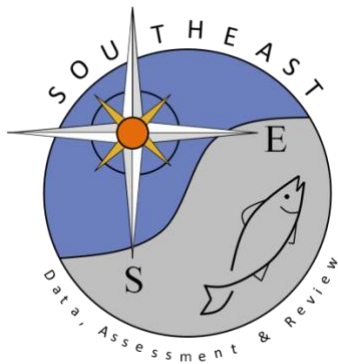# The Distribution of Herbivorous Coral Reef Fishes within Fore-reef Habitats: the Role of Depth, Light and Rugosity

Michael Nemeth and Richard Appeldoorn

SEDAR84-RD-08

January 2024

The Distribution of Herbivorous Coral Reef Fishes within Fore-reef Habitats: the Role of Depth, Light and Rugosity

Michael Nemeth[1] and Richard Appeldoorn[1]

[1]University of Puerto Rico, Department of Marine Sciences, PO Box 908, Lajas, Puerto Rico 00667
michaelnemeth@hotmail.com

Abstract.—Examining the relationship between habitat characteristics and utilization patterns by herbivorous fishes on coral reefs will add to our understanding of the factors that influence the abundance and distribution of this important group. The abundances of parrotfishes (Scaridae) and surgeonfishes (Acanthuridae) on fore-reef habitats were sampled along an inshore-offshore gradient to provide for within reef and cross-shelf comparisons in relation to the environmental parameters of depth and topographic relief. Temporally replicated visual surveys were conducted along permanent belt transects (100m^2) at three depth intervals (3, 10, 15 m) to obtain data on fish species density and lengths, which were used to calculate biomass. The roving herbivorous fish assemblage was dominated by three species of parrotfishes *(Scarus iseri, Sparisoma aurofrenatum* and *S. viride)* and three surgeonfishes *(Acanthurus bahianus, A. chirurgus* and *A. coerulus).* Overall the biomass of both families was highest at 3m compared to 10 or 15m (p<0.05). However, the relative decrease in biomass across depths for both families was greatest at inshore reefs where water transparency is lowest. The mean biomass for both families differed between inner and mid-shelf reefs at 10 and 15 m (p<0.05) but not at 3m. Fish biomass was correlated to reef topographic relief at 3m for parrotfishes (p<0.05) and at all three depth intervals for surgeonfishes (p<0.05). Overall patterns of herbivore biomass across the shelf reflect differences in light penetration, suggesting that fish may be responding to algal productivity. Thus, within fore-reef habitats along a cross-shelf gradient water transparency and topographic relief may interact to structure biomass patterns.

Keywords.—Herbivorous fishes, depth, light, rugosity, cross-shelf

Introduction

Algal grazing by reef fishes is an important ecological process with practical significance to the management and conservation of coral reefs (Mumby et al. 2006, Hughes et al. 2007). The process of herbivory has been shown to play a key role in structuring the benthic community on coral reefs (Hixon and Brostoff 1996; Smith et al. 2001; Belliveau and Paul 2002). In areas of high grazing on benthic algae, the algal assemblage is dominated by crustose coraline algae with cropped algal turfs (Littler et al. 2006). This affects the interaction between macroalgae and corals, particularly in enhancing coral recruitment, and is seen as a fundamental determinant of coral reef resilience (Mumby et al. 2007).

Fishes from the family Acanthuridae (surgeonfishes) and Scaridae (parrotfishes) are important herbivores on Caribbean coral reefs in terms of biomass (Lewis and Wainwright 1985) and are found commonly on fore-reef habitats from 1 to 30 m. Surgeonfishes and parrotfishes are commonly harvested with fish traps, nets, and spears in the Caribbean (Munro 1983). High fishing intensity has led to a reduction in abundance and mean size in these groups, and in some locations has been correlated with increased macroalgal cover (Williams and Polunin 2001). Understanding the distribution of the herbivorous fish assemblage is important because the consequences of grazing depend in part on spatial abundance patterns (Mumby et al. 2006, Paddack et al. 2006).

The abundance and distribution of herbivorous coral reef fishes can vary spatially along a cross-shelf gradient, by depth and among the different habitats within a reef. On the Great Barrier Reef the abundance,

at the family level, of surgeonfishes and parrotfishes was higher on offshore reefs compared to near shore reefs (Russ 1984a, Gust et al. 2001). Within a reef, studies have shown that the highest densities of roving herbivorous fishes are often found on the shallow fore-reef and reef crest (Russ 1984b, Lewis and Wainright 1985, Fox and Bellwood 2007, Hoey & Bellwood 2008). This pattern may be related to food availability and quality since the biomass of roving herbivores has been found to be positively correlated to algal productivity (Russ 2003). The topographic relief of reef habitat is also a major factor in structuring fish communities (Friedlander and Parrish 1998) since fish benefit from abundant reef crevices to escape predation. Yet, this relationship has typically been studied across a wide variety of habitats, from relatively flat sand and algal plains to emergent coral reefs. Little work, has investigated what role rugosity plays in structuring fish distributions on finer, within habitat scales.

It is clear that roving herbivorous fishes are not randomly distributed over coral reefs and that spatial patterns may be related to preferences in habitat characteristics in order to meet requirements for feeding and refuge. This study examines the importance of depth, cross-shelf reef position and topographic relief in structuring the distribution of roving herbivorous fishes in Southwest Puerto Rico. The study focuses on topographic relief only within the fore reef habitat on coral reefs, and examines trends across multiple species within the surgeonfishes and parrotfishes. The resulting spatial and depth related patterns are then used to infer underlying processes structuring herbivorous fish distributions and community structure on fore-reef habitats.

Methods

The density of parrotfishes and surgeonfishes was quantified at six reef sites stratified into inner-shelf (3) and mid-shelf reefs (3) to allow for within reef (across depths) and among reef (cross-shelf) comparisons (Figure. 1). The study was conducted on the fringing coral reefs off of La Parguera, Puerto Rico (N 17° 58.3′, W 67° 02.6′).

A water quality gradient generally exists from inshore to offshore with inner shelf reefs having higher turbidity resulting from local land-based runoff and upstream sources that are carried by the alongshore current. Published values for water transparency ($K_{d\,PAR}$) at the study reefs were used to relate water quality to cross-shelf reef position (Table 1, Bejarano Rodríguez 2006). The study sites were located on the fore-reef along a series of emergent reefs that occur from 1 to 5 km offshore and rise from surrounding unconsolidated bottom at 15-18 meters depth. The general fore-reef profile slopes gently from the surface to ~6 m where the slope becomes steeper down to the reef base.

To determine fish abundance, visual surveys were conducted using SCUBA along belt transects measuring 25 x 4m. At each study reef three depth intervals were selected: 3 (3-5m), 10 (8-10m), and 15 (12-15m). Three replicate transects were established per depth interval and permanently marked with rebar stakes for repeated sampling of the same reef area. Transects were sampled four times per year, corresponding to the four seasons, from 2004 to 2007. All surgeonfishes and parrotfishes within transects were counted, identified to species and their fork length estimated visually. Prior to beginning surveys the observers were trained in estimating fish fork lengths underwater using wooden fish models (Rooker and Recksiek 1992). Topographic relief was sampled once along 10 m of all transects with the chain method to calculate a rugosity index. A light chain was draped loosely over the bottom following the topography. The rugosity index is expressed as the ratio of the chain distance to the linear distance.

Fish length data were used to calculate mean sizes, and biomass was derived utilizing published parameters for length-weight relationships (Bohnsack and Harper 1988). Data were analyzed for differences across depth intervals and between inner and mid-shelf reef strata at the family level. Homoscedasticity of the data was tested with Levene's test. The fish density and biomass data did not meet assumptions of equal variance even after log and
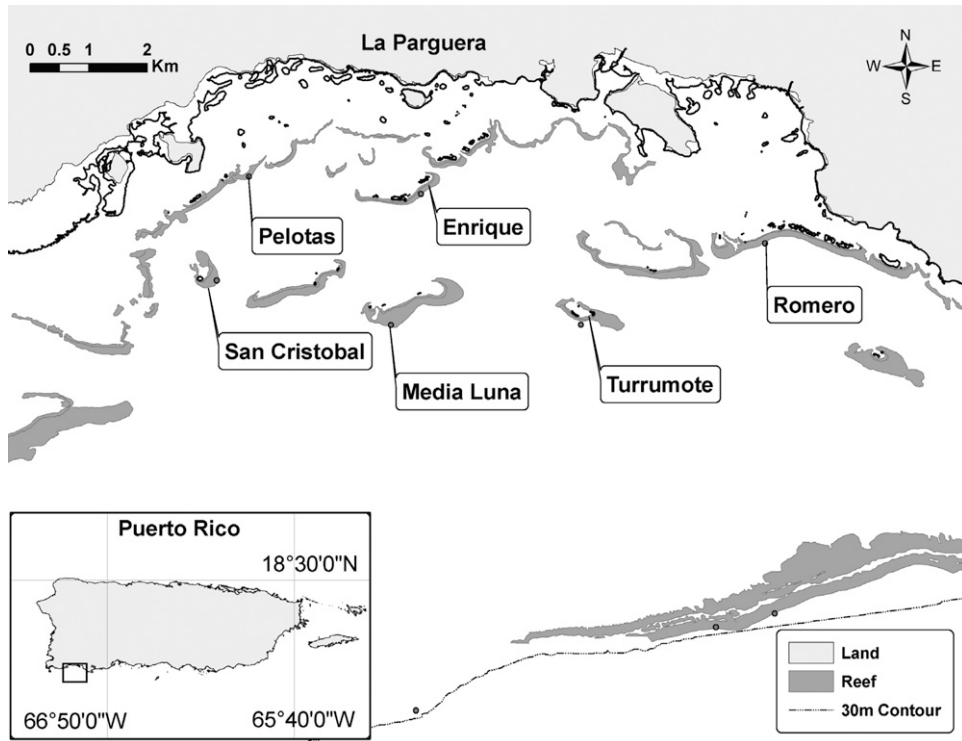
FIG. 1. Map of the study area showing the 6 study reefs, which are divided into two cross-shelf strata for purposes of analyses: inner-shelf (Romero, Enrique, Pelotas) and mid-shelf (Turrumote, Media Luna, San Cristobal).

TABLE 1. Reef sites with cross-shelf strata designation, minimum distance from mainland shoreline and light extinction coefficient. Extinction coefficients from Bejarrano Rodríguez (2006).

Reef Site	Shelf Strata	Offshore Distance (km)	Light Extinction Coefficient (Mean $K_{d\,PAR}$)
Romero	Inner-shelf	1.2	0.19
Enrique	Inner-shelf	1.8	0.20
Pelotas	Inner-shelf	1.5	0.19
Turrumote	Mid-shelf	3.8	0.17
Media Luna	Mid-shelf	4.0	0.17
San Cristobal	Mid-shelf	3.1	0.16

square-root transformations. Therefore the non-parametric Kruskal-Wallis test with the multiple comparisons of mean ranks routine was used to test for significant differences across depth intervals. The Mann-Whitney test was used to compare between inner and mid-shelf strata within each of the three depth intervals. Since data did not

meet parametric assumptions the Spearman rank correlation was used to examine the relationship between fish abundance and rugosity. All tests were implemented using Statistica (2005) software. Annual and seasonal patterns in the abundance data were examined as part of another study and no temporal patterns were evident at the family or species level.

RESULTS

The roving herbivorous fish assemblage on fore-reef habitats in La Parguera is predominantly made up of three species from the surgeonfish family (Acanthuridae) and eight species from the parrotfish family (Scaridae). The surgeonfishes are represented by *Acanthurus bahianus*, *A. chirurgus* and *A. coerulus* with the latter having the highest frequency of occurrence. The parrotfishes are numerically dominated by *Scarus iseri*, *Sparisoma aurofrenatum* and *S. viride* with *S.iseri* having the highest overall

density for parrotfish. Other species of parrotfish were present in the samples but in low abundances, and therefore they were not included in species level analyses. Overall the densities of both families pooled within reef position and across depth intervals were slightly higher on mid-shelf reefs (surgeonfishes: 9.4 verse 10.9 fish/100m² for inner and mid-shelf respectively, parrotfishes: 19.7 verse 23.4 fish/100m² for inner and mid-shelf respectively).

The abundances of parrotfishes and surgeonfishes were distinctly structured in relation to depth on the fore-reef habitat. The overriding pattern is a maximum in density and biomass on the shallow fore-reef with lower abundances deeper on the reef (Figure 2). Pooling across all reef sites the mean biomass of both families for the 3m interval was significantly higher than at the 10 and 15m intervals which did not differ significantly (K-W multiple comparisons p<0.05).

A greater relative difference in biomass was observed between the 3 m interval and the other two depth intervals for the surgeonfishes than for the parrotfishes (Figure 2).

Comparing the biomass of both families within depth intervals and between inner-shelf and mid-shelf reefs revealed that the general trend of decreasing abundances with depth varies between the two reef strata. The overall pattern of higher biomass at 3m than at 10 and 15m was not the same between inner and mid-shelf reefs. The decline in biomass of fish across the depth gradient was of a greater magnitude at the inner shelf reefs when compared to the mid shelf reefs (Figure 2). At the 3 m depth interval the mean biomass for both families did not differ significantly between inner and mid-shelf reef groupings. However, for both the 10 and 15m depth intervals the biomass of both surgeonfishes and parrotfishes was significantly higher on mid-shelf reefs than inner-shelf reefs (Mann-Whitney test, p<0.01).

Individual species exhibited varying degrees of deviation from the general trend of decreasing biomass with depth seen at the family level when pooling all reefs. The three species of surgeonfish all showed highest densities at 3m with a decrease at 10 and 15m (K-W multiple comparisons p<0.01, Figure 3). One species of parrotfish, *Scarus iseri* exhibited a significant decline in
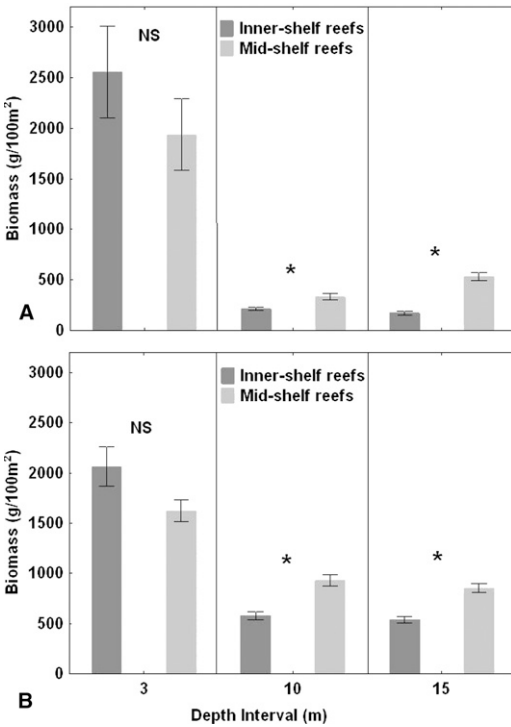

FIG. 2. Mean (± SE) Biomass of (a) surgeonfishes and (b) parrotfishes by depth interval for the two cross-shelf reef strata. Asterisks (*) represent significant differences for comparison between reef position within a depth interval (Mann-Whitney test, p<0.05, n=108).
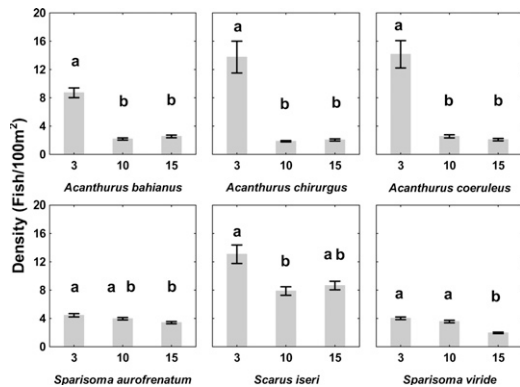

FIG. 3. Mean (± SE) density of most common surgeonfishes (top row) and parrotfishes (bottom row) by depth interval pooled across all reefs. Letters represent groupings of non-significant differences provided by Kruskal-Wallis multiple comparison routine (p<0.05, n=216).

density when comparing the 3m to the 10m depth interval but the 15m interval was not significantly different from the 3 or 10m intervals (K-W multiple comparisons $p < 0.01$, Figure 3). The decrease in density with depth for *Sparisoma aurofrenatum* and *S. viride* was of a lesser magnitude although still evident.

The mean biomass of either family was not significantly correlated to rugosity when pooling all reefs and depth intervals (Spearman Rank Order Correlation = 0.22 for surgeonfishes and 0.07 for parrotfishes). However, when grouping the data at the individual depth intervals rugosity was positively correlated to the biomass of both surgeonfishes and parrotfishes at the 3 m interval (Spearman=0.59 and 0.57 respectively, $p < 0.05$) but only to surgeonfishes at the 10 and 15 m intervals (Spearman=0.68 and 0.67 respectively, $p < 0.05$, Figure 4).

Discussion

Understanding fish distribution patterns in relation to habitat characteristics will provide insight into the processes involved in structuring the fish assemblages across the seascape. The general pattern of highest abundances of roving herbivores on the shallow fore-reef (Lewis and Wainright 1985, Russ 1984b, Fox and Bellwood 2007, Hoey & Bellwood 2008) was also observed in this study indicating that depth is an important descriptor in the distribution of roving herbivores on the fore-reef. Due to large sample size we were able to detect similar but distinct patterns at the species level, even with the high variability typical of visual survey counts of reef fish. Our results also show that the relative intensity of the depth related effect varied by species, so the family level response to depth will depend on the relative abundance and proportions of the species present.

The difference in the depth related pattern between the two families may be due to the predominance of surgeonfishes to form large schools. These schools are most common in shallow fore-reef areas (unpublished data), which may reflect a feeding strategy to overcome the high density of territorial damselfish by overwhelming
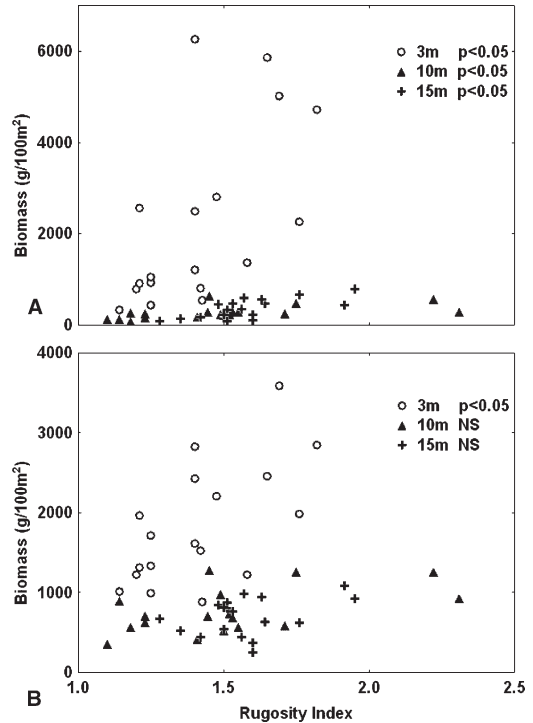

Fig. 4. Correlation between the rugosity index and the mean biomass of (a) surgeonfishes and (b) parrotfishes for the three depth intervals. The p-values are from Spearman Rank Correlation. The mean biomass for each of the fixed transects within each depth at each reef is based on the mean of 12 transects sampled across the 3 year period.

their ability to defend their territories. Parrotfishes seem to have a slightly different strategy in that, while also forming schools to feed in shallow areas, number of fish per school is lower (unpublished data), and proportionally more fish were found deeper compared to sugeonfishes.

It is likely that the physical changes in depth are not affecting the fishes directly, but rather they are responding to some environmental factor that co-varies with depth. The most compelling evidence is that productivity of the algal turf assemblage in shallow habitats correlates positively with the biomass of roving herbivorous fishes (Russ 2003). The usefulness of grouping abundances at higher taxonomic or trophic groupings has been demonstrated previously where the pooled biomass of all species of parrotfish and surgeonfish was inversely correlated to algal cover (Williams

and Polunin 2001). Also, the total biomass of herbivores was used to examine patterns in this assemblage within and among reefs (Wismer et al. 2009).

Although the cross-shelf scale of this study (1-4 km) is limited in an absolute sense compared to previous works from the Great Barrier Reef (5-50km), the cross shelf differences in environmental parameters from open ocean to coastal fringe are the same and should result in even steeper spatial gradients. Cross-shelf variability in community structure similar to that observed on the Great Barrier Reef has previously been documented for La Parguera (Kimmel 1985). In the present study the herbivorous fish assemblage also exhibited a cross-shelf response to reef position that was evident within the overall depth related pattern. Inner-shelf reefs had relatively lower abundances of both surgeonfishes and parrotfishes on the deeper fore-reef compared to mid-shelf reefs, while shallower areas were similar throughout.

Herbivorous fish biomass has been shown to correlate positively with algal turf productivity (Russ 2003), fish may be selecting for areas that have higher food quality. One important factor affecting algal productivity is the availability of light. Clifton (1995) showed spatial differences in turbidity to affect algal turf productivity, with corresponding differences in parrotfish growth and fecundity. In La Parguera, existing data on light availability (Bejarano Rodríguez 2006) show that cross-shelf reef position is related to reef water quality, with inshore reefs having higher coefficients of extinction (Table 1). This is consistent with inner-shelf reefs generally having higher turbidity (unpublished data). Turbidity and light differences would be expected to cause differences in the algal productivity (Clifton 1995, Klumpp and McKinnon 1989). The differences in herbivore biomass at 10 and 15m between inner and mid-shelf strata is seen as a result of fish responding to lower algal productivity in the inshore reefs. Since the amount of light reaching the reef surface may affect benthic primary productivity, water transparency has the potential to influence the algal resources available to herbivorous fishes and thus affect their distribution. This was demonstrated in La Parguera, where the extinction coefficient of light was directly correlated to the density and abundance of herbivorous fishes (Bejarano-Rodríguez 2006).

Topographic relief can influence the distribution of herbivorous fish over reef habitat (Friedlander and Parrish 1998), but separating this factor from depth effects is difficult because they can often co-vary. In this study rugosity was not correlated to fish biomass when samples from all depths were included in the analysis. When separated into discrete depth intervals the confounding effects were minimized and this revealed that habitat areas of high topographic relief are positively correlated with biomass. These results indicate that over the entire fore-reef slope roving herbivorous fishes may be responding more strongly to depth related habitat conditions, such as light level or productivity, than to topographic relief.

In this study, surgeonfishes and parrotfishes did not utilize the entire fore reef habitat equally but instead showed preference for certain habitat characteristics within the fore-reef habitat. The reefs in this study provide a continuous topographically complex habitat patch that extends from the surface to 15m wherein fish can select for optimum habitat characteristics. If herbivores are able to choose optimum habitat in terms of depth, water quality and topographic relief, their distribution patterns and resulting ecological impacts may be related to the spatial mosaic of these characteristics.

Literature Cited

Bejarano Rodríguez, I. 2006. Relationships between reef fish communities, water and habitat quality on coral reefs. M.S. thesis, University of Puerto Rico, Mayagüez.

Belliveau, S. A., and V. J. Paul. 2002. Effects of herbivory and nutrients on the early colonization of crustose coralline and fleshy algae. *Mar. Ecol. Prog. Ser.* 232:105-114.

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* 215:1-31.

Clifton, K. E. 1995. Asynchronous food availability on neighboring Caribbean coral reefs determines seasonal patterns of growth and reproduction for the herbivorous parrotfish *Scarus iserti*. *Mar. Ecol. Prog. Ser.* 116:39-46.

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.

Fox, R. J., and D. R. Bellwood. 2007. Quantifying herbivory across a coral reef depth gradient. *Mar. Ecol. Prog. Ser.* 339:49-59.

Gust, N., J. H. Choat, and M. I. McCormick. 2001. Spatial variability in reef fish distribution, abundance, size and biomass: a multi-scale analysis. *Mar. Ecol. Prog. Ser.* 214:237-251.

Hixon, M. A., and W. N. Brostroff. 1996. Succession and herbivory: effects of differential fish grazing on Hawaiian coral-reef algae. *Ecol. Monogr.* 66:67-90.

Hoey, A. S., and D. R. Bellwood. 2008. Cross-shelf variation in the role of parrotfishes on the Great Barrier Reef. *Coral Reefs* 27:37-47.

Hughes, T. P., M. J. Rodrigues, D. R. Bellwood, D. Ceccarelli, O. Hoegh-Guldberg, L. McCook, N. Moltschaniwskyj, M. S. Pratchett, R. S. Steneck, and B. L. Willis. 2007. Phase shifts, herbivory, and the resilience of coral reefs to climate change. *Curr. Biol.* 17:360-365.

Kimmel, J. J. 1985. A characterization of Puerto Rican fish assemblages. PhD diss., University of Puerto Rico, Mayagüez.

Klumpp, D. W., and A. D. McKinnon. 1989. Temporal and spatial patterns in primary production of a coral-reef epilithic algal community. *J. Exp. Mar. Biol. Ecol.* 131(1):1-22.

Lewis, S. M., and P. C. Wainwright. 1985. Herbivore abundance and grazing intensity on a Caribbean coral reef. *J. Exp. Mar. Biol. Ecol.* 87:215-228.

Littler, M. M., D. S. Littler, and B. L. Brooks. 2006. Harmful algae on tropical coral reefs: Bottom-up eutrophication and top-down herbivory. *Harmful Algae* 5:565-585.

Mumby, P. J., A. R. Harborne, J. Williams, C. V. Kappel, D. R. Brumbaugh, F. Micheli, K. E. Holmes, C. P. Dahlgren, C. B. Paris, and P. G. Blackwell. 2007. Trophic cascade facilitates coral recruitment in a marine reserve. Proc. *Nat. Acad. Sci.* 104(20): 8362-8367.

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

Munro, J. L. 1983. *Caribbean coral reef fishery resources*. Manila: International Center for Living Aquatic Resources Management.

Paddack, M. J., R. K. Cowen, and S. Sponaugle. 2006. Grazing pressure of herbivorous coral reef fishes on low coral-cover reefs. *Coral Reefs* 25:461-472.

Rooker, J. R., and C. W. Recksiek. 1992. The effects of training with fish models in estimating lengths of fish underwater. *Proc. Gulf Caribb. Fish. Inst.* 41:321-331.

Russ, G. R. 1984a. Distribution and abundance of herbivorous grazing fishes in the central Great Barrier Reef. I. Levels of variability across the entire continental shelf. *Mar Ecol Prog Ser.* 20:23-34.

Russ, G. R. 1984b. Distribution and abundance of herbivorous grazing fishes in the central Great Barrier Reef. II. Patterns of zonation of mid-shelf and outershelf reefs. *Mar. Ecol. Prog. Ser.* 20:35-44.

Russ, G. R. 2003. Grazer biomass correlates more strongly with production than biomass of algal turfs on coral reefs. *Coral Reefs* 22:63-67.

Smith, J. E., C. M. Smith, and C. L. Hunter. 2001. An experimental analysis of the effects of herbivory and nutrient enrichment on benthic community dynamics on a Hawaiian reef. *Coral Reefs* 19:332-342.

Williams, I. D., and N. V. C. Polunin. 2001. Large-scale associations between macroalgal cover and grazer biomass on mid-depth reefs in the Caribbean. *Coral Reefs* 19:358-366.

Wismer, S., A. S. Hoey, and D. R. Bellwood. 2009. Cross-shelf benthic community structure on the Great Barrier Reef: relationships between macroalgal cover and herbivore biomass. *Mar. Ecol. Prog. Ser.* 376:45-54.