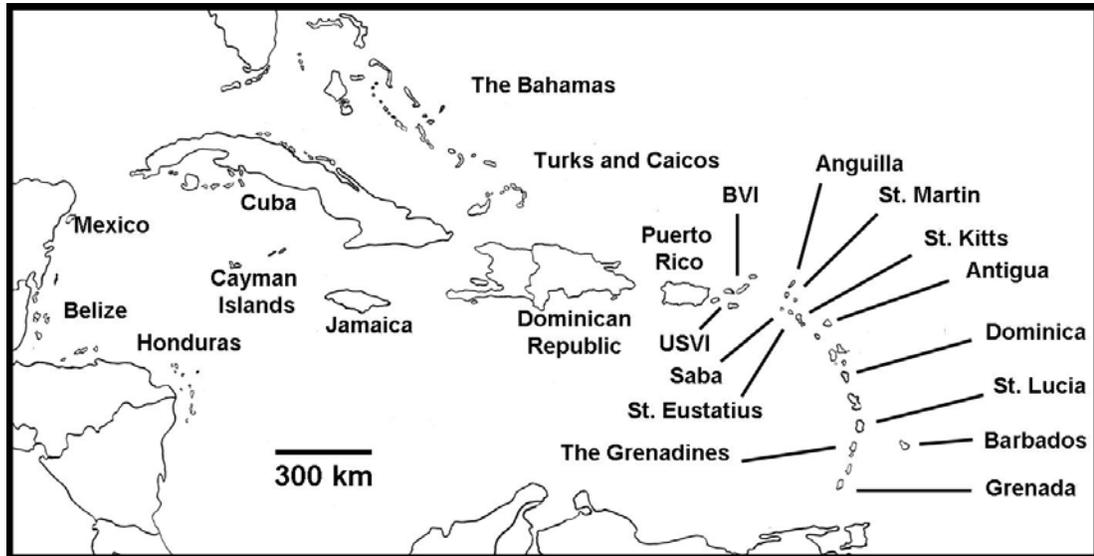


Figure 4.1. Map of Caribbean locations from which predator presence data were gathered. The data were from all locations in which at least 10 volunteer diver surveys were conducted between 1996 and 2006.

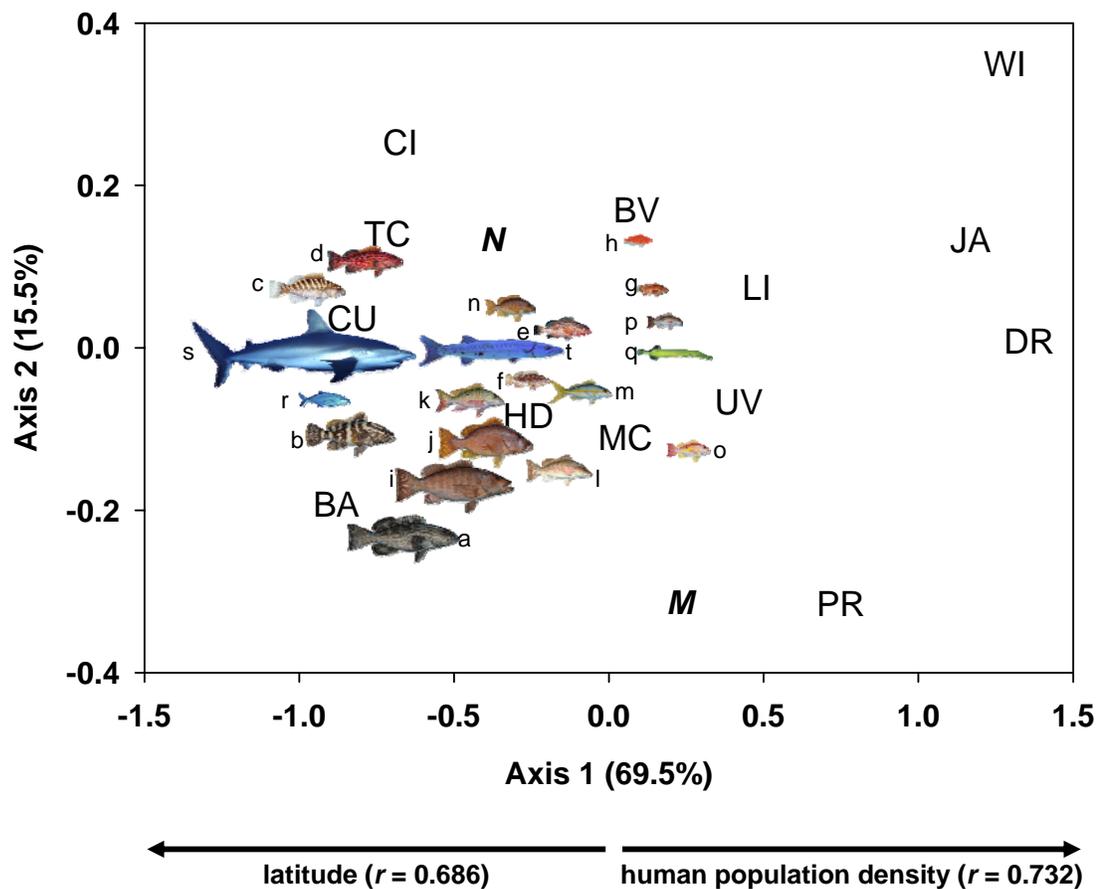


Figure 4.2. NMS ordination of regions in predatory fish space (20 taxa). Regional centroids are displayed: BA (Bahamas); TC (Turks and Caicos); CU (Cuba); CI (Cayman Islands); JA (Jamaica); MC (Mexican Caribbean); BZ (Belize); HD (Honduras); DR (Dominican Republic), PR (Puerto Rico); UV (US Virgin Islands); BV (British Virgin Islands); LI (Leeward Islands); WI (Windward Islands). The axis 1 scores for the two uninhabited islands are italicized: *MI* (Isla de Mona); *NI* (Navassa Island). Along axis 1, latitude increases towards the left and human population density increases towards the right. Taxon codes: a (*Mycteroperca bonaci*); b (*Epinephelus striatus*); c (*M. tigris*); d (*M. venenosa*); e (*E. guttatus*); f (*E. adscensionis*); g (*Cephalopholis cruentata*); h (*C. fulva*); i (*Lutjanus cyanopterus*); j (*L. jocu*); k (*L. analis*); l (*L. griseus*); m (*Ocyurus chrysurus*); n (*L. apodus*); o (*L. synagris*); p (*L. mahogoni*); q (*Aulostomus maculatus*); r (*Caranx* spp.); s (*Carcharhinus* spp.); t (*Sphyrna barracuda*).

Figure 4.3. Maximum published total lengths (A and B) and maximum calculated mass (C and D) for different species of serranids (A and C) and lutjanids (B and D) as a function of the NMS index of human population density. Taxon codes are in caption to Fig. 2. Regression statistics ($n = 8$ species each): (A) serranid maximum lengths ($r^2 = 0.777$, $P = 0.004$); (B) lutjanid maximum lengths ($r^2 = 0.784$, $P = 0.003$); (C) serranid maximum mass ($r^2 = 0.844$, $P = 0.001$); (D) lutjanid maximum mass ($r^2 = 0.795$, $P = 0.003$). NMS scores are from the axis that accounted for the most variation in the data. Axis variation explained and correlation with human population density: (A and C) serranid ordination (axis $r^2 = 0.546$, r with axis = 0.754); (B and D) lutjanid ordination (axis $r^2 = 0.457$, r with axis = 0.496).

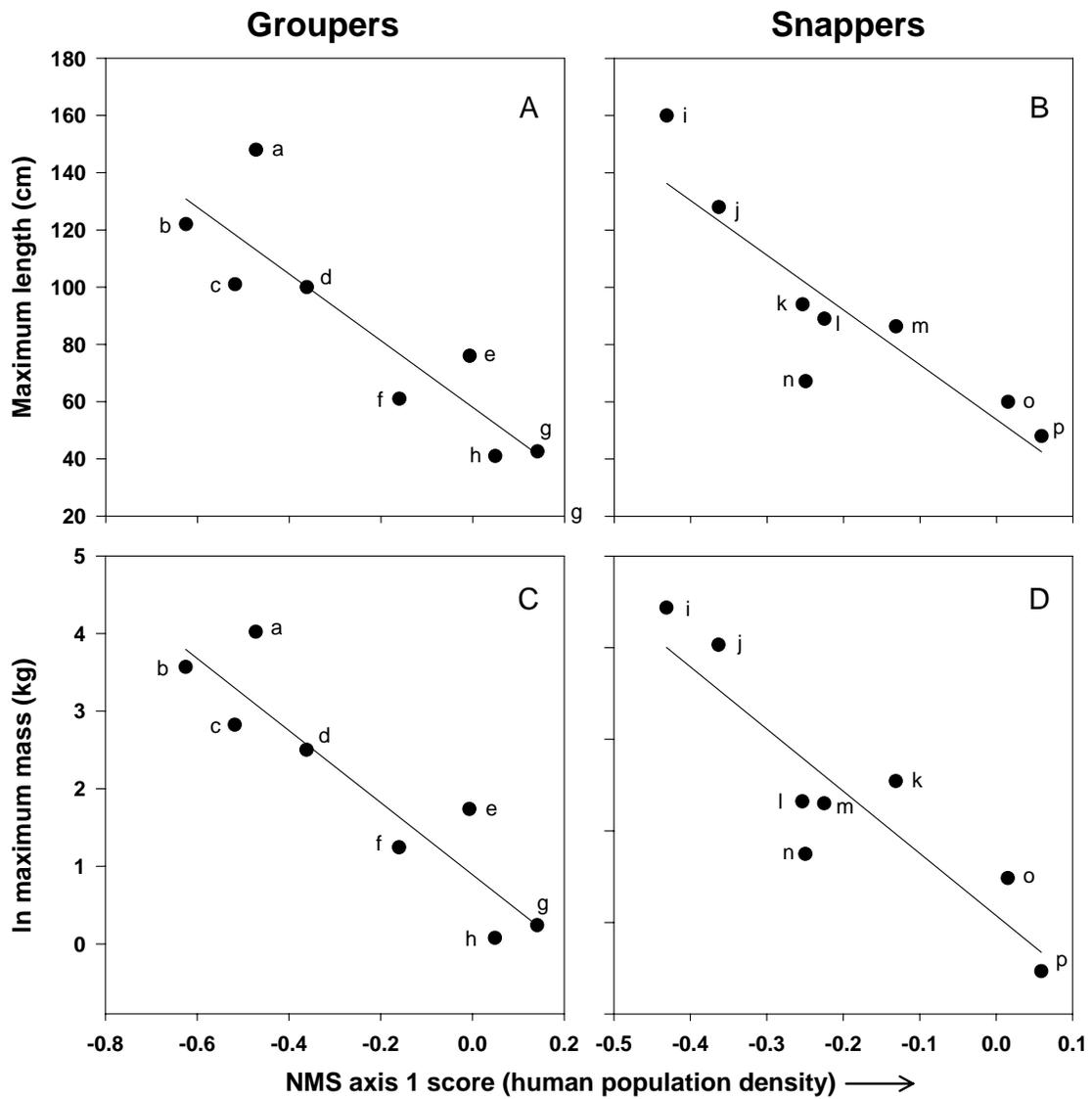


Figure 4.3

Chapter 5: General Conclusions

The research presented in this dissertation clearly demonstrates that fishing can have important effects on marine communities well beyond simple reductions in the populations of targeted species. Predatory fish communities have been greatly altered at both local (Bahamas) and regional (greater Caribbean) scales, primarily due to direct and indirect effects of fishing. In addition, the interactions among fished and unfished predatory species have been affected as a consequence of altered predator communities, with substantial effects on the behavior and foraging activities of predators, as well as the diversity and abundance of their prey.

In Chapter 2, I found that two species of closely related predatory fishes had very different effects on recruitment of other coral-reef fishes. Recruitment to reefs occupied by Nassau grouper (*Epinephelus striatus*; large fished predator) was similar to recruitment to grouper-free control reefs, and was higher in both diversity and abundance than on reefs occupied by coney grouper (*Cephalopholis fulva*; small unfished predator). Several species of coral-reef fishes, including two parrotfishes, a damselfish, and a blenny, recruited in higher abundance to the reefs with the fished piscivore compared to those with the unfished one. Decreased recruitment to reefs occupied by coney grouper was most likely due to intense

predation, whereas Nassau grouper did not appear to have a direct effect on recruitment. Given that previous observational studies had indicated that fishing may cause a shift in relative abundance of these different piscivorous species, this study highlights potential indirect and cascading effects of fishing on coral-reef fishes and possibly the rest of the coral-reef ecosystem.

In Chapter 3, I found that, as the abundance of Nassau grouper increased, the activity levels and growth of coney and graysby (*C. cruentata*; small unfished predator) groupers decreased. Accompanying the effects on the unfished groupers, recruitment of coral-reef fishes increased with higher abundances of Nassau grouper. Different effects on recruitment were once again almost certainly due to predation by the unfished groupers and there was no evidence to indicate that Nassau grouper had a direct effect on other coral-reef fishes. By altering the foraging behavior and thereby reducing predation by the unfished grouper, which appear to be voracious predators on newly recruited fishes, Nassau grouper indirectly enhanced recruitment of coral-reef fishes.

Lastly, the results presented in Chapter 4 indicate that the structure of predatory fish communities on coral reefs across the entire Caribbean region have been greatly altered by humans. As the density of human populations increases, overall predator abundance and diversity decreases, and predator communities

become dominated by only a few, small species. Although factors such as pollution (including eutrophication through increased nitrogen input) and habitat destruction may have contributed to these effects, fishing is the most likely mechanism to have caused these changes in communities of predatory reef fishes (Jenkins 2003, Hawkins and Roberts 2004).

Worldwide, marine fisheries science and management to date has been based primarily on single-species assessments of individual stocks to determine the maximum quantity the fishery is allowed to remove. Unfortunately, the single-species approach has largely been unsuccessful, in part because it has not incorporated the indirect effects of fishing beyond reductions in populations of targeted species. To increase the sustainability of fished populations, fisheries science and management must be reformed to account for both the direct and indirect effects of fishing on marine communities. Ecosystem-based approaches to fisheries management have become the focus for achieving such goals (Pikitch et al. 2004, Francis et al. in press), but research has been sorely needed on the specific ecological mechanisms by which fishing affects marine food webs. This dissertation provides substantial progress towards a better understanding how the effects of fishing can be translated through food webs among both fished and unfished species. It is my hope that these findings will be informative to marine

ecologists and conservation biologists, as well as fisheries scientists and managers, both within and beyond the greater Caribbean region.

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APPENDIX

APPENDIX A. Supplementary Materials, Chapter 4

Data from the Reef Environmental Education Foundation (REEF) volunteer fish monitoring program can be queried from their website (www.reef.org) to generate summary reports of two metrics: 1) percent sighting frequency, and 2) logarithmic-based categorical abundance data. A third metric can be produced by multiplying the first two, which gives a measure of species abundance including ‘zero’ observations. I examined these three metrics of the REEF data relative to presence and abundance of top trophic-level predatory fishes across a gradient of human population density in the Caribbean.

Data of all observed predatory fishes were assigned to one of four abundance categories by the volunteer SCUBA divers: Single (1); Few (2-10), Many (11-100), and Abundant (>100). Percent sighting frequency (SF) is a measure of how often a species was observed. The SF metric is calculated as:

$$SF = 100 * \frac{S + F + M + A \text{ (for each species)}}{\text{(Number of surveys)}}$$

The log abundance metric (DEN) is a measure of how many individuals of a species were observed. The index is a weighted density average, based on observations of the four abundance categories; abundance weight categories are

Single = 1, Few = 2, Many = 3, and Abundant = 4. This weighted density average is calculated as:

$$\text{Den} = \frac{(S * 1) + (F * 2) + (M * 3) + (A * 4)}{\text{(Number of surveys in which species was observed).}}$$

I queried summary reports of both SF and DEN for 11 predatory taxa (Table A.1) from 14 regions throughout the greater Caribbean (Table A.2, REEF 2006). Within each region I chose survey locations (sample units) for which at least 10 surveys had been conducted. I constructed matrices of sample units (SU's) by taxa SF (matrix 1), SU's by taxa DEN (matrix 2), and SU's by taxa SF*DEN (matrix 3). I also constructed an environmental matrix containing categorical variables for the 14 geographic regions and quantitative variables for human population density (people per square kilometer).

The raw data from all three matrices had extremely low Whitaker's beta diversity and low values of the coefficient of variation (CV) for both species and sample units (Table A.3), and therefore did not require data transformation. I identified sample unit outliers using Sorensen's distance measure of 2.0 standard units greater than the overall average among all sample units. The SF data

required removal of two sample unit outliers due to very low total sightings across all species. The SF*DEN data required removal of eight sample unit outliers (Table A.3). Seven of these SF*DEN outliers, which included the two sample units identified as SF data outliers, had low totals and the eighth had an extremely high total across all species. Interestingly, all sample unit outliers identified in the DEN data were from countries of high human population density, and removal of these SU's drastically reduced the magnitude of the gradient of human population density. I therefore used the full matrix for the DEN data.

I ordinated each of the three matrices using non-metric multidimensional scaling (NMS, Kruskal 1964, Mather 1976). I ran all NMS ordinations in PC-ORD 5.14 (McCune & Mefford 1999) using the 'Autopilot Mode' with Sorensen distance measure and random starting configurations. The ordinations of sample units in species space are presented graphically.

NMS ordinations of the SF matrix converged on a stable, 2-dimensional solution (final stress = 17.05, final instability = 0.00048, iterations = 64). The first axis accounted for most of the variation ($r^2 = 0.76$; cumulative $r^2 = 0.86$). Human population density was strongly correlated with axis 1 ($r = 0.73$). The structure of the ordination along the first axis was driven by strong associations of requiem sharks, jacks, tiger grouper, Nassau grouper, black grouper, and barracuda with

sample units located in regions of low human population density, and moderate associations of coney grouper, graysby grouper, and trumpetfish with sample units in high human population density regions (Figure A.1). The structure of the ordination along the second axis appears to have been driven by a weak association of red hind with sample units located in the Turks and Caicos and Puerto Rico versus the Bahamas and the Windward Islands (Figure A.1).

NMS ordinations of the DEN matrix also converged on a stable, 2-dimensional solution (final stress = 11.29, final instability = 0.00041, iterations = 47). The first axis accounted for most of the variation ($r^2 = 0.84$; cumulative $r^2 = 0.96$). Human population density was correlated with axis 1 ($r = 0.47$). The structure of the DEN ordination was driven by strong associations of barracuda, requiem sharks, tiger grouper, black grouper, and Nassau grouper with sample units in low human population regions, and weak associations of graysby grouper, coney grouper, and trumpetfish in sample units located in high human population regions (Figure A.2). No species were strongly correlated with the second axis and no clear patterns among geographic regions emerged.

NMS ordinations of the SF*DEN matrix converged on a stable, 3-dimensional solution (final stress = 11.89, final instability = 0.00040, iterations = 73). Like the SF and DEN analyses, the first axis accounted for most of the

variation ($r^2 = 0.59$), although to a lesser extent than the above ordinations. The second and third axes accounted for 12% and 19% of the variation, respectively (cumulative $r^2 = 0.90$). Human population density was strongly correlated with axis 1 ($r = 0.66$). The structure of the SF*DEN ordination along the first axis was driven by strong associations of requiem sharks, Nassau grouper, tiger grouper, and barracuda with sample units in low human population density regions, and moderate to strong associations of graysby grouper, trumpetfish, and coney grouper in sample units located in high human population density regions (Figure A.3, Figure A.4). The structure of second axis was driven mainly by weak associations of black grouper with sample units from the Greater Antilles (Dominican Republic, Puerto Rico, and Jamaica) versus moderate associations of trumpetfish with sample units from the Lesser Antilles (Leeward and Windward Islands). The structure of the third axis was driven by differences between the Greater Antilles and Bahamas versus the Lesser Antilles and the Turks and Caicos (Figure A.3, Figure A.4). Patterns along the third axis appeared attributable to strong associations of Nassau grouper, tiger grouper, barracuda, and jacks with sample units in the Bahamas and moderate associations of trumpetfish with sample units in the Lesser Antilles.

The NMS ordinations of each of the three metrics of data revealed qualitatively similar patterns of predatory fish assemblages (Table A.4), indicating

that the percent sighting frequency, log abundance, and combined data each described these assemblages relatively well. The general structure and associations between taxa and sample units was consistent across the three data sets, with only minor differences in the magnitudes of correlations between taxa and axes across data types, for all species. Quantitatively, the SF data revealed the strongest relationships between taxa and axes across the gradient of human population density, and therefore appears to be the best choice for ordinating fish predators across a large spatial scale, such as the entire Caribbean.

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Table A.1. Predatory taxa included in the analyses.

Family	Taxa	Common name	Code
Aulostomidae	<i>Aulostomus maculatus</i>	trumpetfish	AUMA
Carangidae	<i>Caranx</i> spp.	jacks	Jack
Carcharhinidae	<i>Carcharhinus</i> spp.	requiem sharks	Shrk
Lutjanidae	<i>Lutjanus</i> & <i>Ocyurus</i> spp.	snappers	Snpr
Serranidae	<i>Cephalopholis cruentata</i>	graysby	CECR
	<i>Cephalopholis fulva</i>	coney	CEFU
	<i>Epinephelus guttatus</i>	red hind	EPGU
	<i>Epinephelus striatus</i>	Nassau grouper	EPST
	<i>Mycteroperca bonaci</i>	black grouper	MYBO
	<i>Mycteroperca tigris</i>	tiger grouper	MYTI
Sphyraenidae	<i>Sphyraena barracuda</i>	barracuda	SPBA

Table A.2. Fourteen regions from which REEF survey data are summarized, including human population density.

Country/region	Code	survey locations	total surveys	people/km2
Belize	BZ	6	1721	12
Bahamas	BA	15	7137	21
Turks and Caicos	TC	10	2581	47
Mexican Caribbean	MC	5	3881	53
Honduras	HD	4	2124	62
Cuba	CU	3	567	102
Leeward Islands	LI	7	1468	131
British Virgin Islands	BV	3	1836	147
Cayman Islands	CI	4	3443	168
Dominican Republic	DR	4	202	183
Jamaica	JA	5	312	248
US Virgin Islands	UV	3	2049	308
Windward Islands	WI	7	1751	356
Puerto Rico	PR	7	929	430

Table A.3. Data adjustments performed on the three data matrices.

	SF		DEN		SF*DEN	
	full	adjust	full	adjust	full	adjust
βD	0.1	0.1	0.1	na	0.1	0.1
samples (rows)	83	81	83	na	83	75
CV of rows	29.4	28.3	19.1	na	22.3	18.4
average skewness	0.8	0.8	0.6	na	0.9	0.8
species (columns)	12	12	12	na	12	12
CV of rows	64.2	64.1	27.8	na	82.6	82.5
average skewness	0.3	0.3	-0.6	na	0.9	0.8

Table A.4. Correlations between taxa and axes for each NMS ordination.

Taxa	SF		DEN		SF*DEN		
	axis 1	axis 2	axis 1	axis 2	axis 1	axis 2	axis 3
	<i>r</i>						
jacks	-0.91	0.15	-0.35	0.26	-0.49	-0.35	0.61
requiem sharks	-0.91	0.15	-0.35	0.26	-0.34	-0.24	0.41
tiger grouper	-0.91	0.15	-0.35	0.26	-0.55	-0.11	0.69
Nassau grouper	-0.84	0.21	-0.24	0.09	-0.59	-0.11	0.80
barracuda	-0.72	0.24	-0.10	0.06	-0.59	-0.35	0.62
black grouper	-0.47	-0.19	-0.30	-0.01	-0.51	0.28	0.25
snappers	-0.36	-0.11	-0.05	0.02	-0.56	-0.37	0.44
red hind	-0.15	0.31	-0.05	0.08	-0.10	-0.35	0.19
coney grouper	0.07	0.09	0.00	-0.01	0.65	0.04	0.43
graysby grouper	0.27	-0.03	-0.01	0.00	0.38	-0.18	-0.21
trumpetfish	0.46	0.06	0.01	-0.02	0.51	-0.68	-0.39

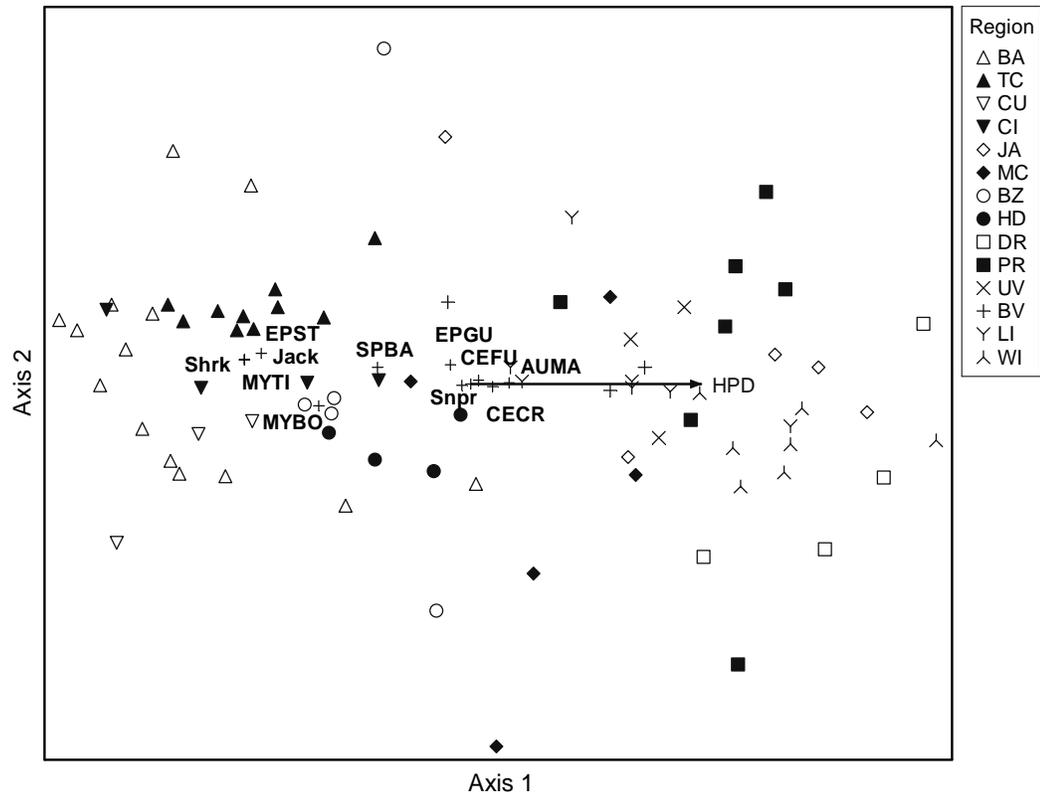


Figure A.1. SF data joint plot of sample units in taxa space, coded by geographic region with species centroids and human population density (HPD) overlay.

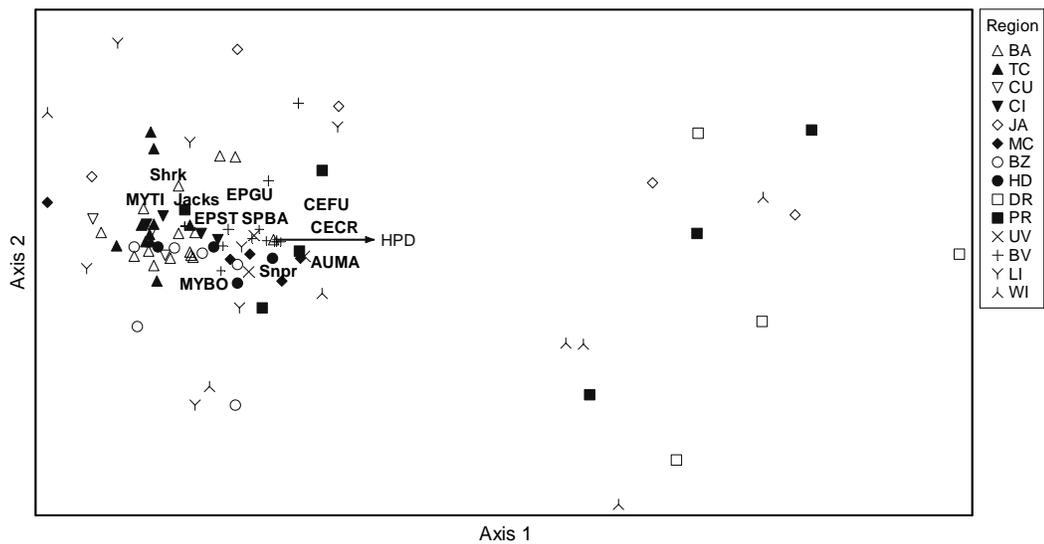


Figure A.2. DEN data joint plot of sample units in taxa space, coded by geographic region with species centroids and human population density (HPD) overlay.

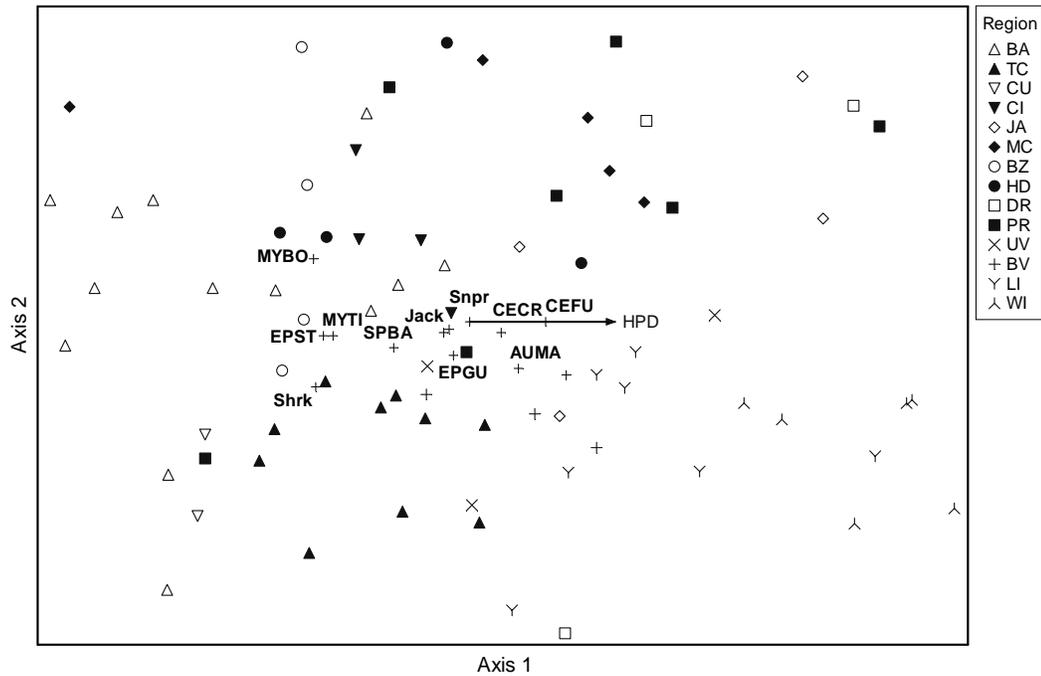


Figure A.3. SF*DEN data joint plot of sample units in taxa space (Axes 1 and 2), coded by geographic region with species centroids and human population density (HPD) overlay.

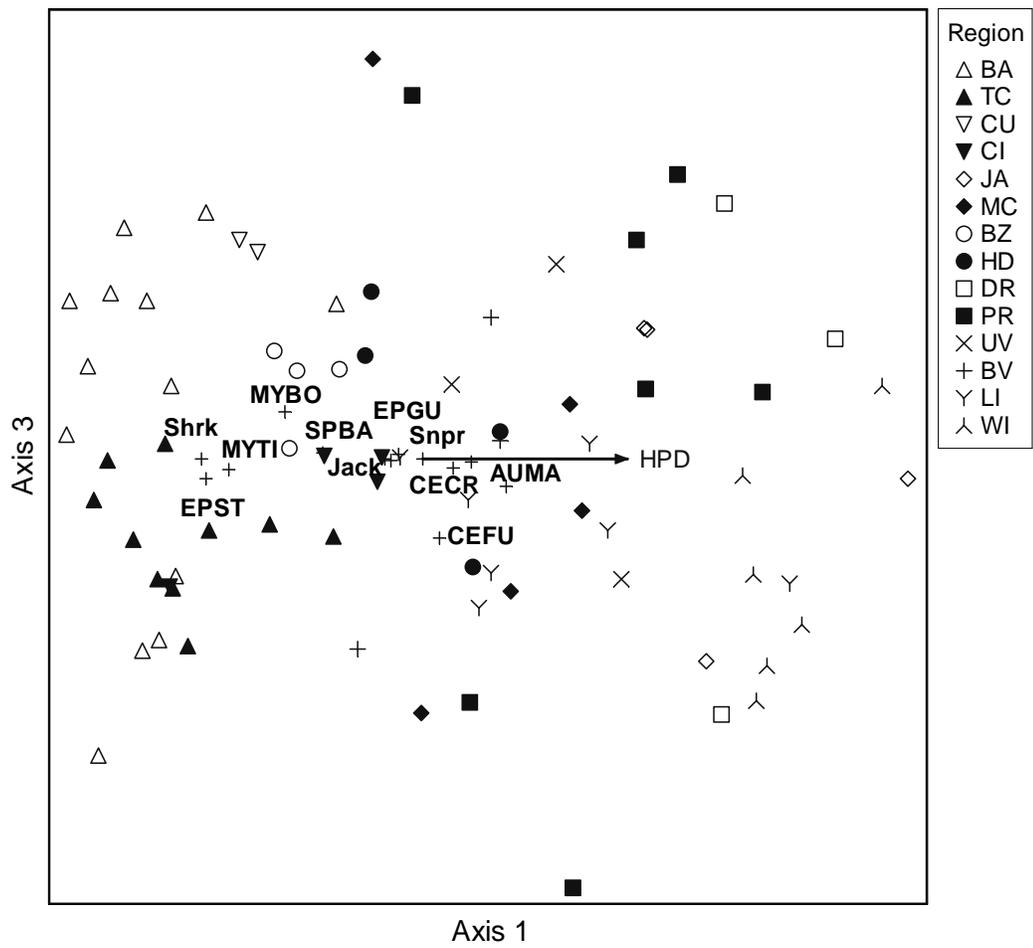


Figure A.4. SF*DEN data joint plot of sample units in taxa space (Axes 1 and 3), coded by geographic region with species centroids and human population density (HPD) overlay.