

## EXPLOITED SPECIES IMPACTS ON TROPHIC LINKAGES ALONG REEF–SEAGRASS INTERFACES IN THE FLORIDA KEYS

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**Abstract.** The removal of fish biomass by extensive commercial and recreational fishing has been hypothesized to drastically alter the strength of trophic linkages among adjacent habitats. We evaluated the effects of removing predatory fishes on trophic transfers between coral reefs and adjacent seagrass meadows by comparing fish community structure, grazing intensity, and invertebrate predation potential in predator-rich no-take sites and nearby predator-poor fished sites in the Florida Keys (USA). Exploited fishes were more abundant at the no-take sites than at the fished sites. Most of the exploited fishes were either omnivores or invertivores. More piscivores were recorded at no-take sites, but most (~95%) were moderately fished and unexploited species (barracuda and bar jacks, respectively). Impacts of these consumers on lower trophic levels were modest. Herbivorous and smaller prey fish (<10 cm total length) densities and seagrass grazing diminished with distance from reefs and were not negatively impacted by the elevated densities of exploited fishes at no-take sites. Predation by reef fishes on most tethered invertebrates was high, but exploited species impacts varied with prey type. The results of the study show that, even though abundances of reef-associated fishes have been reduced at fished sites, there is little evidence that this has produced cascading trophic effects or interrupted cross-habitat energy exchanges between coral reefs and seagrasses.

**Key words:** coral reefs; exploited species; food web interactions; seagrass herbivory; trophic cascade; trophic transfer.

### INTRODUCTION

A great deal of evidence suggests that extensive commercial and recreational fishing has drastically altered the structure of marine ecosystems (e.g., Dayton et al. 1995, Botsford et al. 1997, Coleman et al. 2004). Specifically, the historically intense harvesting of higher order consumers has led to substantial reductions of piscivorous fish biomass worldwide (Hutchings 2000, Christensen et al. 2003, Myers and Worm 2003). As higher order consumers became increasingly rare, fishers shifted their harvesting to lower order consumers, including omnivorous and herbivorous fishes and invertebrates (Pauly et al. 1998, 2000, Steneck et al. 2004). The impacts of these food web changes for the

transfer of primary production to the survivors in higher trophic levels are uncertain. However, current thinking strongly suggests that the intensity of density-dependent interactions and the transmission of primary production to higher trophic levels are much lower in most modern day oceans than they once were (cf. Steneck et al. 2004, Mumby et al. 2006).

Among the other probable impacts of consumer removals are significant reductions in the numbers and strengths of trophic linkages among habitats (Mumby et al. 2004, Valentine and Heck 2005). Although the historical importance of cross habitat transfers of energy in marine food webs is unclear, we do know that once abundant large predators (e.g., groupers, snappers, sharks, and bluefin tuna) fed in multiple habitats to meet their nutritional needs (cf. Dayton et al. 1995, Block et al. 2001, Heithaus et al. 2002, Bonfil et al. 2005). Early studies of coral reefs found that carnivorous fish biomass was three to four times greater than

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herbivore biomass (Goldman and Talbot 1976, Parrish and Zimmerman 1977, Grigg et al. 1984, Polunin 1996). Such inverted biomass pyramids suggest that trophic exchanges between habitats were very important in sustaining reef consumers. While many herbivorous fishes shelter on reefs at night, they commonly forage throughout adjacent seagrass habitats during the day (see review by Valentine and Duffy [2006]). Similarly, many smaller reef-associated carnivores (e.g., grunts and adult lobsters) forage in vegetated habitats at night (e.g., Burke 1995, Cox et al. 1997, Blackmon 2005), and many seagrass-associated fishes and invertebrates figure prominently in the diets of large reef predators (Randall 1965, Ogden 1980, Heck and Weinstein 1989, Eggleston et al. 1998). All of these observations strongly point toward a reliance of reef fishes on seagrass-based production (Nagelkerken et al. 2000, 2001).

Despite increasing documentation of the importance of exogenous inputs of nutrients to reef food webs (Szmant 2002, Leichter et al. 2003), most ecologists still adhere to the view that reef communities are closed entities characterized by tight recycling processes (Hatcher 1997). Although qualitative documentation of the importance of cross-habitat energy exchanges from seagrasses to coral reefs is available (summarized in Valentine and Heck 2005), with few exceptions (Macintyre et al. 1987, Valentine et al. 2007) such transfers have not been quantified. Instead, to estimate production at the base of reef food webs most rely on descriptions of poorly resolved food webs (Link 2002, Dunne et al. 2004), static measures of biomass, and mass balance approximations of the nutritional requirements of larger consumers.

The Florida Keys (USA) are fished heavily year-round (Bohnsack et al. 1994). Because of bans on indiscriminate trap fishing in all waters <30 m in depth, (Bohnsack et al. 1989), fishers now nonselectively target reef piscivores, omnivores, and some invertivores (Ault et al. 2005a, b). Reductions in the density of harvestable lobsters by divers are estimated to range from 55% to 90%, depending on location (Eggleston and Dahlgren 2001). These observations suggest that there has been a reduction of top down pressure on reef food webs (cf. Jackson et al. 2001, Pandolfi et al. 2005), as well as a reduced reliance on the production of adjacent habitats by lower order reef consumers (Valentine and Heck 2005). However, unlike other locations in the Caribbean, herbivorous parrotfishes (Mumby et al. 2006) are not harvested in the Keys.

In 1997, a 10 000 km<sup>2</sup> area surrounding the Florida Keys was designated as a National Marine Sanctuary (the Florida Keys National Marine Sanctuary, FKNMS). Among the consequences of this designation was the establishment of 23 replicate, no-take sites along the Florida Keys Reef Tract (Fig. 1). The designation of no-take sites limited losses of most predators at these sites. These replicated no-take zones provide a unique opportunity to determine the extent to which higher

order consumers control food web composition and productivity, as well as determining the extent to which larger predators control the transfer of energy across habitat boundaries.

Here, we report on a study that used multiple census techniques and direct measures of grazing intensity and predation potential to quantify and compare food web structure in no-take and nearby fished areas. Our goal was to evaluate the impacts of exploited species on energy transfer along the seagrass–coral reef interface in the lower FKNMS. This work builds on the findings of a previous study that documented variation in the intensity of grazing along seagrass–coral reef interface in the Keys, and the probable impacts of higher order consumers on grazing within the region (Valentine et al. 2007).

## METHODS AND MATERIALS

### *Experimental design*

To quantify the impacts of fishing-induced reductions in high order consumer density on the magnitude of trophic transfer among habitats and top down control of community structure within these habitats, we used a simple experimental design that included multiple response variables at multiple distances from replicated fished (predator poor) and no-take (predator rich) coral reefs in the lower Florida Keys. We predicted that there would be elevated densities of exploited fishes at the no-take sites, and that their presence would lead to significant decreases in the abundances and foraging patterns of reef-associated fishes and smaller consumers (herbivores and invertivores) in adjacent seagrass meadows (Fig. 2). Conversely, we predicted that lower exploited fish densities in unprotected areas would allow untargeted consumers to forage freely into seagrasses adjacent to fished reefs. In each case, we predicted that attendant shifts in smaller fish composition and abundance would be reflected in differing rates of grazing intensity and invertebrate survival in seagrasses adjacent to reefs.

### *Description of study sites*

Halpern (Halpern and Warner 2002, Halpern 2003) presented evidence that the establishment of no-take sites rapidly (in one to three years) leads to substantial increases in the density of most exploited fishes (but see recent, alternative findings of Russ and Alcala 2004, McClanahan and Graham 2005, McClanahan et al. 2007). Just two years after the establishment of the no-take zone around Looe Key in the lower Florida Keys there was a near doubling of snapper density and a fourfold increase in grunt density (Clark et al. 1989). No-take sites have also been associated with greater abundances of exploited fishes outside the protected areas (the spillover effect; Holland et al. 1996, Russ and Alcala 1998, McClanahan and Mangi 2000, Roberts et al. 2001; but see Shipp 2003). Thus, the establishment of no-take sites provided us with the opportunity to test the

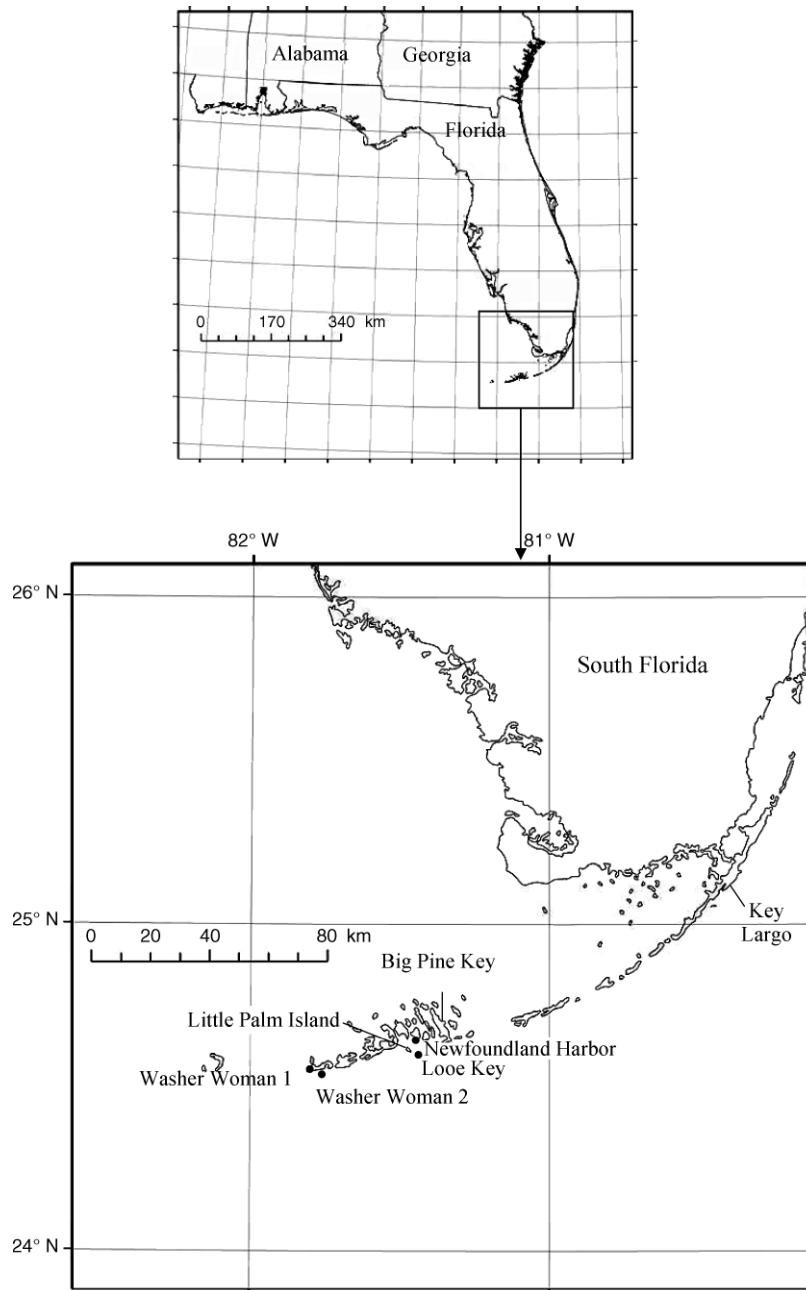


FIG. 1. Study site locations in the lower Florida Keys, USA.

extent to which exploited fishes determine the magnitude of energy exchange in reef food webs.

To minimize the impacts of variation in habitat structure on consumer composition among sites, a significant confounding factor in many prior studies of marine protected areas (MPAs; see Russ et al. 2005), and to assess the extent to which fishing may have altered reef consumer reliance on the production of adjacent habitats, we conducted this study in the lagoonal environments of two fished and two no-take

reefs (Fig. 1). Newfound Harbor ( $24^{\circ}36'56''$  N,  $81^{\circ}23'39''$  W), and Looe Key ( $24^{\circ}32'50''$  N,  $81^{\circ}23'39''$  W) were selected to represent no-take sites. The two fished sites were located along the Washerwoman Reef Tract ( $24^{\circ}32'53''$  N,  $81^{\circ}35'25''$  W and  $24^{\circ}33'19''$  N,  $81^{\circ}33'5''$  W). Each contained isolated patch reefs consisting primarily of the corals *Montastrea* spp., *Diploria* spp., *Siderastrea sidereal*, and *Colpophyllia natans*, along with seagrass habitats on the landward sides of these reefs (e.g., Jaap 1984, Ginsberg et al. 2001).

Predicted effects of piscivorous reef fishes on seagrasses  
and their inhabitants in the marine protected areas

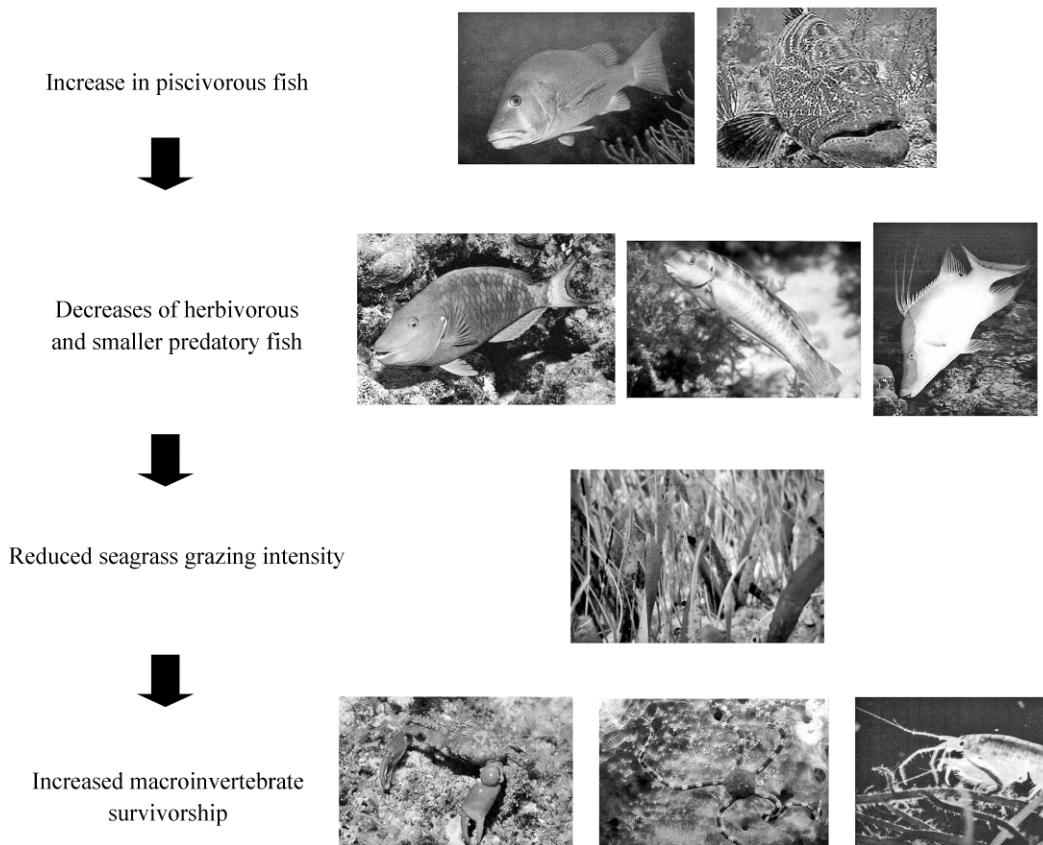


FIG. 2. Predicted impacts of elevated piscivore density at the no-take sites on seagrass grazing. We conducted this study in the lagoonal environments of two fished and two no-take reefs (Fig. 1).

Regrettably, interspersing of treatments among sites was not possible as the designation of the no-take sites by the Florida Keys National Marine Sanctuary office was based on conservation priorities rather than a randomized selection process.

This study was begun five years after the cessation of fishing at Newfound Harbor and 21 years after the cessation of fishing at Looe Key. As such, there should have been adequate time for exploited fishes to have recovered at both sites prior to commencement of this study.

To test our predictions, single navigation lines were anchored at haphazardly chosen locations at the bases of each reef and extended for 30 m into the adjacent seagrass bed. In all cases, except Looe Key, the grassbeds occurred directly adjacent to the reef. At Looe Key, the back reef environment was dominated by multiple small patch reefs. As such, the grass bed began some 3 m away from the reef crest.

Each transect line was established, with the aid of observers on a boat, to lay perpendicular to the reef. Treatment effects were documented during replicated

surveys conducted at sites in May, July, and August of 2002, and in May and August of 2003.

#### *Fish density and composition*

Point counts, belt transect surveys, and baited remote underwater video surveys were used to evaluate the effect of marine protected areas (MPAs) on fish density and composition. SCUBA equipped observers recorded fish composition and density, both near (10 m) and away (30 m) from each reef using the stationary point count method of Bohnsack and Bannerot (1986) with one modification, that being that two intersecting 10 m long lines were used to mark the center of an imaginary cylinder extending upward from the intersection to the water's surface. A diver knelt at the intersection of the lines and identified (to the species level in most cases) and enumerated fishes entering the circle for 15 min. Counts were limited to daylight hours when visibility exceeded 20 m, and the same divers conducted the surveys at each distance during each visit. Because fish composition and density varies greatly on a daily basis

(Sale 1980, Sale and Douglas 1981), point counts were replicated over three days during each survey.

Belt transect surveys, conducted on the same days as the point counts, provided complementary estimates of fish density and composition. To do this, 20 m long  $\times$  1 m wide transect lines were established parallel to each reef edge, both near (1 m) and away (30 m into the seagrass bed) from each reef. A SCUBA equipped observer swam the transect lines with a 1 m long T-Bar. All fish within the 20-m<sup>2</sup> area, determined by the T-bar, were counted and identified. These counts were repeated over the same three days the point counts were conducted during each survey.

Given that some fishes may avoid or be attracted to divers, fish composition and abundance were also recorded using baited remote underwater video (BRUV; Willis and Babcock 2000) in 2003. Replicate digital video cameras (Sony TRV16), secured in underwater housings, and were placed at the same locations used for the point count surveys. Bait (primarily caridean shrimp) held in perforated plastic canisters was placed in front of each camera at a height of 50 cm above the sediment. A 0.25-m<sup>2</sup> quadrat was placed around the bait, and for 30 minutes cameras recorded the abundance and composition of fishes entering the quadrat. These surveys were repeated three times during each survey on the same days that belt transects and point count surveys were conducted.

*Direct measures of grazing intensity and predation potential in seagrasses adjacent to the reefs*

*Grazing intensity.*—Seagrass grazing was quantified as described in Kirsch et al. (2002). To do this, tethered seagrass shoots were placed along the navigation lines at distances of 1, 5, 10, 20, and 30 m from each reef.

Turtlegrass shoots (*Thalassia testudinum*) were collected from Little Palm Island (24°37'7" N, 081°24'25" W; see Goecker et al. [2005] for detailed description of this site) and returned to the lab. Undamaged leaves were severed from the shoots, then digitally scanned (using a Hewlett Packard flat bed scanner), reassembled, and attached to a 0.25 m long sisal line with a clothespin. Each line (or tether) consisted of three evenly spaced shoots. Three tethers were placed at the same distances from the two fished and no-take reefs. Tethers were anchored using wire stakes inserted into the sediment. Clothespins were buried in the sediment, thus simulating the orientation of natural shoots within seagrass beds (Hay 1984). Tethers were retrieved and replaced after 24 hours. Leaves on retrieved tethers were rescanned to estimate grazing intensity. Differences in area between the initial scanning and the final scanning provided estimates of grazing intensity. This process was replicated on the same schedule as the fish surveys.

*Predation potential.*—Established tethering techniques were used to assess fishing impacts on invertebrate survivorship along the reef–seagrass interface (Heck and Wilson 1987, Beck 1997, Acosta and Butler 1999). Three

replicate sets of tethered brittle stars (*Ophioderma*, *Ophiocoma*, and *Ophiothrix* spp.), gastropods (*Turbo* sp.), and spider crabs (predominantly *Mithrax* spp., and some *Pitho* sp.) were placed at the same times and distances from reefs as the seagrass tethers. Each of these taxa is present in seagrass habitats adjacent to the reefs and in the diets of predatory fishes, crabs, and lobsters in the Caribbean, (Randall 1965, Heck and Weinstein 1989, Cox et al. 1997, Eggleston et al. 1997, 1998) and none uses rapid movements to escape from predators.

Brittlestars were tethered by inserting a small needle threaded with 6 lb. test monofilament line at the center of oral disk cover (located dorsally), then pulling it through the mouth (located ventrally). Following extraction, a knot was tied near the center of the dorsal disc cover to secure the line to the brittlestar. Gastropod shells and crab carapaces were tethered by drawing monofilament loops tightly around the organisms after which a drop of cyanoacrylate cement was applied to secure the loop to the animals. In 2003, a second smaller gastropod (*Tegula* sp.) was added to the array of prey used. The absence of tethering artifacts has been shown for brittlestars (Aronson and Heck 1995), crabs (Pile et al. 1996), and gastropods (McClanahan 1992), among others.

Two tethered conspecific prey were attached to a wire stake, and three wire stakes were placed at the same distances from the reefs as the seagrass tethers. Missing tethers were replaced at 24-h intervals, and prey consumption was recorded over the same three days that the fish surveys were conducted. In the few cases when tethered prey were found dead with no evidence of predation, these data were omitted from the analysis. In addition, some tethered invertebrates were monitored using underwater video to observe potential predators.

We evaluated the possibility that differences in aboveground biomass among sites impacted tethered invertebrate survivorship by collecting all shoots contained within three haphazardly located 0.01-m<sup>2</sup> quadrats placed 5 m and 30 m from each reef during each survey. In the laboratory, aboveground biomass was determined after leaves were dried at 60°C to a constant mass.

*Statistical analyses of treatment effects*

*Replicate definition.*—Treatment effects included fishing pressure (via comparisons of measurements made at fished and no-take reefs), and distance from the reef. Because replicate assessments were conducted in each year for two years, survey date was also considered a treatment, except for the baited video transects, which were conducted in a single year.

*Comparison of treatment effects on fish density and the composition of trophic guilds.*—Trophic assignments (see Table 1), as well as fish designations as exploited or not, are based on published reports from the region (Randall 1967, Heck and Weinstein 1989, McAfee and Morgan

1996, Ault et al. 1998, Bohnsack et al. 1999). Evaluations of treatment effects (fishing pressure, distance from reef, and survey date) and their interactions were carried out on piscivore, invertivore, herbivore, and prey fish (species <10 cm total length; Eggleston et al. 1998) density, as well as on exploited taxa, and the extent to which they varied among surveys, using three-way ANOVA. Data were either log- or square-root transformed to satisfy the assumption of homogeneity of variance for ANOVA (Sokal and Rohlf 1981). A two-way ANOVA was used to analyze transformed data collected during baited video surveys, with fishing pressure and distance from the reef as main effects. When significant interactions were detected, comparisons of main effect interactions are simply discussed. In these cases, pairwise comparisons of significant main effects were not conducted. When nonsignificant interactions occurred, they were removed and a customized model was analyzed. When significant impacts of survey date or distance from the reef were detected, post hoc comparisons were conducted using Sheffé's test (Day and Quinn 1989). All parametric statistical analyses were conducted using SPSS Version 11.0 statistical software package (SPSS 2002).

Comparisons of treatment effects on the composition of the piscivore, invertivore, and herbivore guilds were made using the nonparametric analysis of similarity (ANOSIM; fourth-root-transformed) technique (Warwick and Clarke 1991). ANOSIM comparisons of species composition within trophic groups were made using the multivariate nonparametric software package Primer-E (PRIMER-E, Plymouth, UK). Results in all comparisons were considered significant when  $P < 0.05$ .

*Comparisons of treatment impacts on grazing intensity and invertebrate survivorship.*—Main effects (fishing pressure, distance from the reef, and survey date) on losses of tethered seagrass leaves and invertebrates were analyzed, following arcsine square-root transformation, using three-way ANOVA. Daily losses of leaf area (per shoot) and invertebrates (per stake) were averaged. The averages were used in subsequent analyses. When significant impacts of survey date or distance from the reef were detected, post hoc comparisons were conducted.

Comparisons of seagrass biomass were made using the means calculated from the three quadrats placed near and far from the reef, and were analyzed using a three-way ANOVA with levels of fishing pressure (fished vs. no-take sites), distance from the reef (near vs. far), and survey date as factors. If the data did not satisfy the homogeneity of variance assumption, treatment comparisons were made on log-transformed data. In each case, the transformed data satisfied this assumption.

## RESULTS

### *Treatment effects on exploited fishes*

Exploited species comprised 10% and 17% of all fishes recorded in the point and belt transect surveys at the

fished and no-take sites, respectively. The percentage of exploited species recorded during the baited video surveys was also smaller at the fished than at the no-take sites (22% and 34%, respectively).

### *Treatment impacts on food web structure*

*Piscivores.*—More piscivores, both exploited and unexploited species, were recorded at the no-take than at the fished sites (Fig. 3a–c). This pattern did not vary significantly among survey dates ( $P > 0.05$ ). However, exploited species, on average, made up <8% of all piscivores recorded during these surveys. Two-way ANOVA on arcsine-transformed proportions of piscivores recorded in the point counts showed they comprised a greater proportion of the overall pool of fishes at the no-take reefs than at the fished reefs ( $F_{1,36} = 8.52$ ,  $P < 0.006$ ), and more so near reefs than away from them ( $F_{1,36} = 4.56$ ,  $P < 0.04$ ). Results from a three-way ANOVA, however, failed to detect significant impacts of protection, distance from the reef, or date on square-root transformed densities of piscivores recorded during the point counts ( $P > 0.05$ ; Fig. 3a). In large part this was due to episodic encounters with schools of moderately or unexploited transient predators (e.g., great barracuda, and both bar jacks and yellow jacks; Table 1), which comprised 92% of all piscivores recorded.

Similarly, piscivores comprised a significantly greater proportion of fishes counted along belt transects at the no-take than at the fished reefs ( $F_{1,33} = 9.03$ ,  $P < 0.005$ ), with significantly more fishes counted near the reefs than away from them ( $F_{1,33} = 4.84$ ,  $P < 0.035$ ; Fig. 3b). On average, piscivore abundance was nearly nine times greater along the belt transects than was recorded in point count surveys near no-take reefs. Three-way ANOVA detected both significant fishing ( $F_{1,36} = 6.12$ ,  $P < 0.019$ ) and distance effects ( $F_{1,36} = 5.37$ ,  $P < 0.027$ ) on square-root transformed sums of all recorded piscivores. No other significant main effects or interactions were detected.

A three-way ANOVA conducted on square-root transformed densities of piscivores in the baited video surveys also detected significantly more piscivores at no-take than at fished sites ( $F_{1,44} = 4.37$ ,  $P < 0.042$ ), again more so near the reefs ( $F_{1,46} = 4.99$ ,  $P < 0.031$ ; Fig. 3c). Transient piscivores were again numerically dominant, comprising 90% and 100% of all piscivores counted at the fished and no-take sites, respectively. No other significant main effects or interactions between main effects were noted in any of the comparisons.

Because the same three species of transient predators dominated counts in all of the census techniques, we did not evaluate the impacts of main effects on piscivore composition at the study sites. Based on these censuses, piscivorous fish abundance was clearly greater at the no-take sites than at the fished sites.

*Seagrass herbivores.*—All of the observed seagrass herbivores were parrotfishes. Results of three-way

TABLE 1. Trophic assignments for all fishes identified in the visual, belt transect, and baited video surveys.

Scientific name	Common name	Trophic group
<i>Ocyurus chrysurus</i> †	yellowtail snapper	invertivore
<i>Lutjanus analis</i> †	mutton snapper	invertivore
<i>Anisotremus surinamensis</i> †	black margate	invertivore
<i>Haemulon flavolineatum</i> †	French grunt	invertivore
<i>Haemulon plumieri</i> †	white grunt	invertivore
<i>Haemulon sciurus</i> †	bluestriped grunt	invertivore
<i>Haemulon aurolineatum</i> †	tomtate	invertivore
<i>Haemulon parra</i> †	sailors choice	invertivore
<i>Lutjanus synagris</i> †	lane snapper	invertivore
<i>Calamus calamus</i>	saucereye porgy	invertivore
<i>Chaetodon capistratus</i>	four-eye butterflyfish	omnivore
<i>Epinephelus adscensionis</i> †	rock hind	piscivore
<i>Halichoeres bivittatus</i>	slippery dick	invertivore
<i>Lachnolaimus maximus</i> †	hogfish	invertivore
<i>Mycteroperca bonaci</i> †	black grouper	piscivore
<i>Sparisoma chrysopteron</i>	redtail parrotfish	herbivore
<i>Sparisoma radians</i>	bucktooth parrotfish	herbivore
<i>Sparisoma rubripinne</i>	yellowtail parrotfish	herbivore
<i>Sparisoma viride</i>	stoplight parrotfish	herbivore
<i>Sphyaena barracuda</i> †	great barracuda	carnivore
<i>Stegastes partitus</i>	bicolor damselfish	herbivore
<i>Scarus coelestinus</i>	midnight parrotfish	herbivore
<i>Scarus guacamaia</i>	rainbow parrotfish	herbivore
<i>Scarus taeniopterus</i>	princess parrotfish	herbivore
<i>Scarus coeruleus</i>	blue parrotfish	herbivore
Scaridae	unidentified parrotfish	herbivore
<i>Scarus iseri</i>	striped parrotfish	herbivore
<i>Sparisoma aurofrenatum</i>	redband parrotfish	herbivore
<i>Caranx ruber</i>	bar jack	piscivore
<i>Caranx bartholomaei</i>	yellow jack	piscivore
<i>Calamus calamus</i>	jolthead porgy	invertivore
<i>Gerres cinereus</i>	yellowfin mojarra	invertivore
<i>Rachycentron canadum</i> †	cobia	piscivore
<i>Megalops atlanticus</i>	tarpon	piscivore
<i>Stegastes variabilis</i>	cocoa damselfish	herbivore
<i>Stegastes leucostictus</i>	beaugregory damselfish	herbivore
<i>Kyphosus sectatrix</i>	Bermuda chub	invertivore
<i>Halichoeres radiatus</i>	puddingwife	herbivore
<i>Halichoeres garnoti</i>	yellowhead wrasse	invertivore
<i>Thalassoma bifasciatum</i>	bluehead wrasse	invertivore
<i>Halichoeres maculipinna</i>	clown wrasse	invertivore
<i>Halichoeres poeyi</i>	blackear wrasse	invertivore
Labridae	unidentified wrasse	invertivore
<i>Xyrichtys splendens</i>	green razorfish	invertivore
<i>Pomacanthus paru</i>	French angelfish	invertivore
<i>Pomacanthus arcuatus</i>	gray angelfish	invertivore
<i>Acanthurus coeruleus</i>	blue tang	herbivore
<i>Acanthurus chirurgus</i>	doctorfish	herbivore
<i>Acanthurus bahianus</i>	ocean surgeonfish	herbivore
Acanthuridae	immature surgeonfish	herbivore
<i>Lactophrys trigonus</i>	trunkfish	invertivore
<i>Balistes vetula</i>	queen triggerfish	invertivore
Balistidae	unidentified filefish	invertivore
<i>Pseudupeneus maculatus</i>	spotted goatfish	invertivore
<i>Mulloidichthys martinicus</i>	yellow goatfish	invertivore
<i>Lactophrys triquetter</i>	smooth trunkfish	invertivore
<i>Equetus punctatus</i>	spotted drum	invertivore
<i>Aulostomus maculatus</i>	trumpetfish	invertivore
<i>Fistularia tabacaria</i>	bluespotted cornetfish	invertivore
Haemulidae	immature grunt	invertivore
<i>Emblemaria pandionis</i>	sailfin blenny	omnivore
<i>Trachinotus falcatus</i>	permit	omnivore
<i>Chaetodon ocellatus</i>	spotfin butterflyfish	omnivore
<i>Hypoplectrus unicolor</i>	butter hamlet	omnivore
<i>Scomberomorus maculatus</i>	Spanish mackerel	carnivore
<i>Tylosurus crocodilus</i>	houndfish	omnivore
Exocoetidae	halfbeak	omnivore
<i>Ginglymostoma cirratum</i>	nurse shark	invertivore

Note: Identifications are based on the findings of Bohnsack et al. (1999) and Randall (1967).

† Fishes considered by Ault et al. (1998) to be exploited.

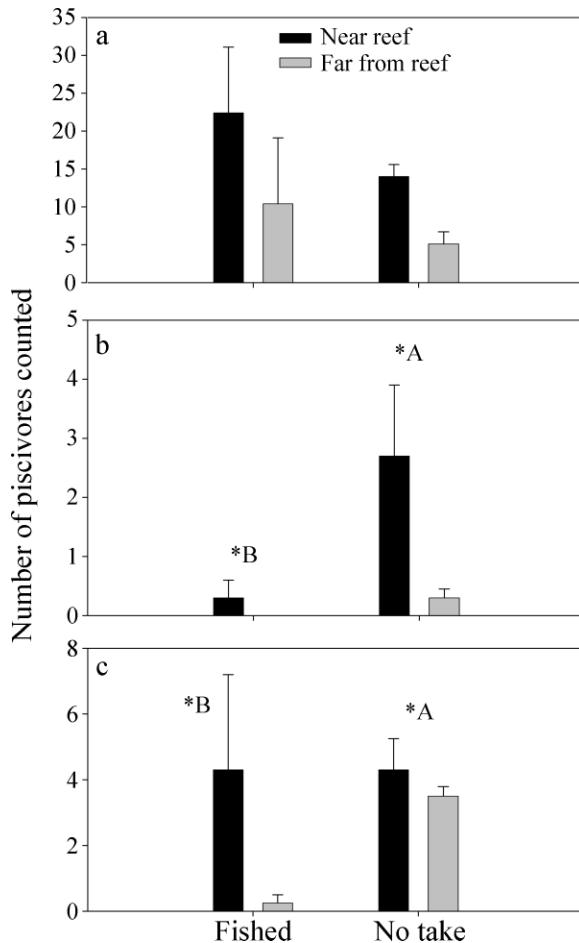


FIG. 3. Piscivore distributional patterns (mean + SE) recorded at the no-take sites (see Fig. 2 legend) and fished sites using (a) point count, (b) belt transect, and (c) baited remote underwater video methods. The two fished sites were located along the Washerwoman Reef Tract (24°32'53" N, 81°35'25" W and 24°33'19" N, 81°33'5" W). Asterisks denote significant differences ( $P < 0.05$ ) within a treatment (fished or no-take) with distance from reef. Uppercase letters denote significant differences ( $P < 0.05$ ) based on fishing pressure: fished vs. no-take sites.

ANOVAs conducted on log-transformed densities of these grazers, recorded during point count and belt transect surveys, found them to be significantly more abundant at the no-take than at the fished sites (point counts,  $F_{1,26} = 18.09$ ,  $P < 0.0001$ ; Fig. 4a; belt transect surveys,  $F_{1,33} = 29.83$ ,  $P < 0.0001$ ; Fig. 4b). In fact, parrotfishes were more than fivefold more abundant at the no-take sites, even though they are not exploited by local fisherman. Overall, parrotfishes comprised a greater proportion of the fish community at no-take sites than at fished sites (point counts,  $F_{1,26} = 6.68$ ,  $P < 0.016$ ; belt transects,  $F_{1,33} = 20.55$ ,  $P < 0.0001$ ). No other significant main effects or interactions between main effects were noted.

We also assessed the extent to which the significant differences between fished and no-take sites were due to

the presence of a greater abundance of larger and perhaps less risk averse, reef-associated herbivores (e.g., stoplight and redbtail parrotfish) at the no-take sites. Log-transformed densities of the sum of all larger species of reef-associated parrotfishes were significantly greater at no-take than at fished reefs ( $F_{1,26} = 11.64$ ,  $P < 0.002$ , and  $F_{1,33} = 10.66$ ,  $P < 0.003$ , point count and belt transect surveys, respectively). While no differences in the density of larger parrotfish species were detected with distance in the point counts ( $P > 0.05$ ; Fig. 5a), larger parrotfishes were significantly more abundant over belt transects near reefs ( $F_{1,33} = 8.24$ ,  $P < 0.007$ ; Fig. 5b). Log-transformed densities of smaller, seagrass-associated parrotfishes (<10 cm in length), those more vulnerable to attack by piscivores, were also significantly greater at no-take sites than at fished sites (point counts,  $F_{1,26} = 23.94$ ,  $P < 0.0001$ ; belt transects,  $F_{1,33} = 29.83$ ,  $P < 0.0001$ ; Fig. 6a, b), more so in point counts near the reefs than away from the reefs ( $F_{1,26} = 9.65$ ,  $P < 0.005$ ).

A two-way crossed ANOSIM conducted on the point count surveys showed that herbivore composition also varied significantly with fishing pressure (Global  $R = 0.249$ ,  $P = 0.002$ ) and distance from the reefs (Global  $R = 0.279$ ;  $P = 0.001$ ). Similarly, a two-way crossed ANOSIM showed that herbivore composition along

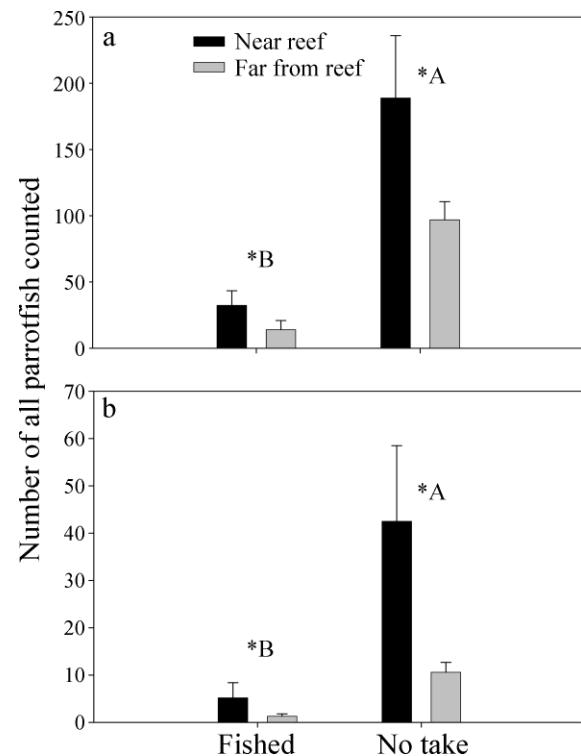


FIG. 4. Parrotfish distributional patterns (mean + SE) recorded at the no-take and fished sites using (a) point count and (b) belt transect surveys. Asterisks denote significant differences ( $P < 0.05$ ) with distance from reef. Uppercase letters denote significant differences ( $P < 0.05$ ) between levels of fishing pressure.

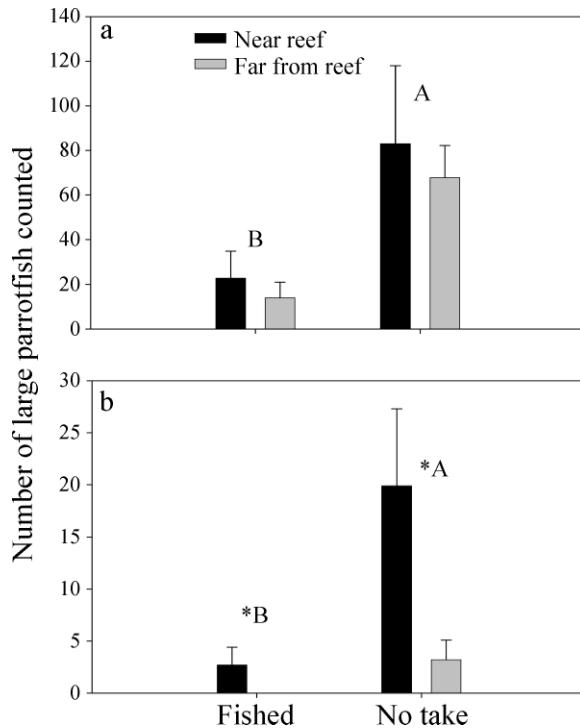


FIG. 5. Large parrotfish species distributional patterns (mean + SE) recorded at the no-take and fished sites using (a) point count and (b) belt transect surveys. Asterisks denote significant differences ( $P < 0.05$ ) with distance from reef. Uppercase letters denote significant differences ( $P < 0.05$ ) between levels of fishing pressure.

the belt transects varied significantly with fishing pressure (Global  $R = 0.24$ ;  $P = 0.007$ ), but not with distance (Global  $R = 0.44$ ;  $P = 0.17$ ). In each case these differences were due to a greater number of reef-associated parrotfishes foraging in seagrasses at the no-take sites.

**Invertivores.**—Invertivores were also significantly more abundant at no-take than at fished sites in all but one of the point count surveys. In that survey, conducted in May 2002, a significant difference in invertivore abundance between fishing treatments was not detected. As a result, a three-way ANOVA conducted on square-root transformed point counts of invertivores found a significant interaction between survey date and fishing pressure ( $F_{3,19} = 4.48$ ,  $P < 0.015$ ; Fig. 7a). Three-way ANOVA conducted on log-transformed invertivore counts on the belt transects also showed them to be significantly more abundant at no-take than at fished sites ( $F_{4,33} = 9.49$ ,  $P < 0.004$ ; Fig. 7b), regardless of survey date ( $P > 0.05$ ). No other significant interactions or distance effects were noted. No significant treatment effects were detected in the baited remote underwater video (BRUV) surveys ( $P > 0.05$ ).

A two-way crossed ANOSIM showed that invertivore composition in the point surveys varied significantly

with distance from the reef (Global  $R = 0.32$ ,  $P = 0.001$ ) and fishing pressure (Global  $R = 0.219$ ,  $P = 0.002$ ). A second two-way crossed ANOSIM showed that total invertivore composition along belt transects varied significantly with fishing pressure (Global  $R = 0.179$ ;  $P = 0.001$ ), but not with distance (Global  $R = -0.022$ ;  $P = 0.64$ ).

#### Lower level trophic interactions

**Prey fish density.**—There was also no evidence that the higher abundances of piscivores or exploited fishes recorded at the no-take sites negatively impact the densities of smaller prey fishes. Comparisons of treatment effects using three-way ANOVA found that the square-root and log-transformed densities of prey fishes (those fishes  $< 10$  cm total length) were significantly greater at the no-take sites than at fished sites (point counts,  $F_{1,26} = 32.36$ ,  $P < 0.000$ ; belt transects,  $F_{1,33} = 6.96$ ,  $P < 0.013$ ), more so in point counts near no-take reefs ( $F_{1,26} = 5.78$ ,  $P < 0.024$ ). No other significant treatment effects or interactions were detected.

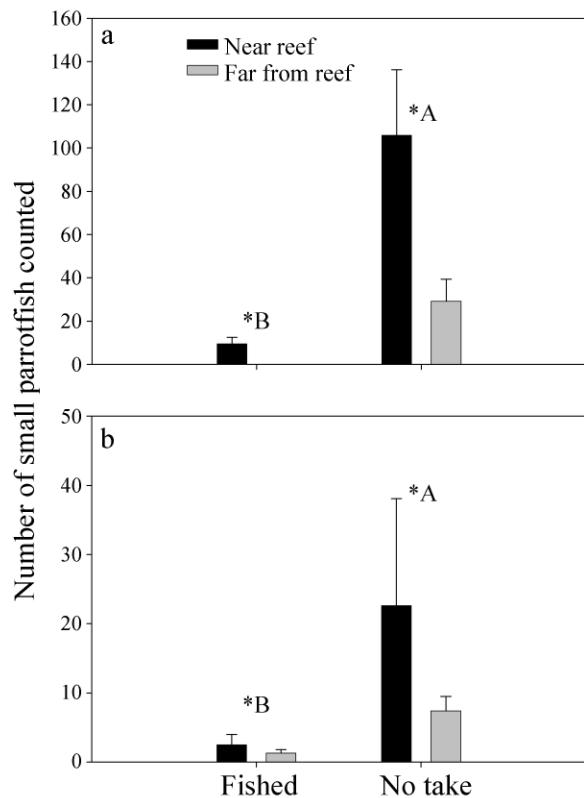


FIG. 6. Small parrotfish species distributional patterns (mean + SE) recorded at the no-take and fished sites using (a) point count and (b) belt transect surveys. Asterisks denote significant differences ( $P < 0.05$ ) with distance from reef. Uppercase letters denote significant differences ( $P < 0.05$ ) between levels of fishing pressure.

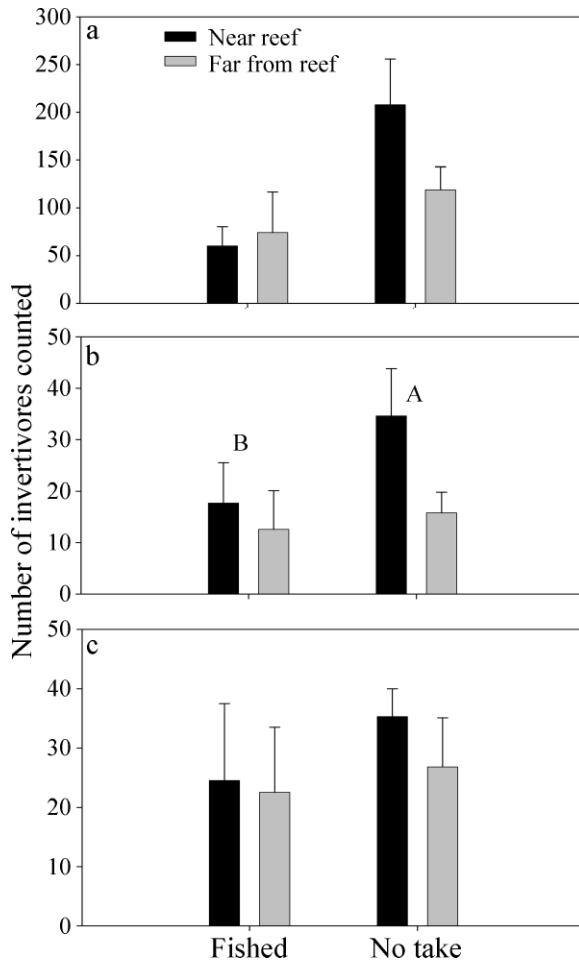


FIG. 7. Invertebrate distributional patterns (mean + SE) recorded at the no-take and fished sites using (a) point count, (b) belt transect, and (c) baited remote underwater video methods. Invertebrate density was not found to vary significantly with distance from the reefs. Uppercase letters denote significant differences ( $P < 0.05$ ) between levels of fishing pressure.

To further explore the impacts of piscivores on smaller prey fishes, we also conducted simple linear regression of square-root transformed counts of the piscivores on similarly transformed counts of small prey fishes for both the point count surveys and the belt transect surveys. The results of these two analyses failed to find any evidence of a significant suppressive effect of piscivores on smaller fishes (point counts,  $F_{1,30} = 0.002$ ,  $P > 0.97$ ,  $R^2 = 0.00005$ ; belt transects,  $F_{1,38} = 0.071$ ,  $P > 0.79$ ,  $R^2 = 0.002$ ). Although the regression analysis of piscivore counts on prey fishes in the point counts was significant, we found no evidence of exploited species in aggregate having a negative impact on prey density (point counts,  $F_{1,30} = 8.47$ ,  $P < 0.007$ ,  $R^2 = 0.007$ ; belt transects,  $F_{1,38} = 0.0001$ ,  $P > 0.997$ ,  $R^2 = 0.00001$ ).

**Seagrass grazing intensity.**—Similarly, we found little evidence that differences in piscivore or exploited species

abundances impacted the grazing of seagrasses in any significant way. A three-way ANOVA failed to detect a significant impact of fishing pressure on grazing intensity date ( $P > 0.05$ ). Grazing did, however, vary significantly with distance from the reefs ( $F_{4,90} = 9.76$ ,  $P < 0.0001$ ) and date ( $F_{4,90} = 2.53$ ,  $P < 0.046$ ). Post hoc comparisons of grazing found the intensity of this consumption was significantly greater on tethers placed at the base of the reef than at any of the other distances. No other significant differences among distances were detected.

**Invertebrate predation potential.**—Results from a three-way ANOVA on arcsine-transformed losses of tethered crabs detected significant effects of survey date ( $F_{4,74} = 3.04$ ,  $P < 0.022$ ), distance from reefs ( $F_{4,74} = 3.5$ ,  $P < 0.011$ ), and fishing pressure ( $F_{1,74} = 15.96$ ,  $P < 0.0001$ ), but no significant interactions ( $P > 0.05$ ). Daily averages of tethered crab losses exceeded 45% in all of the surveys, except in May 2002 when losses were significantly lower (Fig. 8a). Tethered crab losses were significantly greater at fished than at no-take sites (Fig. 8b). Pairwise comparisons failed to detect differences in losses of tethered crabs placed at 5 m and 20 m from each reef (Fig. 8c). Post hoc comparisons of distances, however, show that losses were significantly greater near than far from reefs. Video recordings of attacks on tethered crabs showed that most were conducted by either reef-associated porgies (*Calamus calamus*) or hogfish (*Lachnolaimus maximus*) foraging in grass beds near reefs. Slippery dicks (*Halichoeres bivittatus*) were also observed to attack tethered crabs at times.

Losses of tethered brittlestars were consistently high (>75% of all individuals placed at the study sites on most dates) regardless of fishing pressure or distance from reefs ( $P > 0.05$ ). In this case, attacks were conducted primarily by wrasses and porgies. Overall, the losses of large tethered gastropods were very low (<2%), and they varied significantly among survey dates and between levels of fishing pressure (time  $\times$  fishing pressure interaction,  $F_{3,38} = 3.73$ ,  $P < 0.02$ ). This significant interaction resulted from losses of large gastropods being greater at the fished sites in August of 2002 and May of 2003 and higher at the no-take sites in May 2002. No treatment effects were noted for July 2002 or August 2003. In contrast, losses of small gastropods were, on average, higher (~60%) than the larger gastropods. Some 20% more of these prey were consumed at fished than at no-take sites resulting in there being significantly more small gastropods being consumed at the fished than at the no-take sites ( $F_{1,33} = 4.58$ ,  $P < 0.02$ ), regardless of distance from the reef ( $P > 0.05$ ). Small gastropod losses were also significantly greater in August of 2003 than in May of 2003 ( $F_{1,33} = 6.61$ ,  $P < 0.015$ ).

**Seagrass biomass.**—While seagrass biomass varied significantly with survey date ( $F_{4,31} = 3.05$ ,  $P < 0.031$ ), three-way ANOVA failed to detect significant differences in seagrass biomass between levels of fishing pressure

or among distances from reefs ( $P > 0.05$ ). As such, the interpretation of treatment effects on prey fish density or tethered invertebrate mortality was not confounded by site differences in seagrass biomass.

#### DISCUSSION

Paleoecologists have clearly shown that both increasing abundances and rapid diversifications of higher order consumers over geologic time scales triggered dramatic shifts in the morphology and the composition of their prey (e.g., Vermeij 1977, 1987, Aronson 1992). As such, it is reasonable to expect that shifts in the composition induced by fishing, as well as reductions in the density of higher order consumers, have led to dramatic changes in trophic exchanges within marine food webs (Bruno and O'Connor 2005). In some cases, reductions in the density of modern day higher order consumers have produced important cascading effects on the intensity of interactions among lower trophic levels (Steneck et al. 2004). For the most part, however, these cascades have been found in structurally simple food webs where slow-moving invertebrates (e.g., sea urchins and mussels) are the key intermediates for the transfer of primary production to higher order consumers (e.g., Hay 1984, McClanahan 1998, Shears and Babcock 2003). Of the studies that have looked for broader impacts of overfishing on the structure and productivity of more diverse, highly reticulate food webs (cf. Polis and Strong 1996), the results have been mixed (Strong 1992, Jennings and Polunin 1997, Jennings and Kaiser 1998, Bascompte et al. 2005, Ault et al. 2006). Moreover, none have considered the extent to which changes in exploited fish density have altered the strength of trophic links among habitats.

In general, we found significantly more species and greater densities of fishes, regardless of trophic position, at the no-take than at the fished sites. And while we recorded fewer species of exploited fishes along the seagrass–coral reef boundary than reported for the fore reefs in our study area (cf. Ault et al. 1998), most were significantly more abundant, and comprised a greater proportion of the overall pool of fishes, at no-take than at the fished sites. Recent estimates of exploited piscivore abundance on fore reefs in the Florida Keys are low (Bohnsack et al. 1999, Ault et al. 2006), and that was also true in our study. On average, exploited fishes never accounted for >8% of all piscivores recorded in any survey. Instead, most of the exploited species were either invertivores or omnivores, which were consistently more abundant at the no-take sites.

With only one exception, the census techniques used to evaluate fish community structure consistently detected greater numbers of piscivores at the no-take than at the fished sites. These piscivores were dominated by moderately fished or unfished transient predators, such as jacks (Carangidae) and great barracuda (*Sphyraena barracuda*), which comprised some 92% of all piscivores recorded. Given that historical data on the

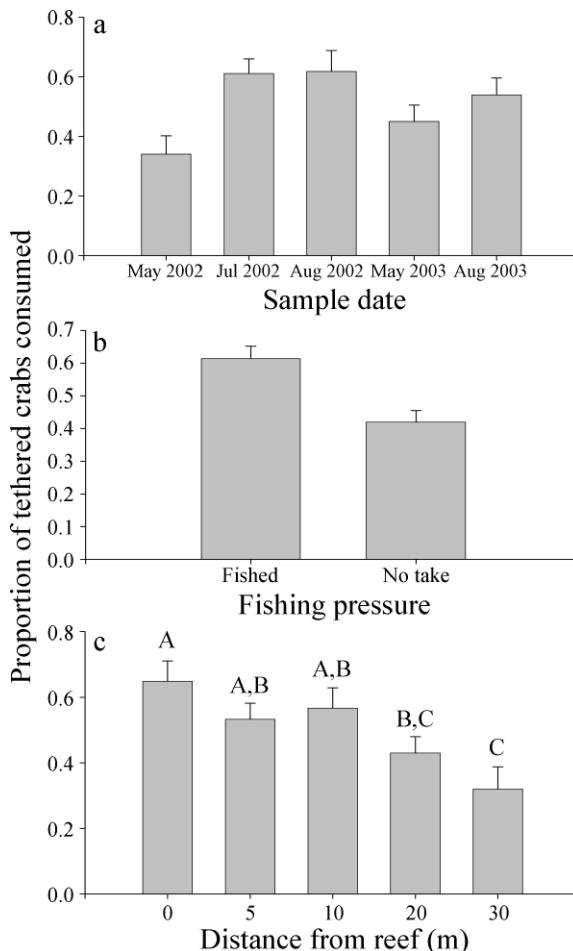


FIG. 8. Proportion of tethered crabs consumed (mean + SE) (a) in each survey, (b) at the fished and no-take sites, and (c) at varying distances from the reefs. Uppercase letters denote significant differences ( $P < 0.05$ ).

relative abundances of these species are lacking (cf. Edgar and Barrett 1999), and the fact that persistent intense commercial fishing throughout the Keys predated the time when scientific investigations began (Viele 2001), it is not clear if the food webs at our protected sites are representative of reef food webs that were present in earlier times (Jennings and Blanchard 2004, Knowlton 2004, National Research Council 2006). Anecdotal reports and commercial fishing records suggest that the composition of organisms in higher trophic levels was probably very different from the composition currently present in the Keys, and that higher order fishes were probably much larger than those recorded in our study (Viele 2001). Still, it is noteworthy that Hixon and Carr (1997) also found transient predators (bar jacks) to be the dominant piscivores at Lee Stocking Island, Bahamas, where fishing pressure is reported to be low. We also do not discount the possibility that exploited piscivores were more abundant at our study sites at night and that some

were hiding during our daytime surveys (Eggleston et al. 1998), although a companion study addressing a separate question found smaller bar jacks to be the only piscivore detected during nocturnal fish surveys (Blackmon 2005). Clearly, there is a need to develop techniques that will allow us to reconstruct the composition of marine food webs, to the extent possible, to determine if in fact the establishment of marine protected areas will restore more food webs to the way they once were (Jennings and Blanchard 2004, Knowlton 2004). Still, if nocturnally active consumers were more abundant at the no-take sites, and they are strong interactors within local food webs, then we should have detected consistently significant differences in the density and composition of smaller fishes (both invertivores and herbivores), and daily losses in our tethering experiments between treatments. This was not the case.

We predicted that significantly fewer lower order consumers (herbivores and invertivores) would be encountered at the no-take sites where exploited fishes (both piscivores and omnivores) were abundant. Counter to our prediction, elevated exploited fish density at the no-take sites was not associated with either lower herbivore or invertivore densities, as significantly more of these two groups were recorded at the no-take sites. On average, parrotfishes were five times more abundant near no-take than at fished sites. These significant differences were not, however, solely attributable to elevated densities of larger reef-associated parrotfish species, whose foraging patterns might have been affected by the elevated densities of piscivores at the no-take sites. Smaller, seagrass-associated parrotfishes were also significantly more abundant at no-take sites. We also predicted that significantly fewer and smaller sized prey fishes would be found at the no-take reefs. This was not the case either, as significantly more of these smaller fishes were recorded at the no-take sites, again where exploited fishes were most abundant. None of the treatment differences were the result of habitat structure as seagrass biomass never varied significantly among sites. We cannot discount the possibility that the no-take sites were always sites of elevated fish abundance and diversity. If true, however, this implies strongly that top down pressures on smaller fishes are not strong. We believe, however, that the more probable explanation for these unexpected results lies in the fact that the lion's share of the exploited fishes found during our surveys was invertivores and not piscivores.

Differences in the densities of herbivores and invertivores were not clearly related to differences in grazing intensity or, in two cases, the predation potential of tethered invertebrates. Tethered crab losses were significantly greater at fished reefs where invertivores were less abundant. So too were losses of small gastropods significantly greater at the fished sites than at the no-take sites. In contrast, both large and small species of parrotfishes were found at higher densities at the same sites where piscivores were found at high density. Leaf

losses on seagrass tethers were significantly greater at the no-take sites where herbivores were more abundant. In most cases, diver observations and video recordings indicated that reef-associated parrotfishes, porgies, and hogfishes, all of which were more abundant at the no-take sites, were responsible for attacks on tethers near the reefs. These weak relationships between differences in consumer density and levels of fishing pressure and losses on the tethers support a recent evaluation of Caribbean reef food webs that concluded that interactions between adjacent trophic levels are diffuse, and that strong trophic cascades are likely to be rare in modern day tropical ecosystems (Bascompte et al. 2005).

Based on our results it seems unlikely that there are strong top down restrictions on the transfer of seagrass-based production to reef consumers. The diver and video observations suggest that strong direct trophic links exist between nearby seagrass meadows and coral reefs. Differences in the composition of consumers in seagrass meadows away from the reefs suggest that the transfer of seagrass-based production to reef consumers passes through smaller wrasses and parrotfish, which in turn are consumed by reef-associated transient predators. In this study, brittlestars, for example, were consumed in great numbers throughout the seagrass habitats at all of the sites. Most frequently these organisms were attacked by seagrass-associated smaller invertivores (primarily wrasses and porgies). Tethered seagrass leaves placed away from the reefs were consumed by smaller seagrass-associated parrotfishes (Valentine et al. 2007). Both of these groups of smaller consumers were observed by our divers or are reported in the literature (Randall 1967, Clifton and Robertson 1993) to be fed on by bar jacks foraging along the seagrass-coral reef boundaries. These observations, plus the magnitude of grazing by larger species of reef-associated parrotfishes reported by Valentine et al. (2007), suggest an important trophic link between reefs and adjacent seagrass meadows and that piscivores now present in unfished areas do not diminish its strength.

There still remain a number of issues to consider before we should conclude that higher order consumers do not control community composition or affect the strength of trophic linkages between habitats. While variation in habitat structure can mask the intensity of density-dependent interactions on reefs (Overholtzer-McCleod 2004), we minimized this possibility by conducting our study in adjacent seagrass meadows whose biomass did not vary significantly among sites. As such, habitat heterogeneity did not confound the interpretation of our data. We can not, however, discount the possibility that in the no-take areas predatory fish biomass has not yet reached the point at which density-dependent processes control food web structure. In a separate analysis, Russ and Alcala (2004) report that higher order predator biomass will not reach an asymptote for a minimum of 40 years after the cessation of fishing. Since neither of our study sites has

been protected for 40 years, it is not clear that the composition of the food web described in this study is representative of that prior to urbanization of the Florida Keys. Finally, we must consider the possibility that the bioenergetic needs of exploited fishes, which seem to comprise a small percentage of the overall pool of fishes in these habitats, are not great enough to significantly impact the transfer of energy between adjacent trophic levels.

In conclusion, we found greater densities of exploited fishes at our no-take study sites. These fishes, however, never comprised more than about 30% of all fishes recorded and, of these, most were invertivores not piscivores. Encounters with exploited piscivores were rare and the piscivore guild was dominated by larger transient predators such as barracudas and jacks. Unexpectedly, most other fish trophic groups were also more abundant at the no-take than at the fished sites. Lack of clear links between piscivore abundance and grazing intensity and tethered invertebrate survivorship suggests that strong trophic cascades do not exist along the seagrass–coral reef boundaries of the Florida Keys. We found evidence from tethered crabs and smaller gastropods at the fished sites that seagrass production reaches reef residents. Our results show that while the abundances of many consumers have been reduced by fishing pressure along the seagrass–coral reef interface, the allochthonous input of seagrass habitat production to reef-associated consumers remains strong.

#### ACKNOWLEDGMENTS

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#### APPENDIX

Results from the statistical analyses of fishing impacts on fish community structure, and predation and grazing intensity along the coral reef–seagrass interface (*Ecological Archives* A018-052-A1)