RELATIONSHIPS BETWEEN REEF FISH COMMUNITIES, WATER AND HABITAT QUALITY ON CORAL REEFS

by

Ivonne Bejarano Rodríguez

A thesis submitted in partial fulfillment of the requirements for the degree of
MASTER OF SCIENCES
In
MARINE SCIENCES
(Biological Oceanography)

UNIVERSITY OF PUERTO RICO
MAYAGÜEZ CAMPUS

2006

Approved by:

Dannie A. Hensley, Ph.D. Member, Graduate Committee	Date
Paul Yoshioka, Ph.D. Member, Graduate Committee	Date
Richard S. Appeldoorn, Ph.D. President, Graduate Committee	Date
Edgardo Ojeda, Ph.D. Representative of Graduate Studies	Date
Nilda E. Aponte, Ph.D. Chairperson of the Department	Date

ABSTRACT

Rapid urban and industrial development is causing water quality deterioration in coastal marine environments. Sediment and nutrient inputs increase water turbidity, limiting light availability and reducing the photosynthetic capacity of the reef. Turbidity can also lead to organism stress, suffocation or death. Consequently, many coral reefs are declining, resulting in a loss of biodiversity and economic yield. This study investigates the relationship between water turbidity, measured as vertical attenuation of PAR (Kd), and coral and fish communities. At 35 reef sites in southwest Puerto Rico spanning a range of water turbidity, Kd was measured, and fish and coral communities were characterized. Coral and fish parameters varied with turbidity, showing higher diversities and abundances in clearer waters. Reef fishes responded to a combination of habitat characteristics. Turbidity, reef rugosity and percentage of live coral were significant variables affecting the reef fish community, and therefore are useful predictors of reef community health.

RESUMEN

El rápido desarrollo urbano e industrial está causando un deterioro en la calidad de las aguas marinas costeras. El aporte de sedimentos y nutrientes incrementa la turbidez del agua, limitando la disponibilidad de luz y reduciendo la capacidad fotosintética del arrecife. La turbidez puede causar stress, asfixia o la muerte de lo organismos. Como consecuencia, muchos arrecifes se están deteriorando, lo cual representa perdidas de la biodiversidad y producción económica. Este estudio investiga las relaciones entre la turbidez del agua, medida como atenuación vertical de PAR (Kd), y las comunidades de peces y corales. En 35 estaciones arrecifales al suroeste de Puerto Rico, abarcando un rango de turbidez del agua, se midió Kd, y se caracterizaron las comunidades de peces y corales. Los parámetros de corales y peces variaron con la turbidez, mostrando diversidades y abundancias mayores en aguas claras. Los peces arrecifales respondieron a una combinación de características del hábitat. La turbidez, la rugosidad del arrecife y el porcentaje de coral vivo fueron variables que afectaron significativamente la comunidad de peces, y por lo tanto se consideran útiles predictores de la salud de las comunidades arrecifales.

DEDICATION

A mis padres, Fernando Bejarano y Sandra Rodríguez, mis hermanos Eliana y Andrés, y la nena que viene en camino, por compartir mi pasión por el mar, apoyarme en lograr mis sueños, y ser la base de mi felicidad, mi orgullo y mi mas inmenso amor.

A Gordito, por ser mi familia en Puerto Rico, darme su amor, apoyo y comprensión, y enseñarme las maravillas de esta hermosa isla y su gente.

A mis buenos amigos, por ser del alma y por ser por siempre.

ACKNOWLEDGMENTS

I want to greatly thank my advisor Dr. Richard S. Appeldoorn for believing in me and giving me the opportunity of being his student and part of the fisheries lab. Thanks for his guidance, patience and support along mi master studies.

I specially thank Dr. Dannie A. Hensley, Dr. Paul Yoshioka and Dr. Edgardo Ojeda, for their technical and science-based comments that contributed importantly to this research. I also appreciate the help of Dr. Roy Armstrong, for his advice in bio-optic aspects and for facilitating the irradiance meters. Maria Cardona helped by sharing time in the field and some bio-optical and algal data. I deeply and sincerely thank my best dive buddy Marco Rosado, and Negrito (Angel L. Camacho), for their unconditional help in the field as well as Godoberto Lopez and Milton Carlo for volunteering on dives. Very special thanks to my lab partners: Michael Nemeth, Michelle Scharer, Tony Marshak, Idelfonso Ruiz and Francisco Pagán. Thanks for being dive buddies, assisting in the field, and helping me to explore the statistical “dimension” using new statistical programs and analyses. I am grateful to Rocio Garcia, Carolina Hincapié, Anabella Zuluaga and Maria Fernanda Barberena for being nice friends and helping me physically and spiritually in this work in so many ways.

My love Gordo, Eddie Rodríguez, was an essential part in this personal success, thanks for encouraging me to be a better professional every day and for making my life so wonderful. I deeply thank my family for being the biggest treasure in my life, without their love and support I would have never reached this achievement.

Funds for this project were provided by Puerto Rico Department of Natural and Environmental Resources (DNER).

TABLE OF CONTENTS

LIST OF FIGURES

LIST OF TABLES

LIST OF APPENDIX

INTRODUCTION

Tropical coastal marine ecosystems are increasingly facing water quality deterioration due to rapid urban and industrial development and poor land-use practices (NOOA, 2000; GESAMP, 2001; Burke & Maidens, 2004; Garcia et al., 2004). Suspended sediments and eutrophication are main factors responsible for the higher turbidities observed in Caribbean coastal waters (Acevedo & Morelock, 1988; Burke & Maidens, 2004; Garcia et al., 2005). Turbidity is likely to be an important physical factor determining health and structure of coral reef communities (Kaye, 1959; Loya, 1976; Rogers, 1979). Increases in turbidity reduce light penetration and limit its availability at the bottom due to increased absorption and scattering by particles suspended in the water column (Jerlov, 1970; Wilber, 1971; Kirk, 1994). Light is crucial for photosynthesis by the zooxanthellae associated with reef building corals (Souter & Linden, 2000) and, consequently, for the normal growth and survival of coral colonies (Kinzie et al., 1984). Similarly, composition and abundance of algal communities are influenced by resource availability such as light, nutrients and substrate (Lapointe et al., 1987; McCook et al., 1997; Fabricius & McCorry, 2006). Light is also critical for vision of fishes (Matz et al., 2006), which can be reduced by turbidity (Lythgoe, 1979) and hence lead to changes in fish social behavior (Berg and Northcote, 1985) and foraging success (Gregory and Northcote, 1993). Also, fish capacity to avoid predators can be affected (Miner and Stein, 1996), and ultimately fish production. In fact, it has been suggested that some vision-mediated fishes could be more adversely affected by deterioration of water transparency. Thus, increasing turbidity could result in loss of diversity for fishes that depend on vision (Seahausen, 2001). Turbidity, by restricting the photic zone, can compress, change and limit the distribution and abundance of reef organisms, and therefore lead to reductions in habitat quality (Fabricius & McCorry, 2006).

Suspended sediments in the water column add to the negative effects of turbidity in coral reef systems. Coral and fish stress responses to sediment burial and abrasion vary from increases in respiration rate, to reductions in growth and feeding, suffocation and in severe cases, death (Abrahams & Kattenfeld, 1997; Bash et al., 2001; Newcombe and MacDonald, 1991; Gregory et al., 1993). Suspended sediments, as a consequence of sand dredging activities, have been reported to potentially reduce reef fish abundance and diversity (Amesbury, 1981), and to modify the trophic structure of fish communities (Harmelin-Vivien, 1992). Therefore, even relatively small increases in turbidity can stress reef organisms and cause community structure to change (Ruiz et al., 1993; Maes et al., 1998) and reefs to degrade.

The distribution and abundance of coral reef fishes are mainly determined by the quality, diversity and availability of suitable habitat (Bouchon-Navarro, 1986; Caley and St. John, 1996; Williams, 1991; Lindberg, 2006) and the habitat preferences of incoming larvae (Booth and Wellington, 1998). Therefore, fish community parameters are usually correlated with specific habitat features. For example, fish richness, abundance (Bell and Galzin, 1984; Sano et al., 1984; Ormond et al., 1996; Lewis, 1997, 1998) and diversity (Gladfender and Gladfender, 1978; Carpenter et al., 1981; Sano et al., 1984; Galzin, 1994; Ormond et al., 1996) are generally correlated with live coral cover. Similar results were found by Booth and Beretta (2002), who studied fish community changes following coral bleaching and subsequent mortality at the Great Barrier Reef (Australia). Luckhurst and Luckhurst (1978), however, found little influence of live coral cover on the structure of reef fish assemblages in the Netherlands Antilles. Reductions in fish recruitment after catastrophic loss of live coral were reported by Doherty et al. (1997).

Larval and juvenile recruitment in reef fish communities have an important role in determining the structure and stability of these communities. Settlement is influenced by habitat selection for substrate types (Williams and Sale, 1981), and many reef fish species prefer to settle on live corals (Booth and Beretta, 2002). In addition, Jones (1998) found that juvenile growth and survival may be substantially affected by the structure of the habitat. Sale and Douglas (1984) suggested reef size (measured as surface area) as another important habitat characteristic predicting fish abundance and richness in coral reef environments. Additional habitat parameters commonly correlated with fish community variables are density of macroalgae (Carr, 1991, 1994a,b; Levin, 1991, 1993), and substratum complexity (Risk, 1972; Luckhurst and Luckhurst, 1978; Gladfelter et al., 1980; Carpenter et al., 1981; Clarke, 1988; Tupper & Boutilier, 1997; Lewis, 1997, 1998; McLain & Pratt, 1999). Thus, substratum complexity studies are useful for assessing fish assemblage structure (Sale, 1991; Hixon and Beets, 1993; Friedlander and Parrish, 1998).

The relationship between reef fishes and coral health is complex, however, and can flow in the other direction: the fish community condition can affect reef health. Herbivory by fishes (and invertebrates) helps control algal abundance in reef systems, thus contributing to maintain coral growth and the recruitment and survival of new coral individuals (Tanner, 1995; Wolanski et al., 2003; McCook et al., 2001). Herbivorous fishes can also generate changes in the algal community they are feeding on (Hughes et al., 1987; Hay, 1997; McCook et al., 2001), for example, modifying the algal community from fleshy, less productive algae to less voluminous but more productive turf algae (Carpenter, 1986). Therefore, a possible imbalance could result in the reef ecosystem when herbivorous fishes, such as parrotfishes, are commercially exploited while other non-commercial fish species, such as damselfishes, remain abundant. Thus, localized extirpations of fish species due to fishing and associated community structure changes can occur (McClanahan, 1994). Food consumption and “farming” activities performed by damselfishes can as well potentially affect reef communities by destroying coral to grow algae that will enhance their food sources. Damselfishes can modify the structure of algal, coral and fish assemblages on coral reefs (Ceccarelli et al., 2001). Herbivorous fish diversity and abundance is also dependent on predatory fish density. Therefore, the health of a coral reef ecosystem can be evaluated not only in terms of growth and reproductive rates, but also in the number of fishes present (Holden and LeDrew, 2001) and fish species abundance. Additionally, planktivorous fishes perform important interactions among coral reefs and trophic pathways. Fishes feeding on plankton canalizes nutrients and energy from the pelagic zone to the reef environment, importing particulate organic and inorganic material to the reef when they excrete dissolved waste products while sheltering on it (Robertson, 1982; Rothans and Miller, 1991).

Coastal development and other human activities, combined with overfishing, have resulted in severe declines of both targeted and non-targeted fish populations (Roberts and Polunin, 1991; Lauck et al., 1998) throughout the region (Hernandez and Sabat, 2000; Christensen et al., 2003). There has been a sharp decline in catch per unit effort (CPUE) in both commercial and recreational fishing for all of Puerto Rico (Appeldoorn et al., 1992). Declining reef fishes contribute to the degradation of other reef communities (Bohnsack, 1993). Eventually, high fishing rates can lead to changes in the reef fish trophic structure (Harmelin-Vivien, 1992). The accelerating degradation and depletion of coral reef resources results in a loss of biodiversity and of the economic yield (Burke & Maidens, 2004; Bruckner et al., 2005).

Understanding and assessing the interactions of physical and biological factors affecting the structure of reef communities is fundamental for coral reef management and conservation.

The present study investigates the relationship between coral and fish communities and water quality measured as the light attenuation coefficient (Kd) of photosynthetically active radiation (PAR). The objectives are (1) to investigate the relationship between the reef fish community and the water quality, (2) to determine the relationship between the reef icthyofauna and the coral reef condition, and (3) to assess the current status of the fishes and live coral in three important areas of southwest Puerto Rico. This investigation may result in a better understanding of the condition and functioning of coral reef ecosystems.

MATERIALS AND METHODS

Study Area

This study was conducted at 35 coral reef sites distributed along southwest Puerto Rico and Mona Island, from January to October 2005 (Figure 1, Appendix 1). Reef sites were selected at a fixed depth of 10 m, to control variations due to other causes rather than water turbidity, and were located in areas of differing water quality: 1) Mona Island, characterized by clear waters, 2) La Parguera, with waters of intermediate turbidity, and 3) Guayanilla and Ponce, possessing turbid waters. The southwest coast is generally dry and warm, and is characterized by a subtropical dry forest life zone (Ewel and Withmore, 1973). Wave energy is typically low, and the insular shelf is wider than the north coast (Garcia et al., 2005). Sierra Bermeja, a series of mountains, separate the coastal plain from the Lajas Valley, and act as an important hydrographic boundary (Ewel and Withmore, 1973). Only small creeks discharge on the southwest coast (Garcia et al. 2005), none in La Parguera area (Ewel and Whitmore, 1973). Coral reefs at La Parguera are located among a broad carbonate shelf, mostly deposited in the Cretaceous (Almy, 1965), which was flooded about 5,000 to 9,000 years ago (Goenaga, 1988). This platform extends approximately 15 km offshore, and possesses emergent fringing reefs, bank-barrier reefs and submerged patch reefs (Morelock et al., 2001). The insular shelf off Guayanilla is characterized by relatively bare rock and reefs on the shelf platform and muddy sediment-floored submarine canyon floors (Morelock et al., 2001). Late in the 1960's a refinery was constructed in the area leading to permanent turbid waters in the bay (Morelock et al., 2001). In addition, ship traffic is active in this area and resuspension of sediments occur (Morelock et

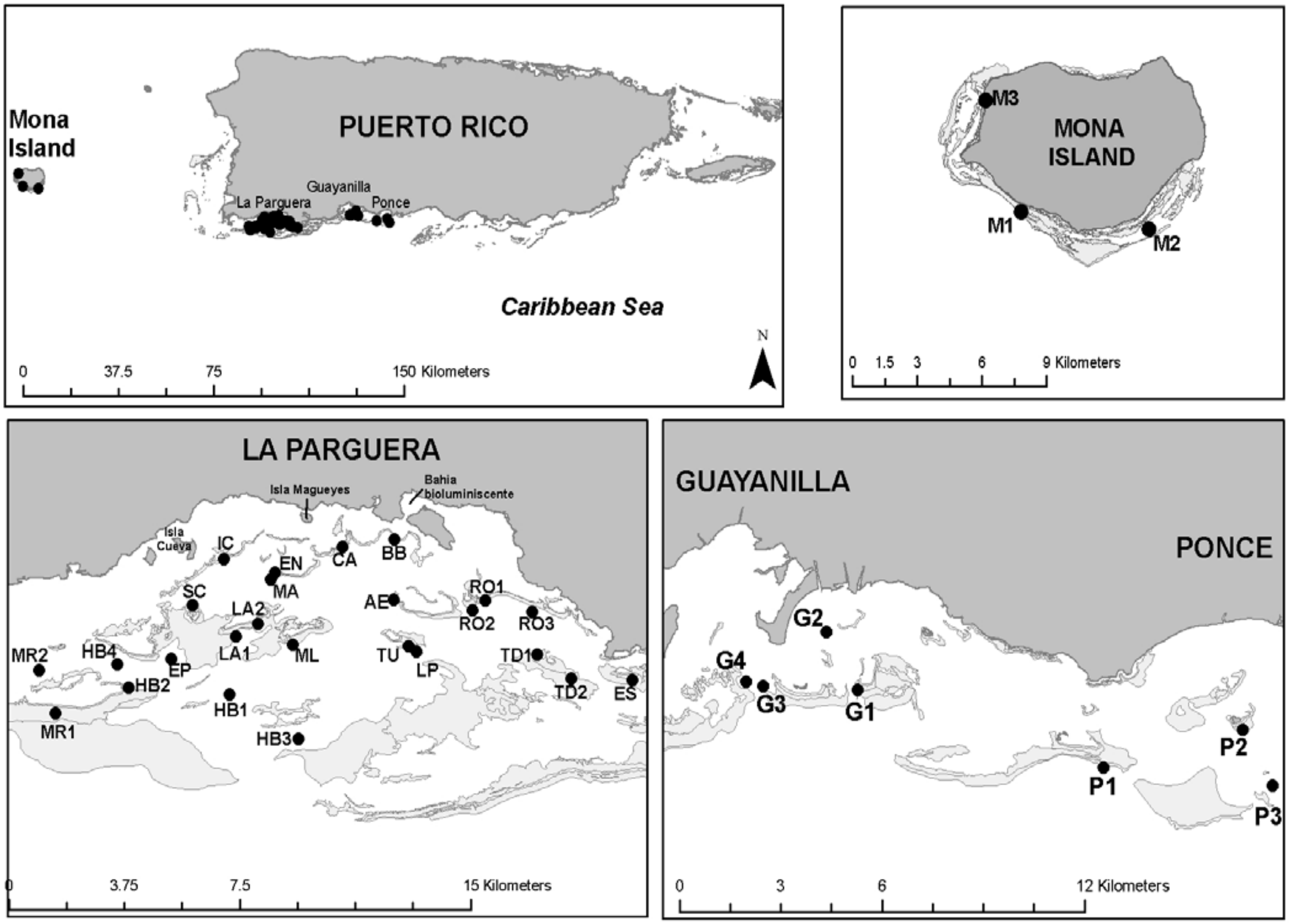

Figure 1. Map of Puerto Rico showing study area and locations in southwest Puerto Rico and Mona Island.

al., 2001). Similarly, west Ponce reefs are subject to a plume of turbid waters resulting from fine-grained sediments resuspended by wave action and ship traffic (Acevedo et al., 1989; Morelock et al., 2001). The shelf in Ponce consists of hard carbonate pavement with thin carbonate sands and small reefs (Morelock et al., 2001). The only emergent reefs are in front of Cayo Ratones and south of Isla Cardona (Morelock et al., 2001). Mona Island is an oceanic natural reserve located in the Mona Passage, midway between the Dominican Republic and Puerto Rico, approximately 70 km from western Puerto Rico. Coral reefs and cliff walls are the main submarine habitats around Mona Island (Scharer, 2001). Coral reefs at Mona are mostly developed in the south of the island, because the platform is wider than on the north, and the wave action is lower (Garcia et al., 2005). Mona's southern coast is surrounded by reef formations, such as spur and groove, fringing and patch reefs; and sandy beaches (Scharer, 2001). There are no rivers on Mona (Cintron et al., 1975), and waters are constantly clear.

Site Selection

The distribution of coral reef ecosystems in the area was determined with the NOAA benthic characterization map (Kendall et al., 2001). Study sites were selected by using ArcMap GIS. Contour depth profiles at 8, 10 and 12 m depth were created in the area, so that reef sites located in that depth range could be differentiated. The geographic coordinates of selected sites were identified and entered into a hand-held GPS unit, with which field sites were located.

Field Methods

Vertical profiles of photosynthetically active radiation (PAR) were obtained from underwater light measurements taken at 1-m depth intervals using a submersible irradiance meter (Li-Cor Biosciences LI-1400) from surface to 10 m depth. Measurements were taken on days with similar climatic conditions, and at the same time period per hour day (8:00 – 10:00) to avoid possible bias. Additionally, light measurements in air were taken from the boat with an external collector for cloud corrections. Kd values (m^{-1}) were estimated following Beer's Law as the slope of the linear regression of the natural logarithm of descendent irradiance (Ed) against depth (z): $\ln Ed(z) = -Kdz + \ln Ed(0)$; where Ed(z) is the ascendent irradiance at z meters, and Ed_o is the ascendent irradiance just below water surface. Because water clarity can be variable on short and seasonal time scales Kd measurements were obtained for multiple days at each site covering both the dry and rainy season. These were used to determine a mean Kd characteristic value for each site, assuming typical climate conditions (e.g., not after strong storms).

Biotic communities were accessed from surveys conducted within a depth range of 8 - 12 m using SCUBA. The fish fauna was characterized using an adaptation of the underwater visual census method (UVC) (Brock 1954), considered the most practical and extensively used technique to access demersal species in shallow-waters (Nagelkerken et al., 2000; Appeldoorn et al., 2003). At each location, fish were identified, counted and lengths estimated in 6 belt transects of 10 x 3 m^2 each, totaling 180 m^2 per site. Because water turbidity varied strongly among sites, these transect dimensions ensured acceptable visibility for fish identification within the census area at any site. Censuses were standardized to 15 min/transect. All fishes passing through or staying within the census area were identified to species, or to the lowest possible taxon. Nomenclature for species followed Eschmeyer (1998). Abundance was determined in groups of 1, 2-5, 6-10, 11-30, 31-50, 51-100, and 100+ to minimize error (Harmelin-Vivien et al., 1985). For body size estimation (standard length [SL]), practice runs prior to sampling were performed to calibrate direct visual estimations by the diver, increasing accuracy and precision (Rooker and Recksick, 1992).

The composition and percent of live coral cover at each reef site were determined along six line transects 10 m long (Loya and Slobodkin, 1971; Loya, 1972). A meter line was laid along reef surface, parallel to the local depth contour. All live coral species lying beneath the meterline were identified to the lowest possible taxon, and the distance they covered (cm) under the meter line were recorded. Data were transformed to percentages. Bottom rugosity was assessed by the ratio of the horizontal distance crossed by a 6 m chain laid following the surface relief (Horizontal distance (m) / 6 m).

By using ArcMap GIS, sites coordinates were entered into NOAA benthic characterization map and the closest linear distance (m) from each point to land was determined.

Statistical Analysis

Fish abundance was the total number of individuals per species, and species richness was the total number of species in the transect area. Species diversity was calculated using the Shannon-Weaver Diversity index (Ludwig and Reynolds, 1988): $H' = -\Sigma\, Pi \ln Pi$; where *Pi* is the proportion of the total number of individuals occurring in species i. Fish weights were estimated with length-weight relationships, following the equation: $W = aL^b$, where W is weight (g), L is length (mm), and a and b are constants taken from Bohnsack and Harper (1988) and Bohnsack (ms).

Normality was corroborated using a Kolmogorov-Smirnov 1-sample test after data transformations (Sokal and Rohlf, 1995). Square-root transformations were applied to vertical light attenuation coefficients (Kd), and coral and fish species richness data; fish abundance and biomass data was log transformed because of their larger variability; and percentage of live coral cover data was arcsine root transformed.

Comparisons using ANOVAs were performed to test for statistical differences ($p \leq .05$) in the fish, coral and water quality parameters among sites. Correlations among these parameters were tested by statistical regressions. However, characteristics of some sites made it necessary to group reefs in different ways for some analysis.

Nonparametric Multidimensional Scaling (NMDS) based on presence/absence of species were conducted to determine similarities in fish species composition among sites using PC-ORD software. Sorensen (Bray Curtis) distance was used, and the environmental parameters were used as secondary matrix.

RESULTS

Differences in the characteristics of some coral reefs were found when sites were visited. Sites HB1, HB2, HB3 and HB4 turn out to be more hardbottom and hence gorgonian dominated, and not reef, which has vertical elevation off the surrounding bottom. Thus, studied sites could be separated in three main groups: 1) Mona Island reefs, possessing the clearest waters, highest fish abundances and intermediate live coral coverage; 2) Sites HB1, HB2, HB3 and HB4 in La Parguera, with relatively clear waters but dominated by soft rather than hermatypic corals; and 3) All other reef sites.

Significant differences were found among sites for almost all biotic and abiotic factors (Table 1). The attenuation coefficient of light ($Kd_{(PAR)}$) was significantly different among sites. Sites at Mona Island had the clearest waters, with the mean value at site M1 (0.064 m^{-1}) being only one-half to one-quarter the values observed at sites along the main island (Table 2). Most sites in La Parguera showed intermediate $Kd_{(PAR)}$ values varying from 0.16 to 0.20 m^{-1}, but lower values ($\leq$ 0.15 m^{-1}) were found at sites HB1, HB2, HB3 and HB4 (eastward off Margarita and in front of San Cristobal and Laurel), and high values (> 0.20 m^{-1}) at Romero (RO2 and RO3), Mario (MA), Enmedio (AE), Caracoles (CA) and site ES, which was located off eastern La Parguera and had the highest $Kd_{(PAR)}$ (0.27 m^{-1}) recorded in this study. Sites located in Guayanilla and Ponce had characteristically turbid waters, with $Kd_{(PAR)}$ values ranging from 0.21 to 0.25 m^{-1}.

Table 1. Results of analysis of variance on transformed parameters compared among study sites.

Parameter	F	p
Kd $_{(PAR)}$	4.74	<0.0001
Rugosity	27.45	<0.0001
Fish species richness	2.23	0.0005
Fish density	3.19	<0.0001
Herbivorous fish density	3.00	<0.0001
Mobile invertebrate feeder fish density	3.47	<0.0001
Mobile invertebrate-piscivorous fish density	1.26	0.1725
Omnivorous fish density	1.52	0.0445
Piscivorous fish density	1.02	0.4452
Sessile invertebrate feeder fish density	1.67	0.0187
Planktivorous fish density	3.95	<0.0001
Fish diversity index (H')	5.08	<0.0001
Fish biomass	2.20	<0.0001
Percent live coral cover	5.03	<0.0001
Coral species richness	3.85	<0.0001

Table 2. Mean values and standard deviation (SD) of the biotic and abiotic parameters measured at coral reef sites along the south coast of Puerto Rico and Mona Island. Maximum and minimum values in bold. Station codes: M#, sites at Mona; G#, sites at Guayanilla; P#, sites at Ponce. In La Parguera station codes have two letters related with reef name, and HB# are hardbottom sites. Herb = Herbivore, Plank = Planktivore, CC = Coral Cover. Densities are number of fish/30 m^2. See Appendix 1 for sites location (coordinates).

Site	Kd $_{(PAR)}$		Fish density		Fish richness		Fish biomass		Herb. ab.		Plank. ab.		% CC		Rugosity	
	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD
M1	**0.064**	**0.007**	**118**	**26.8**	14	1.2	**12713**	**2899**	**34**	**26.1**	**42.5**	**29.9**	0.19	0.0	1.29	0.05
M2	0.083	0.007	77	13.9	10	0.6	3868	697	19	4.0	10.0	2.9	0.17	0.2	1.15	0.04
M3	0.090	0.004	44	15.0	13	6.6	3345	1132	11	5.5	15.5	10.5	0.25	0.1	1.20	0.03
HB1	0.130	0.005	25	7.7	11	3.1	1980	621	17	6.5	**0.0**	**0.0**	0.31	0.1	1.15	0.02
HB2	0.140	0.021	21	11.1	**6**	**2.2**	1707	910	7	5.0	**0.0**	**0.0**	**0.05**	**0.1**	**1.03**	**0.02**
HB3	0.140	0.014	26	11.1	10	4.0	3276	1411	17	6.6	**0.2**	**0.4**	0.32	0.1	1.15	0.07
HB4	0.150	0.027	27	12.7	11	3.6	1975	916	20	10.9	**0.2**	**0.4**	0.24	0.1	1.22	0.03
EP	0.160	0.021	38	5.6	12	6.2	2559	2308	22	17.0	5.9	15.1	0.37	0.0	1.21	0.03
SC	0.160	0.032	40	34.4	**16**	**2.2**	6646	2551	16	9.3	5.8	7.0	0.45	0.2	1.39	0.06
LP	0.160	0.053	25	10.9	13	2.3	912	398	14	8.3	1.8	1.5	**0.46**	**0.1**	1.36	0.04
MR1	0.170	0.019	48	26.2	12	4.4	7027	2842	20	6.6	0.7	1.2	0.28	0.1	1.21	0.03
MR2	0.170	0.021	35	7.6	12	4.0	3571	1320	16	4.6	8.7	8.8	0.26	0.1	1.25	0.04
BB	0.170	0.020	43	15.4	14	3.1	1691	788	12	3.2	14.2	12.1	0.42	0.2	1.28	0.02
LA1	0.170	0.033	26	32.9	9	4.3	1300	1634	9	3.1	8.0	18.6	0.30	0.1	1.10	0.02
TU	0.170	0.020	32	23.0	11	2.8	2721	1965	12	5.7	12.2	24.6	0.42	0.1	**1.48**	**0.03**
ML	0.170	0.012	35	18.0	10	4.6	1521	787	12	4.3	12.2	12.8	0.43	0.1	1.36	0.07
IC	0.190	0.013	46	30.0	12	2.3	6035	2965	22	12.2	8.9	15.6	0.20	0.1	1.35	0.11
TD2	0.190	0.005	20	12.2	9	3.4	1097	658	11	6.9	0.7	1.6	0.25	0.1	1.06	0.03
RO1	0.190	0.051	32	14.1	10	2.1	1259	549	**5**	**2.3**	13.8	7.1	0.24	0.0	1.30	0.03
LA2	0.190	0.037	19	8.3	11	4.0	1674	745	9	6.0	0.7	0.8	0.31	0.1	1.17	0.02
TD1	0.190	0.006	19	6.3	9	5.7	1707	552	9	5.0	**0.0**	**0.0**	0.16	0.0	1.12	0.04
EN	0.200	0.062	26	9.0	11	1.9	2807	996	12	6.3	5.2	5.1	0.35	0.1	1.31	0.02
G1	0.210	0.061	43	16.5	14	3.1	6204	2384	12	6.0	15.0	9.8	0.22	0.1	1.34	0.05
G3	0.210	0.073	49	27.6	13	3.1	6544	3717	18	4.4	19.2	29.2	0.24	0.0	1.25	0.05
P1	0.210	0.032	55	34.5	10	3.4	1573	994	11	3.5	**35.3**	**29.8**	0.16	0.1	1.30	0.05
CA	0.219	0.021	21	8.1	9	3.0	1226	483	11	5.4	4.0	7.9	0.24	0.1	1.20	0.05
RO2	0.220	0.014	18	15.3	7	3.2	890	773	**5**	**4.5**	**0.3**	**0.8**	0.11	0.1	1.14	0.03
RO3	0.220	0.053	23	10.0	8	2.9	1726	743	7	4.5	7.8	8.0	0.25	0.1	1.14	0.03
G4	0.220	0.037	37	19.8	**16**	**3.5**	**510**	**77**	18	3.5	1.7	2.9	0.30	0.1	1.36	0.04
MA	0.230	0.112	18	7.0	10	2.6	688	263	7	3.9	2.3	1.8	0.17	0.1	1.20	0.07
AE	0.230	0.053	18	9.0	9	2.7	1315	657	6	5.1	3.9	6.4	0.18	0.1	1.30	0.07
P2	0.240	0.000	35	12.8	13	2.4	661	144	13	2.0	6.7	8.1	0.14	0.0	1.25	0.05
G2	0.240	0.012	32	9.6	10	2.6	3449	1039	14	7.8	9.7	5.5	0.11	0.0	1.14	0.04
P3	0.250	0.040	32	25.9	9	6.1	956	773	9	4.0	1.3	2.3	0.08	0.1	1.19	0.02
ES	**0.270**	**0.025**	**16**	**7.8**	7	1.7	2327	1154	7	3.3	**0.0**	**0.0**	0.17	0.0	1.14	0.04

A total of 6,400 fishes from 101 species (Appendix 2) and 37 families were observed among all study sites. Significant differences were found among sites in mean values of fish density, species richness, biomass, and diversity index (H') (Table 1). Higher fish densities were found at Mona Island, varying from 44 to 118 fish/30m^2. In La Parguera densities varied from 16 to 48 fish/30m^2 , with site ES having the lowest density observed in the study (16 fish /30m^2). Guayanilla and Ponce sites had densities ranging from 32 to 55 fish/30m^2. Maximum fish species richness (16) occurred in La Parguera, at San Cristobal (SC) and in Guayanilla (G4), while the lowest number of species were recorded in La Parguera at sites HB3 (6), RO2 (Romero, 7) and ES (eastern La Parguera, 7). Fish biomass at site M1 at Mona Island (12,713g) was almost twice that observed at any other site; high values were also observed in La Parguera at Margarita (MR1, 7,027g) and San Cristobal (SC, 6646g), while the lowest values occurred at Guayanilla (G4, 510g) and Ponce (P2, 661g) (Table 2).

There were significant differences among sites in mean densities of herbivores, planktivores, omnivores, sessile invertebrate feeders and mobile invertebrate feeders (Appendix 3, 4, 5, 6, 7), while densities of mobile invertebrate-piscivorous feeders and piscivores (Appendix 8, 9) among sites were not significantly different (Table 1). The highest mean densities of herbivorous (34/30m^2) and planktivorous fishes (43/30m^2) were recorded at Mona Island (M1), whereas the lowest herbivore densities (5/30m^2) were found in La Parguera at Romero (RO1 and RO2). Densities of planktivores were $< 1/30m^2$ at sites RO2, HB4 and HB2, while at sites HB3, HB1, TD1 and ES planktivorous fishes were absent (Table 2).

Ordination by Nonparameteric Multidimensional Scaling analysis of fish species composition explained 59% of the variance with axis 1 and another 18% of the variance with axis 2. The orthogonality for ordination was 92%. A nonparametric multi-response permutation procedure (RMPP) showed significant differences (A = 0.10599, $p < 0.0001$) among the four areas: (1) Mona Island, (2) La Parguera, (3) Guayanilla and (4) Ponce (Figure 2). However, Mona Island exerted a strong influence in this ordination because the main vectors were Kd $_{(PAR)}$ and distance from land, both of which were extreme at Mona Island sites.

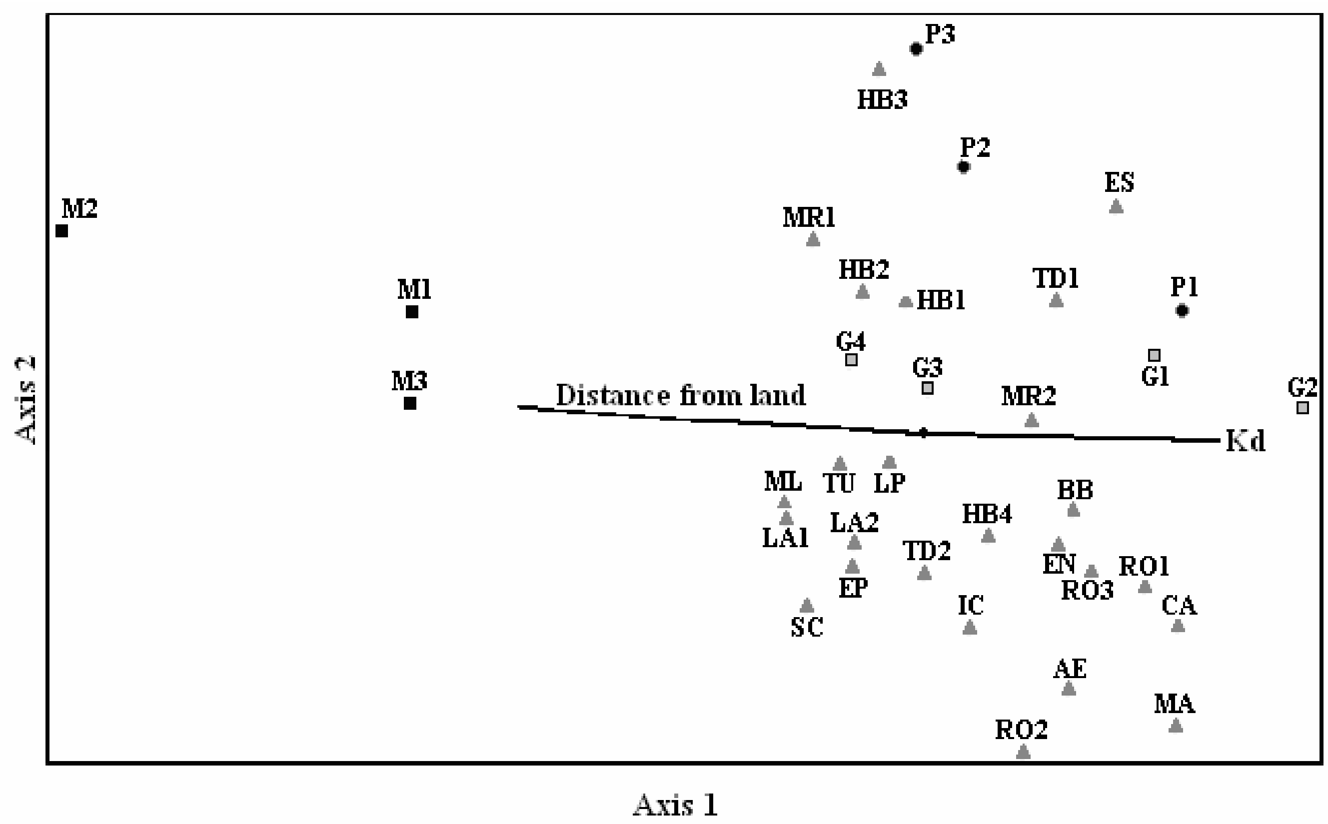

Figure 2. Nonparametric multidimensional scaling ordination analysis comparing species composition among all sites. Areas: Mona Island (black squares); La Parguera (triangles), Guayanilla (gray squares); and Ponce (black circles).

Significant differences in mean values of percent live coral cover and coral species richness were found among sites (Table 1). Highest percentages of live coral cover were observed in La Parguera at Los Pinaculos (LP, 46%) and San Cristobal (SC, 45%). Minimum values of live coral cover were recorded at sites HB3 (5%) in La Parguera, P3 (8%) in Ponce, and G2 (11%) at Guayanilla. The highest mean coral species richness was observed at Media Luna (ML, 9) in La Parguera and the lowest at Ponce (P1, 3) and Guayanilla (G2, 3) (Table 2). Reef rugosity also differed among sites (Table 1), varying from 1.03 at site HB3 to 1.48 at Turrumote (TU) in La Parguera (Table 2).

Distance from land showed a significant negative correlation with water turbidity (r^2 = 0.7374, $p < 0.0001$) (Figure 3). Although, Mona Island data had a strong effect in this regression, the correlation was still significant when those sites were excluded from the analysis (r^2 = 0.39, p = 0.0001).

When % live coral cover was regressed against water turbidity for all sites, the correlation was not significant (Figure 4). However, when Mona Island and the hardbottom gorgonian (HB1, HB2, HB3 and HB4) sites were excluded from the analysis a strong correlation was found (Figure 5).

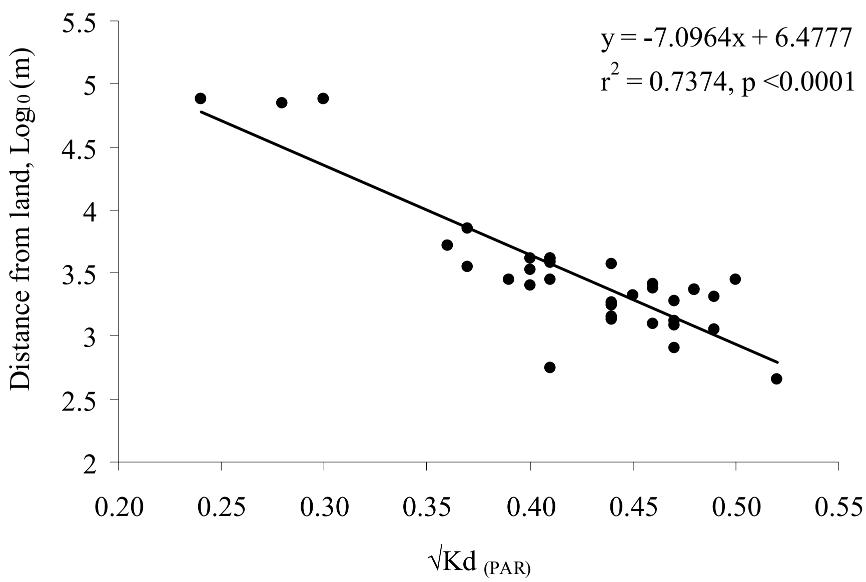

Figure 3. For all sites, regression between the vertical attenuation coefficient of light ($\sqrt{Kd}_{(PAR)}$) and distance from land.

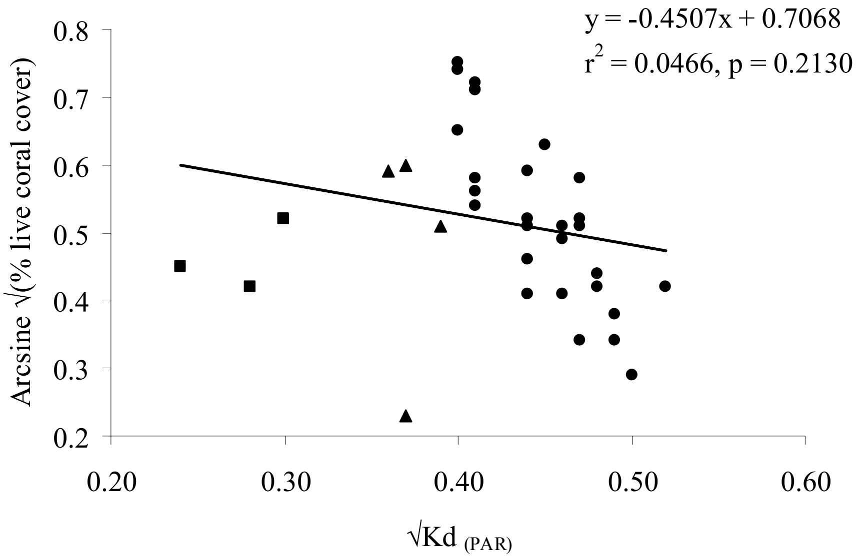

Figure 4. For all sites, regression between the vertical attenuation coefficient of light and % live coral cover. Squares represent Mona Island sites, triangles are hardbottom sites, and circles represent all other sites.

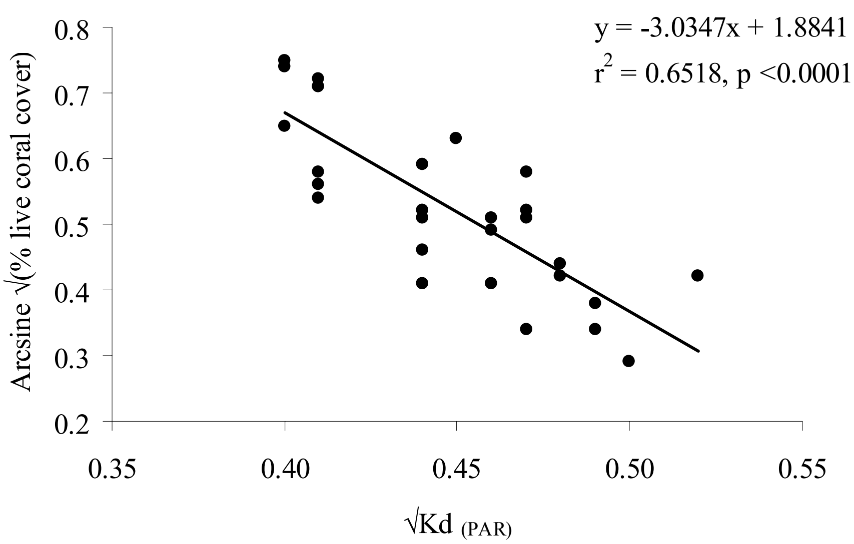

Figure 5. Regression between the vertical attenuation coefficient of light and % live coral cover excluding Mona Island and hardbotton sites.

In reverse fashion, the relationships between water turbidity and mean fish density and mean fish biomass (Figures 6, 7) were significant but were driven by the extreme values for the Mona Island sites. Thus, while excluding Mona Island and the hardbottom sites still resulted in trends of decreasing fish abundance and biomass with increasing turbidity, the regressions were not statistically significant.

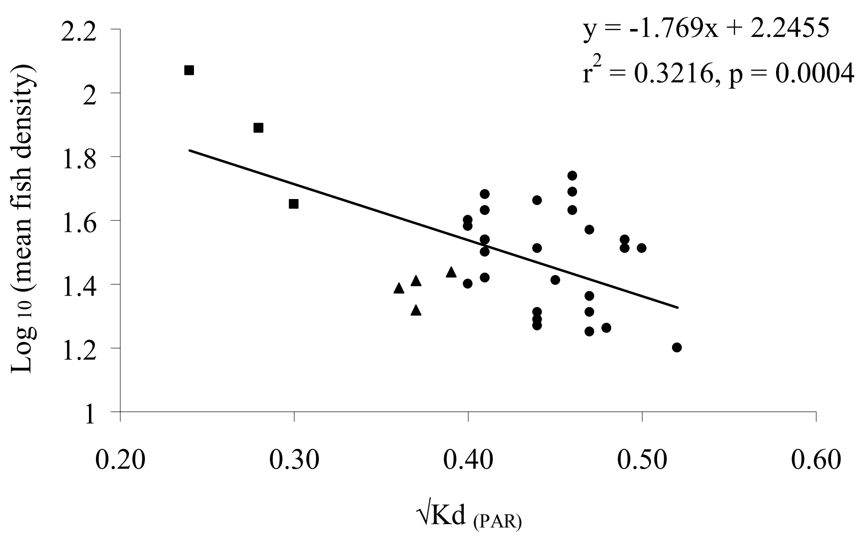

Figure 6. For all sites, regression between the vertical attenuation coefficient of light and mean fish density. Squares represent Mona Island sites, triangles are hardbottom sites, and circles represent all other sites.

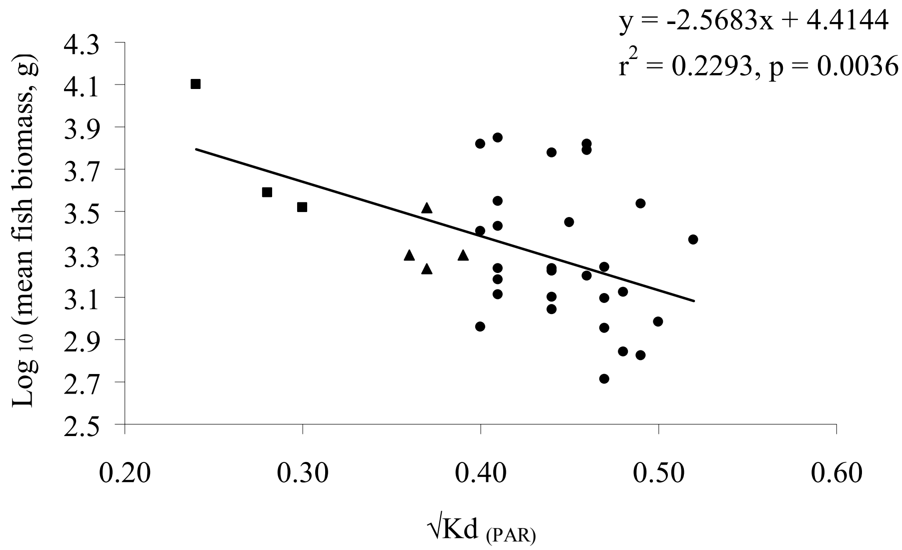

Figure 7. For all sites, regression between the vertical attenuation coefficient of light and mean fish biomass. Squares represent Mona Island sites, triangles are hardbottom sites, and circles represent all other sites.

Mean abundance of herbivore was negatively correlated with turbidity for all sites (Figure 8) and when Mona Island and the hardbottom sites were excluded, although the explained variance was much reduced (Figure 9).

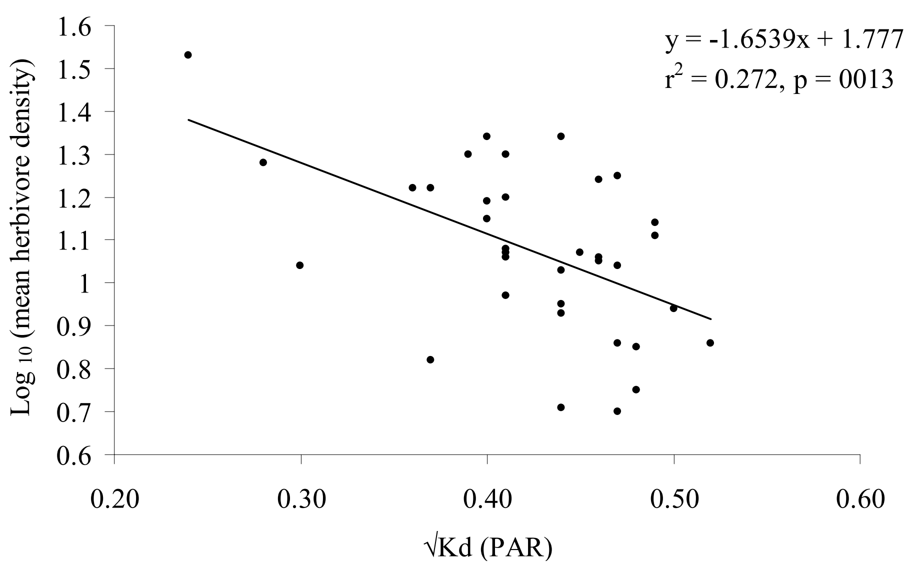

Figure 8. For all sites, regression between the vertical attenuation coefficient of light and mean herbivore density.

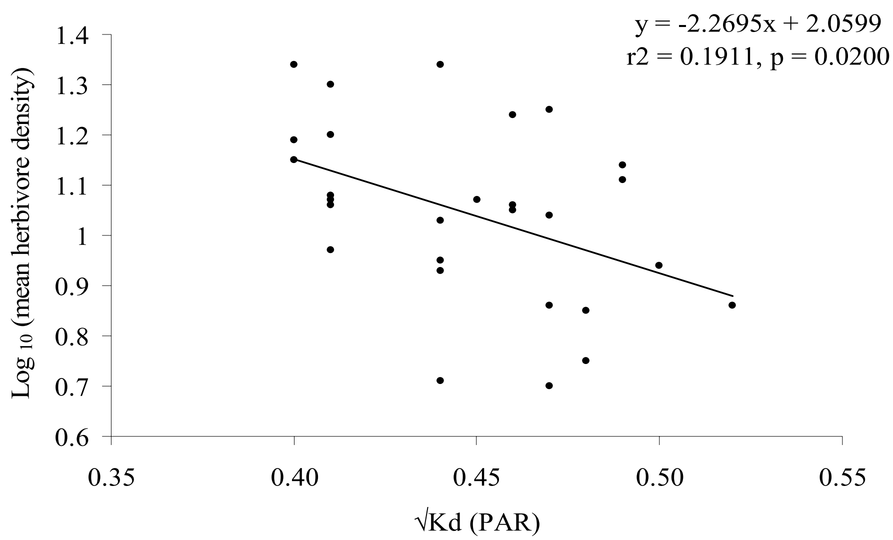

Figure 9. Regression between the vertical attenuation coefficient of light and mean herbivore density, excluding Mona Island and hardbottom sites.

The fish community also was found to be significantly affected by parameters other than water turbidity. For example, reef rugosity was the main factor predicting fish species richness (Figure 10) and fish density (Figure 11).

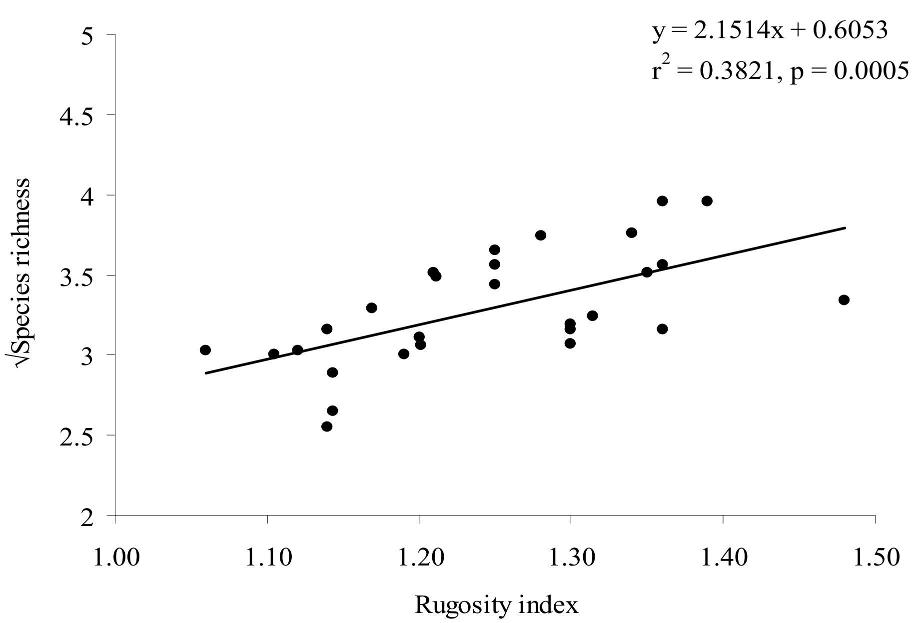

Figure 10. Regression between reef rugosity and fish species richness.

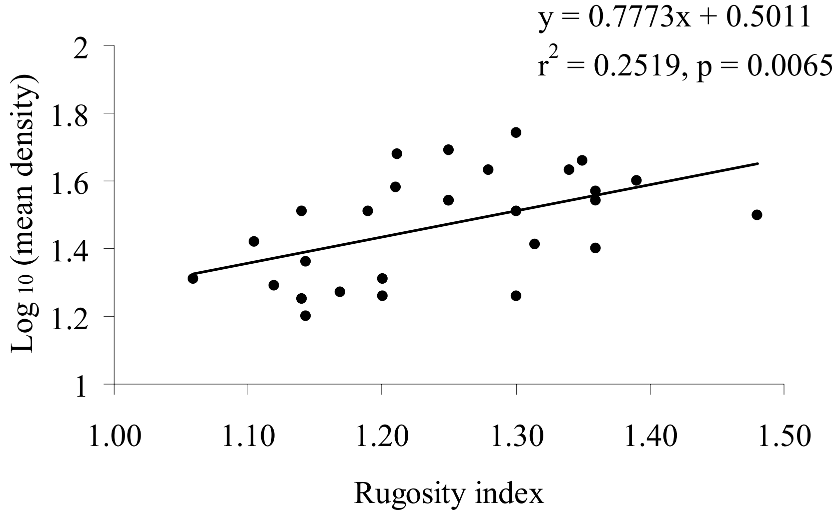

Figure 11. Regression analysis between reef rugosity and mean fish abundance (Log 10).

Other fish community parameters such as fish diversity (H') (Figure 12) and mean planktivore abundance (Figure 13) showed positive relationships with reef rugosity.

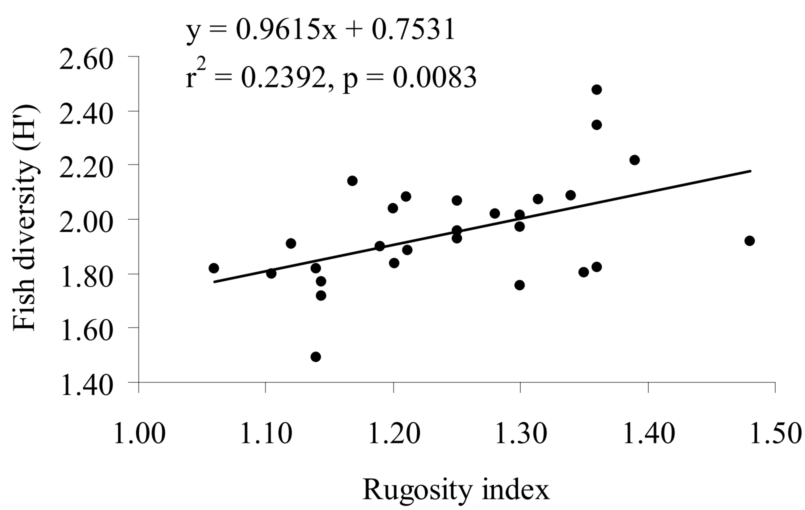

Figure 12. Regression between reef rugosity and fish diversity (H').

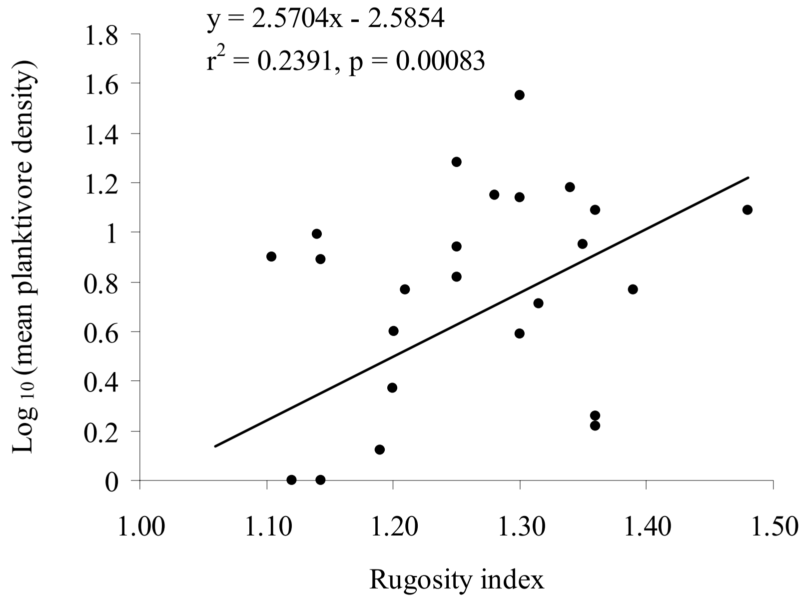

Figure 13. Regression between reef rugosity and mean planktivore density.

In addition, % live coral cover was found to have a significant positive effect on fish species richness (Figure 14), fish diversity (H') (Figure 15), and mean densities of herbivore (Figure 16).

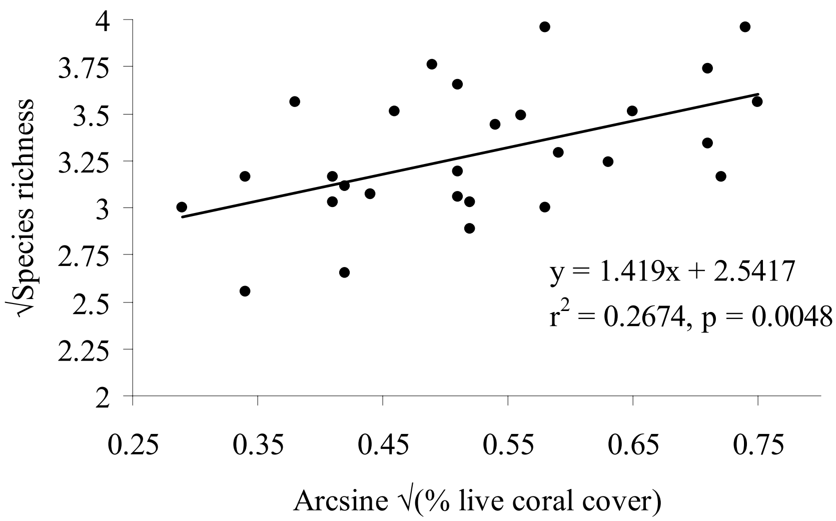

Figure 14. Regression between % live coral cover and fish species richness.

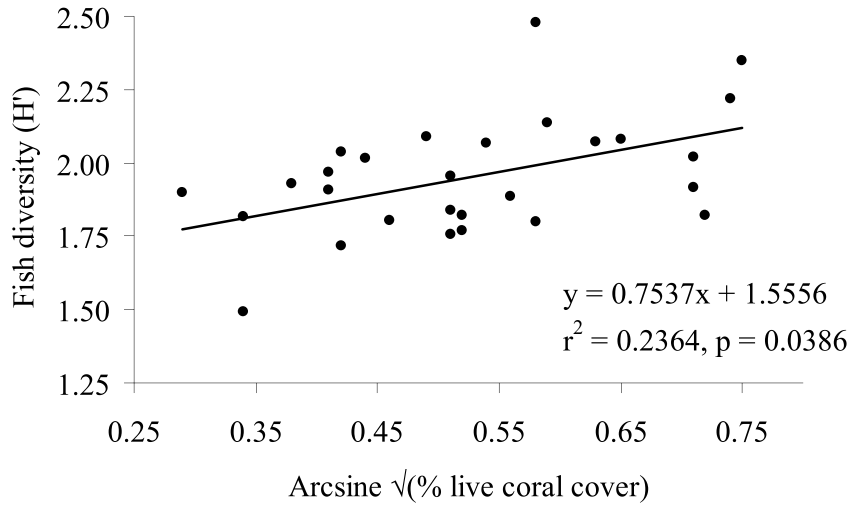

Figure 15. Regression between % live coral cover and fish diversity index.

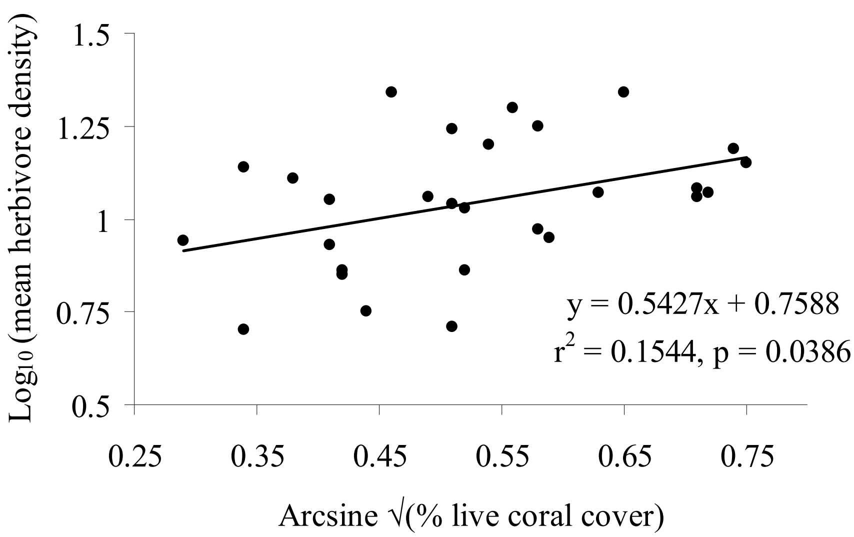

Figure 16. Regression between % live coral cover and mean herbivore density.

DISCUSSION

This study shows that reef fish and coral communities significantly differ among variable conditions of water turbidity. There was a general tendency of finding lower percentages of live coral cover, fish densities, species richness and fish biomass as water turbidity increased. This is supported by the highest fish densities recorded at the site with the clearest waters (M1, Mona Island), and the lowest at the most turbid site (ES, La Parguera). Fish biomass was also maximum at M1, and minimum at the turbid reefs off Guayanilla and Ponce. Nevertheless, there were strong reasons for dividing the sites into three types: Mona Island, hardbottom reefs and all other sites.

While site M1 at Mona had the highest fish density and biomass, Mona Island is an oceanic marine protected area located far from urban development and is partly protected from fishing pressure. Therefore, the higher fish densities and biomass found at these sites could be more related to lower levels of fishing pressure rather than higher water clarity. Over all sites at Mona Island, fish species richness and percentages of live coral cover were intermediate compared to other areas. The oceanic location, the strong currents along the Mona Passage, limited larval dispersal across the channel (Rojas-Ortega and García Sais, 2002; Taylor and Hellberg, 2003; Baums et al., 2006), differences in geomorphic features, and the limited habitats available (mangrove, sea weeds) in Mona Island could be limiting factors determining some fish and coral community attributes. Nevertheless, clear waters at Mona Island did have significant effects on community structure. For example, *Melichthys niger* was limited to Mona Island sites, and was always present in high densities, whereas off La Parguera the clear waters required by this species are limited to the edge of the insular shelf in depths of 25 m, beyond the range of the present study.

The highest fish biomasses off Puerto Rico proper were found at San Cristobal (SC) and Margarita (MR1), sites with relatively clear waters ($Kd_{(PAR)}$ = 0.16, 0.17, respectively). Maximum fish species richness occurred in San Cristobal (SC) as well, but also at Guayanilla (G4) which was more turbid. However, more typical were sites RO2 and Es in La Parguera, which had low species richness under highly turbid conditions. Highest percentages of live coral cover were observed at Pinnacles (LP) and San Cristobal (SC), the reef sites with the clearest waters in La Parguera. The lowest percentages of live coral cover in reef sites were observed in the turbid waters of Ponce and Guayanilla.

Lower fish species richness and very low percent coral cover were found at site Hb3, but this site is better characterized as hardbottom, as opposed to a coral reef proper. Hard ground reefs are mostly flat platforms largely covered by turf algae, encrusting sponges, and scattered patches of stony corals (Prada, 2002; Garcia et al., 2005). Thus, different structural features and therefore different biotic characteristics were found at this site.

Regression analyses suggest that seawater turbidity is an important factor determining coral reef organisms health. The most dramatic effect was observed on the coral community, but turbidity was also found to influence fish structure. The status of coral reefs in Puerto Rico is considered one of the most critical in the Caribbean (Goenaga and Boulon, 1991), as a consequence of increasing degradation of the water quality, due mainly to a rapid urban and industrial development in recent years. In southwestern Puerto Rico, coral reefs off Mayaguez Bay and Ponce have experienced significant degradation, particularly those located close to the shoreline (Garcia et al., 2005). Similar trends are reported for the inshore coral reef epibenthic communities in the northeastern Puerto Rico (Mckenzie and Benton, 1972; Goenaga and Citrón, 1979; Goenaga and Boulon, 1992; Hernandez-Delgado, 1992). Overall causes for this degradation include eutrophication (Goenaga, 1991), increases in water turbidity and suspended particulate matter (Goenaga, 1986, 1988; Zuluaga, 2003), bleaching (Goenaga et al., 1989; Goenaga and Canals, 1990) and disease (Weil et al., 2002), among others.

Hernandez and Sabat (2000) found differences in the structure of coral and reef fish communities in an offshore anthropogenic environmental gradient and reported reefs farther offshore possessed healthier coral and fish communities. However, effects of anthropogenic environmental stress and fishing pressure could not be separated. In the present study, distance from land was only significantly correlated with water turbidity, and definitive relationships across all sites were not observed because of the oceanic location of Mona Island (extreme distance) and the biotic and abiotic differences found in hardbottom sites (low percentages of live coral cover, species richness and fish densities) located relatively far from land. Similarly, a strong correlation among percentage of live coral cover and turbidity was found only after excluding Mona Island and the hardbottom gorgonian sites. Thus, in this study, coral and fish community structure varied along a turbidity gradient not necessarily offshore oriented. Mean fish density and biomass appeared to respond to turbidity changes. However, decreases in those fish community parameters were only significant if Mona Island sites were not considered in the regression.

Fish density was uncorrelated to turbidity for only two groups: the piscivores and mobile invertebrate-piscivorous feeders. Overfishing could be responsible for this lack of significance, as these groups represent the snappers, groupers, grunts and jacks, which are the largest and most desirable species (Matos-Caraballo, 2004). Overfishing, combined with coastal development and other human activities, has resulted in severe declines of both targeted and non-targeted fish populations (Roberts and Polunin, 1991; Lauck et al., 1998) throughout the region (Christensen et al., 2003). There has been a sharp decline in catch per unit effort (CPUE) in both commercial and recreational fishing, and shifts to smaller fish and recruitment failures have being reported for all of Puerto Rico (Appeldoorn et al., 1992). Fisheries developed in coral reefs can lead to changes in the reef fish trophic structure (Harmelin-Vivien, 1992).

In contrast to other studies, where turbid coral reefs possessed high percent algal cover and more abundant herbivorous fish (Hernandez, 2000; Zuluaga, 2003), the present study found mean herbivore density to be negatively correlated with water turbidity. In a complementary study in the same areas, Cardona and Armstrong (unpublished data) showed that algal cover also decreased with turbidity. Measures of algal cover were very variable in clear and intermediate turbid waters, but were particularly low at Kd values larger than 0.22 m^{-1}. This suggests that light limitation in very turbid waters could be severely affecting coral and algal communities, turning the general trend between water quality, percent algal cover and herbivorous fish density into a negative relationship. Similar results are reported by Rogers (1979) after shading 20 m^2 of reef area for five weeks; resulting limitations in light availability lead to losses in algal biomass, which in turn appeared to cause a decrease in damselfish abundance.

This study suggests that water turbidity is an important attribute influencing coral and reef fish communities. However, reef fish community parameters were correlated with multiple rather than single habitat factors. In addition to water turbidity, reef rugosity and percentage of live coral cover were factors significantly affecting the reef fish community. This indicates that reef fishes are responding to a combination of habitat characteristics. Because some of these factors are interrelated (Appendix 10, 11), it becomes difficult to differentiate between direct and indirect effects. A complex of parameters influencing fish community structure is typical of coral reefs (Ormond et al., 1996), and due to the heterogeneous and dynamic nature of these systems, some factors can indirectly affect others (Alveizon et al., 1985).

An example of this may be seen at Guayanilla site G4, which, although more turbid, had high fish species richness. This site was also characterized by high fish densities and low biomasses, because most of the fishes present were at juvenile stages. Turbidity may have a positive anti-predator effect on small species and juvenile fish (Utne-Palm, 2002). Suspended particles in the column water diminish contrast by increasing scattering, consequently affecting long-distance vision that would otherwise aid large piscivores to detect prey (Utne-Palm, 2002). The negative impact turbidity may have on predation success is considered one factor explaining why juveniles of many marine and anadromous species use turbid environments, such as estuaries (Blaber and Blaber, 1980; Gregory and Levings, 1998). It has been also suggested that turbidity favors juvenile fish by enabling them to perform "risky" activities that increase feeding rates (Gregory and Northcote, 1993) and migratory activities away from shelter (Ginetz and Larkin, 1976).

The variability in the vertical relief, or rugosity, is another important attribute of habitat complexity; it reflects and governs the spatial distribution and density of many reef organisms (Sale, 1991; Sebens, 1991; McCormick, 1994). Although the nature of the influence that rugosity exerts over fish communities is still open, this study agrees with those that consider rugosity a good predictor of species richness (Luckhurst and Luckhurst, 1978), density (Gladfelter and Gladfelter, 1978; Luckhurst and Luckhurst, 1978; McClanahan, 1994; Friedlander and Parrish, 1998; Syms and Jones, 2000; Eagle et al., 2001), and diversity (H') (Talbot, 1965; Risk, 1972; Talbot and Goldman, 1972; Luckhurst and Luckhurst, 1978). Rugosity enhances habitat quality by increasing structure and refuge, and facilitates migration for most reef fishes (Jenkins and Southerland, 1997). In particular, microhabitats provided by corals enhance net settlement and offer refuge from predation (Hixon and Beets, 1993). Furthermore, the elevated reef structure interacts with water flow leading to higher concentrations of plankton and nutrient retention (Choat and Bellwood, 1991). Thus, the positive relationship found between reef rugosity and planktivore densities could result from higher plankton and nutrient availability in more complex reefs. Rugosity also provides the abundant shelter needed by small planktivores, which often school in high densities as a protection from predation (Szmant, 1997).

Separating the effects of live coral cover and habitat heterogeneity is complicated, as live corals possess high structural complexity. Thus, fish density, diversity (H') and planktivore abundance were also correlated with percentage of live coral cover. Percent coral cover has long been recognized as a factor affecting fish community structure (Nagelkerken, 1977; Luckhurst and Luckhurst, 1978; Bell and Galzin, 1984; Bell et al., 1985; Sano et al., 1984; Ormond et al., 1996). Corals offer specific habitats for some fish larvae to settle (Sweatman, 1985), their associated complexity provides refuge (Munday et al., 1997), and their polyps constitute a food source for some fish species (Guzman and Robertson, 1989). Therefore, variations in coral cover should affect fish community structure.

The present study indicates that water turbidity, reefs rugosity and percent live coral cover can be useful predictors of the fish community variables. However, the effect these have over coral and fish communities can vary depending on level and duration of exposure. Because remote sensing has the potential to assess the spatial extent and level of water turbidity, in terms of the light attenuation coefficient (Kd_{PAR}), and can provide an idea of the substrate complexity, results found in this study could be useful for coastal marine resource management and conservation if data are incorporated into appropriate models to evaluate and monitor coral reef ecosystems in a synoptic scale. Nevertheless, as also shown in this study, such models must be empirically based as relationships can vary among areas.

CONCLUSIONS

Seawater turbidity is an important factor determining coral reef organisms health, affecting more dramatically the coral community but also influencing the fish community structure. Therefore, coral and fish parameters vary along a turbidity gradient. Signs of degradation, such as low percentages of live coral cover, fish densities, species richness and fish biomass, are stronger in turbid waters. Reefs located in clearer waters are characterized by higher values of these community parameters. However, reef sites have to be similar in order to such trends to be observed. In this study, for example, sites were divided into three types (Mona Island, hardbottom reefs and all other sites) because of differences in their biotic and abiotic characteristics. Possible overfishing could be occurring on piscivores and mobile invertebrate-piscivorous feeders, which are the largest and most desirable fish species. Light limitation in very turbid waters could be leading to losses in algal and coral biomass, which in turn appear to cause a decrease in herbivore density. Turbidity however, appear to represent refuge from large predators for small fishes.

Reef fishes respond to a combination of habitat characteristics, rather than single factors. Seawater turbidity, reef rugosity and percentage of live coral cover are variables significantly affecting the reef fish community, and therefore, are useful predictors of reef community health. However, the effect these attributes exert over coral and fish communities can vary depending on level and duration of exposure. Results found in this study should be considered in the development of remote sensing appropriate models for evaluation and monitor of coastal marine resources in a synoptic scale.

LITERATURE CITED

Abrahams, M. and M. Kattenfeld. 1997. The role of turbidity as a constraint on predator-prey interactions in aquatic environments. Behavioral Ecology and Sociobiology 40(3): 169-174.

Acevedo, R. and J. Morelock. 1988. Effects of terrigenous sediment influx on coral reef zonation in southwestern Puerto Rico, p. 189-194. In Choat, J.H., D. Barnes, MA. Borowitzka, J.C. Coll, P.J. Davies, P. Flood, B.G. Hatcher, D. Hopley, P.A. Hutchings, D. Kinsey, G.R. Orme, M. Pichon, P.F. Sale, P. Sammarco, C.C. Wallace, C. Wilkinson, E. Wolanski and O. Bellwood (eds.) Proceedings of the 6th International Coral Reef Symposium: Vol. 2: Contributed Papers. Townsville, Australia.

Acevedo, R., J. Morelock and R.A. Olivieri. 1989. Modification of coral reef zonation by terrigenous sediments stress. Palaios 4: 92-100.

Almy, C. 1965. Parguera Limestone, Upper Cretaceous Mayaguez Group, Southwestern Puerto Puerto. Ph.D. Thesis, Rice University, Houston Tx, USA.

Alveizon, W., R. Richardson , P. Pitts and G. Serviss. 1985. Coral zonation and patterns of community structure in Bahamian reef fishes. Bull. Mar. Sci. 36:304-318.

Amesbury, S.S. 1981. Effects of turbidity on shallow-water reef fish assemblages in Truk,Eastern Caroline Islands. Proceeding of the Forth International Coral Reefs Symposium, Manila. Vol 1.

Appeldoorn, R.S., J. Beets, J. Bohnsack, S. Bolden, D. Matos, S. Mayers, A. Rosario, Y. Sadovy and W. Tobias. 1992. Shallow water reef fish stock assessment for the U.S. Caribbean. NOOA Technical Memorandum NMFS-SEFSC-304, 70pp.

Appeldoorn, R.S., A. Friedlander, J. Sladek-Nowlis, P. Usseglio and A. Mitchell-Chui. 2003. Habitat connectivity in reef fish communities and marine reserve design in Old Providence-Santa Catalina, Colombia. Gulf. Carib. Res. 14: 61-77.

Bash, J., C. Berman and S. Bolton. 2001. Effects of turbidity and suspended solids on salmonids. (Report No. WA-RD 526.1). Seattle: Washington State Transportation Centre.

Baums, I.B., C.B. Paris and L.M. Cherubin. 2006. A bio-oceanographic filter to larval dispersal in the Caribbean. Limnology and Oceanography 51: 1969-1981.

Bell, J.D. and R. Galzin. 1984. Influence of live coral cover on a coral reef fish communities. Marine Ecology Progress Series 15: 265-274.

Bell J.D., M.L. Harmelin-Vivien and R. Galzin. 1985. Large scale spatial variation in abundance of butterflyfishes (Chaetodontidae) on Polynesian reefs. Proc 5th Int Coral Reef Symp 5: 421-426.

Berg, L. and T.G. Northcote. 1985. Changes in territorial, gill-flaring, and feeding-behaviour in juvenile coho salmon (Oncorhynchus kisutch) following short-term pulses of suspended sediment. Canadian Journal of Fisheries and Aquatic Sciences 42(8): 1410-1417.

Blaber, S.J. and T.G. Blaber. 1980. Factors affecting the distribution of juvenile estuarine and inshore fishes. J. Fish Biol., 17, 143–162.

Bohnsack, J.A. 1993. The impact of fishing on coral reefs. Pages C8-C12 in, Global Aspects of Coral Reefs: Health, Hazards, and History. June 10-11, 1993. University of Miami, Miami, FL.

Bohnsack, J.A. and D.E. Harper. 1988. Length-weight relationships of selected marine reef fishes from the southeastern United States and the Caribbean. NOAA Tech. Mem. NMFS-SEFC-215, 31 p.

Booth, D.J. and G.A. Beretta. 2002. Changes in fish assemblage after a coral bleaching event. Marine Ecology Progress Series 245: 205-212.

Booth, D.J. and G. Wellington. 1998. Settlement preferences in coral-reef fishes: Effects on patterns of adult and juvenile distributions, individual fitness and population structure. Coral Reefs 13:81-89.

Bouchon-Navarro, Y. 1986. Partitioning of food and space resources by chaetodontid fishes on coral reefs. Journal of experimental Marine Biology and Ecology 103: 21- 40.

Brock, R.E. 1954. A preliminary report on a method of estimating reef fish populations. J. Wild. Mgmt. 18: 297-308.

Bruckner, A., K. Buja, L. Fairey, K. Gleason, M. Harmon, S. Heron, T. Hourigan, C. Jeffrey, J. Kellner, R. Kelty, B. Leeworthy, G. Liu, S. Pittman, A. Shapiro, A. Strong, J. Waddell and P. Wiley, 2005. Environmental and Anthropogenic Threats to Coral Reef Ecosystems. p.12-44 in Waddell, J. (ed.), 2005. The State of Coral Reef Ecosystems of the United States and Pacific Freely Associated States: 2005. NOAA Technical Memorandum NOS NCCOS 11. NOAA/NCCOS Center for Coastal Monitoring and Assessment's Biogeography Team. Silver Spring, MD. 522 pp.

Burke, L. and J. Maidens. 2004. Reefs at Risk in the Caribbean. Worlds Resources Institute, Washington. 81 p. Caley, J.M. and J. St John. 1996. Refuge availability structures assemblages of tropical reef fishes. Journal of Animal Ecology 65: 414-428.

Carpenter, R.C. 1986. Partitioning herbivory and its effects on coral reef algal communities. Ecological Monographs 56: 345-363.

Carpenter, K.E., R.I. Miclat, V.D. Albaladejo and V.T. Corpuz. 1981. The influence of substrate structure on the local abundance and diversity of Phillipine reef fishes. Proc. 4th. Int. Coral Reef Symp. 2:497-502.

Carr, M.H. 1991. Patterns, mechanisms, and consequences of recruitment of a temperate marine reef fish. PhD dissertation, University of California, Santa Barbara.

Carr, M.H. 1994a. Predicting the response of reauitment of temperate reef fishes due to changes in macrophyte density caused by disturbance. In: Stouder DJ. Fresh K (eds) Theory and application in the feeding ecology of fishes. Belle Baruch Marine Institute Series, Univ of South Carolina Press, Columbia.

Carr, M.H. 1994b. Effects of macroalgal dynamics on recruitment of a temperate reef fish. Ecology 75:1320–1333.

Ceccarelli, D.M., G.P. Jones and L.J. McCook. 2001. Territorial damselfishes as determinants of the structure of benthic communities on coral reefs. Oceanography and marine biology:

an annual review. Gibson, R.N. (ed.); Barnes, M (ed.), Atkinson, RJA (ed.) London Taylor Francis. 39: 355-389.

Choat, J. and D.R. Bellwood. 1991. Reef fishes: Their history and evolution. In: P. Sale (Ed.), The ecology of fishes on coral reefs, p. 39-66. Academic Press. San Diego, CA.

Christensen, J.D., C.F.G. Jeffrey, C. Caldow, M.E. Monaco, M.S. Kendall and R.S. Appeldoorn. 2003. Cross-shelf habitat utilization patterns on reef fishes in Southwestern Puerto Rico. Gulf and Caribbean Research 14(2): 9-27.

Cintron, G., J. Thurston, J. Williams and F. MacKenzie. 1975. Caracteristicas de la plataforma insular de Isla de Mona. Pp 69-91. In: Proceedings of the 2nd Symposium of the Department of Natural Resources, San Juan, P.R.

Clarke, R.D. 1988. Chance and order in determining fish-species composition on small coral patches. J. Exp. Mar. Biol. Ecol. 115:197-212.

Doherty, P.J., A.A. Thompson, K. Osborne and I.R. Miller. 1996. Catastrophic loss of hard coral cover from reefs in the southern Great Barrier Reef and the impact on reef fish recruitment. Abstracts 8th Int. Coral Reef Symp., June 24-29, 1996, Panama.

Eagle, J., G. Jones and M. McCormick. 2001. A multi-scale study of the relationships between habitat and the distribution and abundance patterns of the three coral reef angelfishes (Pomacanthidae). Mar. Ecol. Pro. Ser. 214:253-265.

Eschmeyer, W.N. 1998. Catalog of fishes. Special Publication, California Academy of Sciences, San Francisco. 3 vols. 2905 p.

Ewel, J.J. and L. Withmore. 1973. The ecological life zones in Puerto Rico and the U.S. Virgin Islands. Forest Service Research Paper ITF 18, U.S. Department of Agriculture, 18 pp.

Fabricius, K.E. and McCorry, D. 2006. Changes in octocoral communities and benthic cover along a water quality gradient in the reefs of Hong Kong. Marine Pollution Bulletin 52: 22-33.

Friedlander, A.M. and J.D. Parrish. 1998. Habitat characteristics affecting fish assemblages on a Hawaiian coral reef. J Exp Mar Biol Ecol 224:1–30.

Galzin, R., S. Planes, V. Dufour and B. Salvat. 1994. Variation in diversity of coral reef fish between French Polynesian atolls. Coral Reefs 13(3): 175-180.

Garcia-Sais, J.R., R.S. Appeldoorn, A. Bruckner, C. Caldow, J.D. Christensen, C. Lilyestrom, M.E. Monaco, J. Sabater, E. Williams and E. Diaz. 2005. The State of Coral Reef Ecosystems of Puerto Rico. p.91-134 in Waddell, J. (ed.), 2005. The State of Coral Reef Ecosystems of the United States and Pacific Freely Associated States: 2005. NOAA Technical Memorandum NOS NCCOS 11. NOAA/NCCOS Center for Coastal Monitoring and Assessment's Biogeography Team. Silver Spring, MD. 522 pp.

GESAMP. 2001. Protecting the oceans from land-based activities. Land-based sources and activities affecting the quality and uses of the marine , coastal and associated freshwater environment. United Nations Environment Program, Nairobi, 168 pp.

Ginetz, R.M. and P.A. Larkin. 1976. Factors affecting rainbow trout (Salmo gairdneri) predation on migrant fry of sockeye salmon (Oncorhynchus nerka). J. Fish. Res. Board Can., 33, 19–24.

Gladfelter, W.B. and E.H. Gladfelter. 1978. Fish community structure as a function of habitat structure on West Indian patch reefs. Rev. Biol. Trop. 26(1):65-84.

Gladfelter, W.B., J.C. Ogden and E.H. Gladfelter. 1980. Similarity and diversity among coral reef fish communities: A comparison between tropical western Atlantic (Virgin Islands) and tropical central Pacific (Marshall Islands) patch reefs. Ecology 61: 1156-1168.

Goenaga, C. 1986. Los arrecifes costaneros en Puerto Rico: Estado actual e implicaciones sociales. Bol. Cien. Sur. 13(2):78-91.

Goenaga, C. 1988. The distribution and growth of Montastrea annularis (Ellis and Solander) in Puerto Rican inshore platform reefs. Ph.D. Thesis, University of Puerto Rico, Mayaguez PR, USA, 186 pp.

Goenaga, C. 1991. The state of coral reefs in the wider Caribbean. Interciencia 16:12-20.

Goenaga, C. and G. Cintrón. 1979. Inventory of the Puerto Rican Coral Reefs. Department of Natural Resources, Coastal Zone Management Program, San Juan PR, USA, 190 pp.

Goenaga, C. and M. Canals. 1990. Island-wide coral bleaching in Puerto Rico: 1990. Caribb. J. Sci. 26(3-4):171-175.

Goenaga, C. and R.H. Boulon, Jr. 1991. The State of Puerto Rican and U.S. Virgin Islands Corals. Caribbean Fishery Management Council, Hato Rey, Puerto Rico. 66 pp.

Goenaga, C. and R. H. Boulon. 1992. The State of Puerto Rican and U.S. Virgin Islands Corals: An Aid to Managers. Report submitted to Caribbean Fisheries Management Council, Hato Rey, P.R. 66 pp.

Goenaga, C., V. P. Vicente and R. Armstrong. 1989. Bleaching induced mortalities in reef corals from La Parguera, Puerto Rico: A precursor of change in the community structure of coral reefs? Caribbean Journal of Science, 25:59-65.

Gregory, R.S. and C.D. Levings. 1998. Turbidity reduces predation on migrating juvenile Pacific Salmon. Trans. Am. Fish. Soc., 127, 275–285.

Gregory, R.S. and T.G. Northcote. 1993. Surface, planktonic, and benthic foraging by juvenile chinook salmon (Oncorhynchus tshawytscha) in turbid laboratory conditions. Canadian Journal of Fisheries and Aquatic Sciences 50: 233-240.

Guzmán, H.M. and D.R. Robertson. 1989. Population and feeding responses of the corallivorous pufferfish *Arothron meleagris* to coral mortality in the eastern Pacific. Mar. Ecol. Prog. Ser. 55: 121-131.

Harmelin-Vivien, H. 1992. Impact of human activities on coral reef fish communities in French Polinesya. Cybium 16 (4): 279-289.

Harmelin-Vivien, M.L., J.G. Harmelin, C. Chauvet, C. Duval, R. Galzin, P. Lejeune, G. Barnabé, F. Blanc, R. Chevalier, J. Duclerc and G. Lasserre. 1985. Evaluation des peuplements et populations de poissons. Méthodes et problémes. Revue Écologie (Terre et Vie) 40: 467-539.

Harmelin-Vivien M, J.G. Harmelin, C. Chauvet, C. Duval, R. Galzin, P. Lejeune, G. Barnabé, F. Blanc, R. Chevalier, J. Duclerc, G. Lasserre. 1985. Evaluation des peuplements et populations de poissons. Méthodes et problémes. Revue Écologie (Terre et Vie) 40: 467-539.

Hay M.E. 1997. The ecology and evolution of seaweed-herbivore interactions on coral reefs. Coral Reefs 16S: S67-S76.

Hernandez-Delgado, E.A. 1992. Coral reef status of northeastern and eastern Puerto Rican waters: Recommendations for long-term monitoring, restauration and coral reef management plan. Report submitted to the Caribbean Fishery Management Council, Hato Rey, P.R., December 1, 1992. 87 pp.

Hernández E. 2000. Effects of anthropogenic stress gradients in the structure of coral reef fish and epibenthic communities. University of Puerto Rico, Rio Piedras Campus. PhD. Thesis.

Hernandez-Delgado, E.A. and A.M. Sabat. 2000. Ecological status of essential fish habitats through and anthropogenic environmental stress gradient in Puerto Rican coral reefs. Proceedings of the Gulf and Caribbean Fisheries Institute. Creswell, R. L. (ed.), 51: 457-470.

Hixon M.A. and J.P. Beets. 1993. Predation, prey-refuges, and the structure of coral-reef fish assemblages. Ecol Monogr 63(1):77–101.

Holden, H. and E. Ledrew. 2001. Hyperspectral discrimination of healthy versus stressed corals using in situ reflectance. Journal of Coastal Research 17 (4): 850-858.

Hughes T., D. Reed and M. Boyle. 1987. Hervibory on coral reefs: Community structure following mass mortalities of sea urchins. J. Exp. Mar. Biol. Ecol. 113, 39-59.

Jenkins, G. and C. Southerland. 1997. The influence of habitat structure on nearshore fish assemblages in a southern Australian embayment: colonization and turnover rate of fishes associated with artificial macrophyte beds of varying physical structure. J. Exp. Mar. Biol. Ecol. 218:103-125.

Jerlov, N.G. 1970. Light in Marine Ecology. Vol 1. Edited by O. Kinne, Wiley Interscience, New York, pp. 95-102.

Jones, G.P. 1988. Experimental evaluation of the effects of habitat structure and competitive interactions on the juveniles of two coral reef fishes. Journal of Experimental and Marine Biology and Ecology 123: 115-126.Kaye, C., 1959. Shoreline features and quaternary shoreline changes, Puerto Rico. US Geological Survey Prof. Paper. 317-B : 49-140.

Kendall, M.S., M.E. Monaco, K.R. Buja, J.D. Christensen, C.R. Kruer, M. Finkbeiner and R.A. Warner. 2001. (On-line). Methods Used to Map the Benthic Habitats of Puerto Rico and the U.S. Virgin Islands URL: http://biogeo.nos.noaa.gov/projects/mapping/caribbean/startup.htm. Also available on U.S. National Oceanic and Atmospheric Administration. National Ocean Service, National Centers for Coastal Ocean Science Biogeography Program. 2001. (CD-ROM). Benthic habitats of Puerto Rico and the U.S. Virgin Islands. Silver Spring, MD: National Oceanic and Atmospheric Administration.

Kinzie, R.A., P.L. Jokiel and R. York. 1984. Effects of light of altered spectral composition on coral zooxanthellae associations and on zooxanthellae in vitro. Mar. Biol. 78, 239-248.

Kirk, J.T.O. 1994. Light and photosynthesis in aquatic ecosystems. Cambridge University Press, London.

Lapointe, B.E., M. Littler and D. Littler. 1987. A comparison of nutrient limited productivity in macroalgae from Caribbean barrier reef and from mangrove ecosystem. Aquat. Bot. 28:243-255.

Lauck, T., C.W. Clark, M. Mangel and G.R. Munro. 1998. Implementing the precautionary principle in fisheries management through marine reserves. Ecological applications 8(1): Supplement: Ecosystem Management for Sustainable Marine Fisheries. S72-S78 pp.

Levin, P.S. 1991. Effects of microhabitat on recruitment variation in a Gulf of Maine reef fish. Mar Ecol Prog Ser 75:183–189.

Levin, P.S. 1993. Habitat structure, conspecific presence, and spatial variation in the recruitment of a temperate reef fish. Oecologia 94:176–185.

Lewis, A.R. 1997. Effects of experimental coral disturbance on the structure of fish communities on large patch reefs. Marine Ecology Progress Series 161: 37-50.

Lewis, A.R. 1998. Effects on the experimental coral disturbance dynamics on fishes on large patch reefs. Journal of Experimental Marine Biology and Ecology 230(1): 91-110.

Lindberg, W.J., T.K. Frazer, K.M. Portier, F. Vose, J. Loftin, D.J. Murie, D.M. Mason, B. Nagy and M.K. Hart, 2006. Density-Dependent Habitat Selection and Performance By A Large Mobile Reef Fish. Ecological Applications: Vol. 16, No. 2, pp. 731–746.

Loya, Y. 1972. Community structure and species diversity of hermatypic corals at Eilat, Red Sea. Mar. Biol. 13: 100-123.

Loya, Y. 1976. Effects of water turbidity and sedimentation on the community structure of Puerto Rican corals. Bull. Mar. Sci. 26(4):450-466.

Loya, Y. and L.B. Slobodkin. 1971. The coral reefs of Eilat (Gulf of Eilat , Red Sea). Proc. Zool. Soc. London 28: 117-140.

Luckhurst, B.E. and K. Luckhurst. 1978. Analysis of the influence of substrate variables on coral reef fish communities. Marine Biology 49: 317-323.

Ludwig, D. and J.F. Reynolds. 1988. Statistical ecology. Wiley, New York.Lythgoe, J.N. 1979. The Ecology of Vision. Oxford University Press, New York.

Maes J, P.A. Van Damme, A. Taillieu and F. Ollevier. 1998. Fish communities along an oxygen-poor salinity gradient (Zeeschelde estuary, Belgium). J Fish Biol 52: 534-546.

Matos-Caraballo, D. 2004. Puerto Rico/NMFS Cooperative Fisheries Statistics Program. April 2001-March 2004. Final Report submitted to the National Marine Fisheries Service by the Fisheries Research Laboratory, Department of Natural and Environmental Resources, San Juan. 83 pp.

Matz, M.V., N.J. Marshall and M. Vorobyev. 2006. Are corals colorful? Photochem. Photobiol. 82: 345-35.

McClanahan, T.R. 1994. Kenyan coral reef lagoon fish: effects of fishing, substrate complexity, and sea urchins. Coral Reefs 13: 231-141.

McCook L.J., I.R. Price and W. Klumpp. 1997. Macroalgae on the GBR: Causes or consequences, indicators or models of reef degradation? Proc. 8th Int. Coral Reef Symp. 1:1852-1856.

McCook L.J., J. Jompa and G. Diaz-Pulido. 2001. Competition between corals and algae on coral reefs: a review of evidence and mechanisms. Coral Reefs 19:400-417.

McCormick, M.I. 1994. Comparison of field methods for measuring surface topography and their associations with a tropical reef fish assemblage. Mar. Ecol. Prog. Ser. 112: 87-96.

Mckenzie, F. and M. Benton. 1972. Biological inventory of the waters and keys of north-east Puerto Rico. Final report submitted to the Division of Natural Resources, Department of Public Works, San Juan, P.R. 90 pp.

Miner, J.G. and R.A. Stein. 1996. Detection of predators and habitat choice by small bluegills: Effects of turbidity and alternative prey. Transactions of the American Fisheries Society. 125(1): 97-103.

Morelock, J., N. Schneiderman and W.R. Bryant. 1977. Shelf reefs, southwestern Puerto Rico. Pp. 17-28. In: Frost, S.H., M.P. Weiss and J.B. Saunders (eds.) Reefs and Related Carbonates-Ecology and Sedimentology, American Asociation of Petroleum Geologists, Studies in Geology 4.

Morelock, J., W.R.Ramirez, A.W.Bruckner and M.Carlo. 2001. Status of coral reefs, southwest Puerto Rico. Caribbean Journal of Science Special Publication N_o. 4.

Munday, P.L., G.P. Jones and M.J. Caley. 1997. Habitat specialisation and the distribution and abundance of coral-dwelling gobies. Mar. Ecol. Prog. Ser. 152,227 -239.

Nagelkerken, W.P. 1977. The distribution of the Graysby Petrometopon cruentatum (Lacepede) on the coral reef at the southwest coast of Curaçao. Proceedings of the Third International Coral Reef Symposium, 311-315.

Nagelkerken, I., G. van der Velde, M.W. Gorissen, G.J. Meijer, T. van't Hof and C. den Hartog. 2000. Importance of mangroves, seagrass beds and the shallow coral reef as a nursery for important coral reef fishes, using a visual census technique. Est. Coast. Shelf Sci. 51: 31-44.

Newcombe, C.P., and D.D. MacDonald. 1991. Effects of Suspended Sediments on Aquatic Ecosystems. North American Journal of Fisheries Management 11:72-82, 1991

NOAA Coastal Ocean Program Decision Analysis Series No.21. COASTAL The Potential Consequences of Climate Variability and Change. A report of the National Coastal Assessment Group for the U.S. Global Change Research Program. October 2000.

Ormond, R.F.G., J.M. Roberts and R.Q. Jan. 1996. Behavioural differences in microhabitat use by damselfishes (Pomacentridae): implications for reef fish biodiversity. Journal of Experimental Marine Biology and Ecology 202:85-95.

Prada, M.C. 2002. Mapping of benthic habitats off southwest Puerto Rico using side scan sonar technology. Ph.D. Dissertation, UPR-Mayaguez.

Risk W. 1972. Fish diversity on a coral reef in the Virgin Islands. Atoll Res. Bull. 153:1-6.

Roberts, C.M. and N.V.C. Polunin. 1991. Are marine reserves effective in management of reef fisheries? Reviews in Fish Biology and Fisheries 1: 65-91.

Robertson, D.R. 1982. Fish feces as fish food on Pacific coral reef. Marine Ecology Progress Series 7: 253-265.

Rogers, C. 1979. The effect of shading on coral reef structure and function. J. Exp. Mar. Biol. Ecol. 41:269-288.

Rojas-Ortega, J. and J. García Sais. 2002. Characterization of the ichthyoplankton within the Mona Channel with emphasis on coral reef fishes. Proc. Gulf Caribb. Fish. Inst. 55: 348 – 361.

Rooker, J. and C. Reicksiek. 1992. The effects of training with visual fish models in estimating lengths of fish underwater. Gulf Carib. Fish. Inst. 41:321-331.

Rothans, T.C. and A.C. Miller. 1991. A link between biologically imported particulate organic nutrients and the detritus food web in reef communities. Marine Biology 110: 145-150.

Ruiz, G. M., Hines, A. H. and Posey, M. H. 1993. "Shallow water as a refuge habitat for fish and crustaceans in non-vegetated estuaries: An example from Chesapeake Bay," Marine Ecology Progress Series 99, 1-16.

Sale PF (1991) Habitat structure and recruitment in coral reef fishes. In: Bell SS, McCoy ED, Mushinsky HR (eds) Habitat structure, the physical arrangement of objects in space. Chapman and Hall, New York, pp 197–210.

Sale, P.F. and W.A. Douglas. 1984. Temporal variability in the community structure of fish on coral patch reefs and the relation of community structure to reef structure. Ecology 65(2): 409-422

Sano, M., M. Shimizu and Y. Nose. 1984. Changes in structure of coral reef fish communities by destruction of hermatypic corals: observational and experimental views. Pacific Science 38: 51-79.

Scharer, M.T. 2001. A Survey of the epibiota of Hawksbill sea turtles (Eretmochelys imbricata) of Mona Island, Puerto Rico. 2001. University of Puerto Rico, Mayaguez. MS thesis.

Sebens, K.P. 1991. Habitat structure and community dynamics in marine benthic systems. In: Bell SS, McCoy ED, Mushinsky HR (eds) Habitat structure: the physical arrangement of objects in space. Chapman and Hall, London, pp 211-234.

Seehausen, O. 2001. Predictions about vision-mediated consequences of water transparency for fish community ecology. Abstract from the 44th Conference on Great Lakes Research. Great Lake Science: making it relevant. USA. International Association for Great Lakes Research. p.121.

Sokal, R.R. and F.J. Rohlf. 1995. Biometry. The principles and practice of statistics in biological research, 3rd Ed., Freeman & Co., NY, 850 pp.

Souter, D and O. Linden. 2000. The health and future of coral reef systems". Ocean and Coastal Management 43:657-688.

Sweatman, H.P.A. 1985. The influence of adults of some coral reef fishes on larvalrecruitment. Ecol. Monog. 55: 469-485.

Syms, C. and G. Jones. 2000. Disturbance, habitat structure and the dynamics of a coral-reef fish community. Ecology 81:2714-2729.

Szmant A. M. 1997. Nutrient effects on Coral reefs: A hypothesis on the importance of topographic and trophic complexity to reef nutrient dynamics. Proc 8th Int. Coral Reef Sym. 2:1527-1532.

Talbot, F.H. 1965. A description of the coral structure of Tutia Reef (Tanganyika Territory, East Africa) and its fish fauna. Proc . Zool . Soc . London 145 : 431-470 .

Talbot, F.H. and B. Goldman. 1972. A preliminary report on the diversity and feeding relationships of the reef fishes of One Tree Island, Great Barrier Reef System. Proc Symp Corals and Coral Reefs, 1969. J. Mar. Biol. Assoc., India, pp. 425–444.

Tanner, J.E. 1995. Competition between scleractinian corals and macroalgae: An experimental investigation of coral growth, survival and reproduction. J. Exp. Mar. Biol. Ecol. 151-168.

Taylor, M. and M. Hellberg. 2003. Genetic evidence for local retention of pelagic larvae in a Caribbean reef fish. Science 299: 107-109.

Tupper, M. and R. G. Boutilier. 1997. Effects of habitat on settlement, growth, predation risk and survival of a temperate reef fish. Marine Ecology Progress Series. 151: 225-236.

Utne-Palm, A.C. 2002. Visual feeding of fish in a turbide environment: Physical and behavioural aspects. Marine and Freshwater Behaviour and Physiology. 35(1-2): 111-128.

Weil, E., I. Urreiztieta and J Garzon-Ferreira. 2002. Geographic variability in the incidence of coral and octocoral diseases in the wider Caribbean. pp. (2): 1231-1237. In: Proceedings of the 9th International Coral Reef Symposium.

Wilber, C.G. 1971. Turbidity in Marine Ecology. Vol 1. Edited by O. Kinne, Wiley Interscience, New York, pp. 1157-1165.

Williams, D.McB. 1991. Patterns and processes in the distribution of coral reef fishes. In: Sale, PF. Ed. The Ecology of Fishes on Coral Reefs. Academiv Press, New York. Pp, 437-474.

Williams, D.McB. and P.F. Sale. 1981. Spatial and temporal paterns of recruitment of juvenile coral reef fishes to coral habitats within 'One Tree Lagoon', Great Barrier Reef. Marine Biology 65: 245-253.

Wolanski, E., Richmond, R., McCook, L. and Sweatman, H. 2003. Mud, Marine Snow and Coral Reefs American Scientist, Volume 91.

Zuluaga, A. 2003. Fish and epibenthic community structure in eight reefs with contrasting environmental conditions. MSc. thesis. University of Puerto Rico, Rio Piedras Campus. 61 pp.

Appendix 1. Station locations and coordinates (decimal degrees).

Site	Location	Area	Latitude	Longitude
M1	Carmelitas	Mona	18.0612	67.9207
M2	Punta Ingleses	Mona	18.0544	67.8671
M3	Carmelitas	Mona	18.1051	67.9354
Hb1	Margarita-San Cristobal	La Parguera	17.9208	67.0669
Hb3	Margarita-San Cristobal	La Parguera	17.9086	67.0469
Hb2	Margarita-San Cristobal	La Parguera	17.9228	67.0964
Hb4	Margarita-San Cristobal	La Parguera	17.9292	67.0997
Ep	El Palo	La Parguera	17.9306	67.0839
Sc	San Cristobal	La Parguera	17.9456	67.0778
Lp	Los Pinaculos	La Parguera	17.9327	67.0123
Mr1	Margarita	La Parguera	17.9158	67.1179
Mr2	Margarita	La Parguera	17.9275	67.1227
Bb	Bahia bioluminiscente	La Parguera	17.9636	67.0188
La1	Laurel	La Parguera	17.9368	67.0651
Tu	Turrumote	La Parguera	17.9342	67.0147
Ml	Media Luna	La Parguera	17.9346	67.0485
Ic	Isla Cueva	La Parguera	17.9582	67.0686
Td2	Turrumote 2	La Parguera	17.9252	66.9671
Ro1	Romero	La Parguera	17.9468	66.9923
La2	Laurel	La Parguera	17.9404	67.0586
Td1	Turrumote 2	La Parguera	17.9318	66.9770
En	Enrique	La Parguera	17.9544	67.0536
G1	Cayo Caribe	Guayanilla	17.9646	66.7358
G3	Fanduco	Guayanilla	17.9656	66.7611
P1	Ratones	Ponce	17.9453	66.6704
Ca	Caracoles	La Parguera	17.9615	67.0340
Ro2	Romero	La Parguera	17.9440	66.9961
Ro3	Romero	La Parguera	17.9437	66.9785
G4	Fanduco	Guayanilla	17.9667	66.7655
Ma	Mario	La Parguera	17.9525	67.0548
Ae	Arrecife Enmedio	La Parguera	17.9469	67.0190
P2	Cardona	Ponce	17.9546	66.6332
G2	Guayanilla	Guayanilla	17.9793	66.7441
P3	Tazmania	Ponce	17.9407	66.6254
Es	Este	La Parguera	17.9247	66.9494

Appendix 2. Fish species codes and trophic categories (T.C.) (H: herbivore; MI: mobile invertebrate feeder; MI/P: mobile invertebrate-piscivorous feeder; P: piscivore; SI: sessile invertebrate feeder; Z: planktivore).

Species	Code	T.C.	Species	Code	T.C.	Species	Code	T.C.
Acanthurus bahianus	ABAH	H	Haemulon sciurus	HSCI	MI	Stegaste variabilis	SVAR	O
Acanthurus chirurgus	ACHI	H	Holacanthus ciliaris	HCIL	MI	Aulostomus maculatus	AMAC	P
Acanthurus coeruleus	ACOE	H	Holocentrus adscensionis	HADS	MI	Bothus lunatus	BLUN	P
Coryphopterus dicrus	CDIC	H	Holocentrus rufus	HRUF	MI	Caranx crysos	CCRY	P
Coryphopterus lipernes	CLIP	H	Hypoplectrus chlorurus	HCLO	MI	Caranx ruber	CRUB	P
Melichthys niger	MNIG	H	Hypoplectrus guttavarius	HGUT	MI	Chloroscombrus chrysurus	CCHR	P
Microspathodon chrysurus	MCHR	H	Hypoplectrus indigo	HIND	MI	Gymnothorax miliaris	GMIL	P
Ophioblennius atlanticus	OATL	H	Hypoplectrus nigricans	HNIG	MI	Gymnothorax moringa	GMOR	P
Scarus iserti	SISE	H	Hypoplectrus puella	HPUE	MI	Mycteroperca venenosa	MVEN	P
Scarus taeniopterus	STAE	H	Hypoplectrus sp	HYSP	MI	Scomberomorus cavalla	SCAV	P
Scarus vetula	SVET	H	Hypoplectrus unicolor	HUNI	MI	Sphyraena barracuda	SBAR	P
Sparisoma atomarium	SATO	H	Lachnolaimus maximus	LMAX	MI	Synodus foetens	SFOE	P
Sparisoma aurofrenatum	SAUR	H	Lutjanus mahogoni	LMAH	MI	Synodus intermedius	SINT	P
Sparisoma chrysopterum	SCHR	H	Malacanthus plumieri	MPLU	MI	Chaetodipterus faber	CFAB	SI
Sparisoma viride	SVIR	H	Mulloidichthys martinicus	MMAR	MI	Chaetodon capistratus	CCAP	SI
Stegastes diencaeus	SDIE	H	Myrichthys breviceps	MBRE	MI	Chaetodon ocellatus	COCE	SI
Stegastes fuscus	SFUS	H	Neoniphon marianus	NMAR	MI	Chaetodon sedentarius	CSED	SI
Stegastes leucostictus	SLEU	H	Pseudupeneus maculatus	PMAC	MI	Chaetodon striatus	CSTR	SI
Stegastes partitus	SPAR	H	Serranus tigrinus	STIG	MI	Holacanthus tricolor	HTRI	SI
Stegastes planifrons	SPLA	H	Thalassoma bifasciatum	TBIF	MI	Pomacanthus arcuatus	PARC	SI
Anisotremus virginicus	AVIR	MI	Cephalopolis cruentata	CCRU	MI/P	Pomacanthus paru	PPAR	SI
Balistes vetula	BVET	MI	Cephalopolis fulva	EFUL	MI/P	Abudefduf saxatilis	ASAX	Z
Bodianus rufus	BRUF	MI	Epinephelus guttatus	EGUT	MI/P	Amblycirrhitus pinos	APIN	Z
Calamus penna	CPEN	MI	Lutjanus analis	LANA	MI/P	Chromis cyanea	CCYA	Z
Diodon hystrix	DHYS	MI	Lutjanus apodus	LAPO	MI/P	Chromis multilineata	CMUL	Z
Equetus punctatus	EPUN	MI	Lutjanus griseus	LGRI	MI/P	Clepticus parrae	CPAR	Z
Gerres cinereus	GCIN	MI	Lutjanus synagris	LSYN	MI/P	Coryphopterus personatus	CPER	Z
Haelichoeres garnoti	HGAR	MI	Ocyurus chrysurus	OCHR	MI/P	Gramma loreto	GLOR	Z
Haelichoeres maculipinna	HMAC	MI	Odontoscion dentex	ODEN	MI/P	Haemulon striatum	HSTR	Z
Haemulon aurolineatum	HAUR	MI	Canthigaster rostrata	CROS	O	Malacoctenus sp	MALA	Z
Haemulon carbonarium	HCAR	MI	Coryphopterus glaucofraenum	CGLA	O	Myripristis jacobus	MJAC	Z
Haemulon chrysargyreum	HCRY	MI	Gobiosoma dilepsis	GDIL	O	Priacanthus cruentata	PCRU	Z
Haemulon flavolineatum	HFLA	MI	Gobiosoma evelynae	GEVE	O	Priacanthus sp	PRSP	Z
Haemulon plumieri	HPLU	MI	Lactophrys triqueter	LTRI	O			

Appendix 3. Herbivore total abundances per site. See Apendix 2 for species codes.

Site	ABAH	ACHI	ACOE	CDIC	CLIP	MCHR	MNIG	OATL	SATO	SAUR	SCHR	SDIE	SFUS	SISE	SLEU	SPAR	SPLA	STAE	SVET	SVIR	Total
MR1	26	1	17			10				20		5	12	7	4	14		2		3	121
IC	11	18	1			1				8				7	10	3	26	35		34	154
MR2	2			4					3	6				8	13	18	18	19		4	95
CA		2		2		2				4			3	5	8	6	23	4		7	66
EP	11	4	8			13		1		8			24	31	2	17	2	11		21	153
HB4	6	2	7	1						17				10	4	2	27	34		11	121
BB		2		3						4			3	11	20	4	17	3		2	69
RO2	7		1	1						5				1	14			1			30
TD2	4					2				9		4	3	14	7	10	1	6		4	64
ES	12		1							29	1				19	1				2	65
LA1	2		2			4				7		4	12	9		7	1	1		7	56
RO3		3		2						11				3	15	1	2	2		4	43
AE													2	1	6	7	17	8		1	42
TU	8	6	6			3				5		1	3	15	6	3	1	8		7	72
SC			25			9				2			1	11	8	24		10		4	94
RO1		1	1			1				6					17	1	1			3	31
G1	2	1	6		6					13				11	8	16		5	1		69
G2		2								1			1	10	9	6	10			2	41
G3	12		9		11					6			2	10	9	36		8		2	105
G4	7	1	2			2				8				2	3	10		2		16	53
P1	6	5								10	1			1	4	4				3	34
P2	5									3			10	7	1	9		4			39
P3	2	1								8				5	1	3		4		2	26
MA		1								7				2	9	3	8	2		7	39
M1	7		3			1	50			1						74					136
M2			1			14	14	3		1				1		43					77
M3	5		3			3	2	2		1			1			26				1	44
HB3	10		1	1						14						12		1		1	40
ML	3		2			7				4			6	5	5	16	6	13		3	70
LP	8	3	3	6		1				10				21	5	9	1	10		9	86
EN	1	1	2							9			2	14	19	2	16	1		3	70
LA2			2							12			2		11	6	10	1		9	53
HB2	11		3			12				9		1	25	1	3	11	8	2		13	99
HB1	19		2			1			1	14				20	2	9		22		9	99
TD1	14									6				1	5	8		15		2	51
Total	201	54	108	20	17	86	66	6	4	278	2	15	112	244	247	421	195	234	1	196	2507

Appendix 4. Planktivore total abundances per site. See Apendix 2 for species codes.

Site	APIN	ASAX	CCYA	CMUL	CPAR	CPER	GLOR	HSTR	MALA	MJAC	PCRU	PRSP	Total
MR1		4											4
IC						60	2						62
MR2						13	39						52
CA						23				1			24
EP				40						1			41
HB4							1						1
BB						80	5						85
RO2							2						2
TD2			4										4
ES													0
LA1	1		5	40		1	1						48
RO3						31	16						47
AE						5	9						14
TU			5	53	10		4		1				73
SC			5	11			15		1	3			35
RO1		4				48	30	1					83
G1		14				74				2			90
G2						29							29
G3		6	9			100							115
G4			3							2			5
P1						106							106
P2						10				10			20
P3										4			4
MA						26	1						27
M1			56	70	36		4			4			170
M2	1		16	22	1								40
M3			18	40			3				1		62
HB3													0
ML			6	61			6						73
LP		2	1			1	7						11
EN						27	3		1				31
LA2			1				2					1	4
HB2										1			1
HB1													0
TD1													0
Total	2	30	129	337	47	634	150	1	3	28	1	1	1363

Appendix 5. Omnivore total abundances per site. See Apendix 2 for species codes.

Site	CGLA	CROS	GDIL	GEVE	LTRI	SVAR	Total
MR1							0
IC	3			13		3	19
MR2		7		1	2	2	12
CA		2		10	1	1	14
EP				4		1	5
HB4		3	8	3			14
BB		7		9			16
RO2		4		11			15
TD2		3	1	13		1	18
ES			1	34	1		36
LA1		4		6			10
RO3		3		9			12
AE		1		10		2	13
TU		8	1	7			16
SC			2	11		4	17
RO1		3		6			9
G1		5		4			9
G2		1		2		1	4
G3		2		5			7
G4		2		2			4
P1		1		2			3
P2	1			1			2
P3							0
MA		7	1	8		1	17
M1				3			3
M2				1			1
M3				2	1		3
HB3		2		5			7
ML		4		7			11
LP		4	3	8			15
EN		9	5	11		2	27
LA2		8		7			15
HB2						6	6
HB1		2		3			5
TD1		5		15	1		21
Total	4	97	22	233	6	24	386

Appendix 6. Sessile invertebrate feeder total abundances per site.
See Apendix 2 for species codes.

Site	CCAP	CFAB	COCE	CSED	CSTR	HTRI	PARC	PPAR	Total
MR1	7								7
IC	17						4	5	26
MR2	7						1		8
CA							1		1
EP	15						4		19
HB4	3								3
BB	24						3		27
RO2	5	3					1		9
TD2	17								17
ES	10						2		12
LA1	2								2
RO3	13								13
AE	9		1				1		11
TU	3						1		4
SC	8						1		9
RO1	4				1		1		6
G1	7	2	1		1		4		15
G2			1				1		2
G3	6					1			7
G4	17			1	1				19
P1	2								2
P2	4		2						6
P3	6								6
MA	13				2		3		18
M1	4								4
M2						2			2
M3				1					1
HB3	20								20
ML	11								11
LP	9								9
EN	2						2	1	5
LA2	5								5
HB2	3				1		1		5
HB1	12								12
TD1	13								13
Total	278	5	5	2	6	3	31	6	336

Appendix 7. Mobile invertebrate feeder total abundances per site. See Apendix 2 for species codes.

Site	AVIR	BRUF	BVET	CPEN	DHYS	EPUN	GCIN	HADS	HAUR	HCAR	HCIL	HCLO	HCRY	HFLA	HGAR	HGUT	HIND	HMAC	HNIG	HPLU	HPUE	HRUF	HSCI	HUNI	HYSP	LMAH	LMAX	MBRE	MMAR	MPLU	NMAR	PMAC	STIG	TBIF	Total
MR1			1					2						16	8			1				1								1				58	88
IC	1			1				3	2		2	6		10	1							1					3								30
MR2							2	2						2	4										1				1					11	23
CA								1		1		5		6					1					1							1				16
EP				1				4		1	3	1		2	3	1					1	2												20	39
HB4											2	1		1						2	1			1			1		1					8	18
BB	3					1		1	6			7		7							2			1					6					4	38
RO2								2				2		2						26			7												39
TD2		1						2		3		2		2						1															11
ES	1							3				1		6	3								1		1		1					4			21
LA1								1			1	1		1	1		1					1												31	38
RO3	1							5		5		1		1		1					1			1										1	17
AE								2				8		4			1			2					1							1	2		21
TU												3		4	1									1			1						1	4	15
SC								7		4		1		5	1	1				2				1			1		5			1	1	46	76
RO1						1	2	5				2		1	1									1		2	2							38	55
G1	3	1						2						3										1					2					12	24
G2	1													1									1						4					11	18
G3	4	1						2				2	1	11	5								1	2	1								1	19	50
G4		1						2						2	8								1									2	1	5	22
P1	5													4							1													5	15
P2								1						1	7										1								3	23	36
P3								1							2								1									1	1	1	7
MA	3					1			1	1	2	11								1		1			2										23
M1		6						4							1							4											1	130	146
M2		1																																180	181
M3														1	3							3							3				2	46	58
HB3			5					2							16													1	4					30	58
ML												1									2											1		35	39
LP								1				3		3	3		1					1	1		1								1	11	26
EN	1							3				11																							15
LA2					1	1		4			1	1		1	1		1				2				3		1						1	8	26
HB2								2						1	2					1									1			3		29	39
HB1				1				2		1				2	5					1									3			1		12	28
TD1					1	1		2				2		1	3	1				6				1			1		1						20
Total	23	11	6	3	2	5	4	68	9	16	11	72	1	101	79	4	4	1	1	42	10	14	13	11	11	2	11	1	31	1	1	14	15	778	1376

Appendix 8. Mobile invertebrate-piscivorous feeders total abundances per site. See Apendix 2 for species codes.

Site	CCRU	EFUL	EGUT	LANA	LAPO	LGRI	LSYN	OCHR	ODEN	Total
MR1					4			3		7
IC	2		1		6			4		13
MR2	2		2		2					6
CA	1									1
EP				1	4			3		8
HB4		1			1			3		5
BB	4	1	1		4	7		3		20
RO2	1		1	3				6		11
TD2			1		3			4		8
ES	2		1		1		1	3		8
LA1	1				1					2
RO3					6					6
AE	1				1	1		2		5
TU								3	1	4
SC				1	4			1	1	7
RO1	2				1		1	4	1	9
G1	6			5	6			8		25
G2	1									1
G3	3		1		1			2	1	8
G4	1				3			4		8
P1	1				1			1		3
P2	1									1
P3		1						2		3
MA								1		1
M1	3	1	1							5
M2	3	2								5
M3	2				1					3
HB3										0
ML					2					2
LP					1			1		2
EN	1				3	1				5
LA2					2			5		7
HB2	1									1
HB1			1					3		4
TD1	1							8		9
Total	40	6	10	10	58	9	2	74	4	213

Appendix 9. Piscivore total abundances per site. See Apendix 2 for species codes.

Site	AMAC	BLUN	CCHR	CCRY	CRUB	GMIL	GMOR	MVEN	SBAR	SCAV	SFOE	SINT	Total
MR1					61								61
IC										15	1		16
MR2	1				11								12
CA	1												1
EP	1											1	2
HB4	2												2
BB													0
RO2													0
TD2													0
ES													0
LA1	1												1
RO3	1												1
AE	2		1			1							4
TU					7								7
SC	1					1						1	3
RO1	1												1
G1	1		20		1				3				25
G2					1								1
G3													0
G4													0
P1							1						1
P2													0
P3					50								50
MA	1												1
M1	2			3				1		1			7
M2					2								2
M3		1		5									6
HB3													0
ML	2					1							3
LP												1	1
EN													0
LA2	2												2
HB2					4								4
HB1													0
TD1					2								2
Total	19	1	21	8	139	3	1	1	3	16	1	3	216

Appendix 10. Trellis diagram of all the correlations (r^2) for all sites (H: herbivores, MI: mobile invertebrate feeders, MI/P: mobile invertebrate-piscivores, O: omnivores, SI: sesile invertebrate feeders, Z: planktivores).

	Reef rugosity	Distance from Land	% live coral cover	Coral richness	Fish richness	Fish density	Fish biomass	Fish H'	H density	MI density	MI/P density	O density	P density	SI density	Z density
Kd	<0.001	0.737	0.047	0.029	0.059	0.322	0.229	0.012	0.272	0.446	0.002	0.318	0.025	0.070	0.024
Reef rugosity		0.001	0.290	0.028	0.426	0.149	0.030	0.247	0.078	0.001	0.008	0.011	0.014	0.011	0.223
Distance from land			0.002	0.131	0.018	0.290	0.128	0.022	0.136	0.452	0.003	0.287	0.034	0.130	0.038
% live coral cover				0.387	0.293	0.008	0.015	0.314	0.108	0.004	0.003	<0.001	0.008	0.001	0.013
Coral richness					0.011	0.175	0.054	0.118	0.005	0.191	0.013	0.059	0.023	0.022	0.029
Fish richness						0.369	0.134	0.486	0.437	0.104	0.074	0.047	0.090	0.024	0.149
Fish density							0.364	<0.001	0.487	0.501	0.103	0.265	0.140	0.007	0.393
Fish biomass								0.012	0.331	0.159	0.045	0.079	0.216	0.033	0.109
Fish H'									0.084	0.050	0.001	0.025	<0.001	0.047	<0.001
H density										0.160	0.008	0.173	0.130	0.003	0.028
MI density											0.016	0.546	0.044	0.019	0.101
MI/P density												0.001	0.229	0.203	0.015
O density													0.007	0.035	0.079
P density														0.062	<0.001
SI density															0.013

Appendix 11. Trellis diagram of all the correlations (r^2) excluding Mona Island and harbottom sites (H: herbivores, MI: mobile invertebrate feeders, MI/P: mobile invertebrate-piscivores, O: omnivores, SI: sesile invertebrate feeders, Z: planktivores).

	Reef rugosity	Distance from Land	% live coral cover	Coral richness	Fish richness	Fish density	Fish biomass	Fish H'	H density	MI density	MI/P density	O density	P density	SI density	Z density
Kd	0.117	0.259	0.652	0.116	0.194	0.125	0.092	0.080	0.191	0.087	0.012	0.036	0.001	<0.001	0.034
Reef rugosity		0.090	0.276	0.014	0.382	0.252	0.046	0.239	0.114	0.045	0.003	0.006	0.027	0.022	0.239
Distance from land			0.074	0.009	0.030	0.027	0.002	0.072	0.047	0.031	0.054	0.008	0.003	0.032	0.002
% live coral cover				0.353	0.267	0.048	0.038	0.236	0.154	0.029	<0.001	0.011	0.005	<0.001	0.046
Coral richness					0.004	0.070	0.008	0.006	0.004	0.027	0.006	0.002	0.026	0.011	0.015
Fish richness						0.481	0.114	0.569	0.516	0.253	0.103	0.121	0.100	0.119	0.132
Fish density							0.239	0.065	0.476	0.306	0.115	0.173	0.172	0.026	0.385
Fish biomass								0.001	0.243	0.035	0.067	0.015	0.208	0.007	0.104
Fish H'									0.215	0.016	0.013	0.008	<0.001	0.086	0.005
H density										0.102	0.019	0.125	0.179	0.019	0.061
MI density											0.012	0.388	0.022	0.004	0.032
MI/P density												0.001	0.286	0.288	0.004
O density													<0.001	0.001	0.142
P density														0.100	0.018
SI density															0.020