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Effects of a marine reserve on recruitment of grunts (Pisces: Haemulidae) at Barbados, West Indies

Mark Tupper[a,b] & Francis Juanes[c]
[a] *Bellairs Research Institute of McGill University, St. James, Barbados, WI*
[b] *Present address: School for Field Studies, P.O. Box 007, Turks & Caicos Islands, South Caicos, British West Indies (e-mail: sfstci@tciway.tc)*
[c] *Graduate Program in Organismal and Evolutionary Biology and Department of Forestry and Wildlife Management, University of Massachusetts, Amherst, MA 01003, U.S.A.*

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Synopsis

The effects of a non-extractive marine reserve on the recruitment dynamics of haemulid fishes and their predators on Barbados coral reefs were studied using visual census and mark-recapture methods. Size and abundance of piscivores (including large adult grunts) known to prey on grunts were greater within the reserve than on adjacent reefs, whereas size and abundance of older juvenile grunts did not differ between protected and exploited reefs. Recruitment and early juvenile abundance were lower within the reserve and were inversely related to predator density (including adult conspecifics). Patterns in density of new recruits may also have been influenced by oceanographic patterns of supply of larvae. Thus, although protection has a significant positive effect on the size and abundance of large carnivorous fishes, higher predation pressure within a reserve may serve to reduce juvenile recruitment within the reserve. At some size/age, cumulative recruitment due to lower size-specific predation mortality results in higher density within the reserve. This increased density is maintained by the absence of fishing mortality within the reserve. Despite maintaining high spawning biomass of several large, commercially exploited species that may export larvae to downstream areas, the Barbados Marine Reserve appears to be a local sink for juvenile grunts.

Introduction

Fisheries for demersal reef fishes are of particular importance to many developing countries, where large numbers of people are dependent on them both for income and as their main source of protein (Roberts & Polunin 1991). Reef fisheries are typically multispecific and fishes are harvested using a wide variety of methods (Munro & Williams 1985). The complexity of these fisheries poses particularly serious management problems (Roberts & Polunin 1991, Russ 1991, Medley et al. 1993). The establishment of marine reserves closed to fishing (except in some cases to recreational or subsistence fishing) has been promoted as a viable alternative where traditional approaches to fisheries management are not practical (Plan Development Team[1], Roberts & Polunin 1991, Medley et al. 1993). Potential advantages of marine reserves have been reviewed by several authors (Plan Development Team[1], Roberts & Polunin 1991, Roberts 1995), but the main value of a marine reserve is thought to be as a breeding and nursery area to maintain recruitment over a wider region (Medley et al. 1993). To date, reserves tend to be primarily a conservation measure; enhancement of the fishery remains a secondary objective (Medley et al. 1993).

One of the characteristics of exploited reef areas is the very low abundance or virtual absence of large carnivorous fishes, particularly groupers (Serranidae) and large snappers (Lutjanidae) (Ferry & Kohler 1987, Koslow et al. 1988, Roberts & Polunin 1991, Russ 1991, Medley et al. 1993). Marine reserves have proved

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[1] Plan Development Team. 1990. The potential of marine fishery reserves for reef fish management in the U.S. southern Atlantic. NOAA tech. Memo NMFS-SEFC-261, Miami. 40 pp.

effective in preserving stocks of such species (Roberts & Polunin 1991). It is now well documented that the abundances and average sizes of large carnivorous fishes increase within protected areas (Roberts & Polunin 1991, Rakitin & Kramer 1996).

The increases in average size found in reserve areas must indicate primarily an increase in longevity (Roberts & Polunin 1991). However, the effects of protection on mortality may be size-dependent. Goeden (1979) reported that mortality of juvenile (<3 years old) *Plectropomus leopardus* in heavily fished areas of the Great Barrier Reef was lower than in an unfished area, whereas mortality of adults was higher in heavily fished areas than in an unfished area. He suggested that density-dependent competition caused higher juvenile mortality on the unfished reef. Evidence of density-dependent post-settlement mortality and recruitment exists for coral reef fishes in Barbados (Hunt von Herbing & Hunte 1991, Tupper & Hunte 1994), Hawaii (Stimson 1990), and the British Virgin Islands (Forrester 1995), and for temperate demersal and reef fish in Nova Scotia (Tupper & Boutilier 1995a,b). Post-settlement mortality may also be expected to decrease outside reserves in response to decreased predation pressure resulting from lower densities of large piscivorous fishes.

Marine reserves are likely to have substantially higher rates of overall fish production than exploited areas (Roberts & Polunin 1991). Fecundity of fishes typically increases as a power of length (Wootton 1990). Since the average size of fishes is higher in reserve areas, small reserves could potentially produce as many eggs as much larger areas of unprotected reef (Roberts & Polunin 1991, Man et al. 1995). This provides the basis for the claim that reserves can act as sources of recruits for unprotected areas – a major premise for the establishment of marine reserves (Roberts & Polunin 1991, Medley et al. 1993).

If increased catches in areas adjacent to reserves do not result from recruitment, they will result from emigration of fishes from the reserve. Generally, reef fishes are strongly site-attached (Sale 1980), although the scale of movement varies among species (Jones 1991, Rakitin & Kramer 1996). Large and schooling species tend to move farther than small or solitary species. Many species show ontogenetic shifts in habitat use, where individuals typically settle into shallow inshore habitats but move offshore as they grow. In the Caribbean, grunts usually settle into seagrass beds, then move onto reefs several weeks later (McFarland 1979). This behavior may reduce predation pressure on juvenile grunts by allowing them to avoid reef-associated predators until they are larger and less vulnerable to predation (Shulman 1985). In Barbados, however, seagrass beds are scarce, and grunt juveniles generally settle directly onto reefs (Tupper 1989). Newly settled grunts remain closely associated with the substrate for one to two weeks, but as they grow they forage farther from the reef. The small, site-attached settlers may be particularly susceptible to post-settlement mortality if densities of older grunts or other piscivorous predators are high (Shulman et al. 1983, Shulman 1984, 1985, Hixon & Beets 1993).

Many species of reef fish also migrate considerable distances to forage (Hobson 1973, Helfman 1993) or to reproduce (Shapiro 1987). Adult grunts may undertake daily foraging migrations of up to 500 m (Ogden & Erlich 1977, Burke 1995). These migrations may take fish across reserve boundaries, reducing the difference in abundance between reserves and exploited areas. Moreover, fish may emigrate from reserves to avoid competition from high densities of conspecifics. However, given a sufficiently large reserve, a strong gradient of fishing pressure across the reserve boundaries might overcome the effects of cross-boundary migration. To date, emigration of fishes from reserves has rarely been investigated and the results are inconclusive. Alcala & Russ (1990) and Russ & Alcala (1996), suggested emigration of fishes from Sumilon Island Reserve in the Philippines as an explanation for higher catches on reefs adjacent to the reserve. Buxton & Allen (1989) found no emigration of tagged fish from a South African reserve. Bryant et al.[2] found substantial movement (over 18 km for *Lutjanus griseus*) of tagged sport fishes into and out of Florida Bay in Everglades National Park. However, given the relatively limited home range of most coral reef fishes, Roberts & Polunin (1991) suggested that significant enhancement of fisheries by emigration alone would likely be restricted to within 1 km of a reserve.

In summary, the establishment of marine reserves leads to increased size and abundance of exploited species, particularly those most vulnerable to fishing gear (Rakitin & Kramer 1996). This in turn may lead to increased fecundity and production, with a 'spillover effect' causing higher levels of recruitment in

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[2] Bryant, H.E., M.R. Dewey, N.A., Funicelli, G.M. Ludwig, D.A. Meineke & J. Mengel. 1989. Movement of five selected species of fish in Everglades National Park. Bull. Mar. Sci. 44: 515 (abstract).

the area surrounding the reserve. However, increased production within the reserve may be offset to some degree by density-dependent growth and mortality. The objectives of this study were to investigate the size and abundance of grunts and selected piscivorous reef fishes within and outside a marine reserve in Barbados. In addition, we monitored the settlement, growth, mortality, and movement of juvenile grunts within and outside the reserve. Data were collected on three species of grunt: tomtate, *Haemulon aurolineatum*; French grunt, *Haemulon flavolineatum*; and smallmouth grunt, *Haemulon chrysargyreum*. These species are among the most common commercially exploited fishes on Barbados reefs (Hunte[3], Tupper 1989, Rakitin & Kramer 1996). The study attempted to answer the following specific questions: (1) Does the abundance of adult grunts of trappable size ($\geq$15 cm; Rakitin & Kramer 1996) and of other large piscivorous fishes differ between the reserve and adjacent areas? (2) Do rates of settlement, mortality and emigration of juvenile grunts differ between sites within and outside the reserve, and are these differences related to the abundance of conspecific adults and/or piscivorous predators?

Methods

The study was conducted on nine fringing reefs, spanning a 7 km section of the west (leeward) coast of Barbados, WI (59°38′W, 13°09′–13°12′N, Figure 1). Three of the study reefs were located within the Barbados Marine Reserve, which is approximately 2.2 km north to south and averages about 800 m east to west. Three reefs were situated north of the reserve; the remaining three were south of the reserve. The distance separating adjacent study reefs averaged 780 m. A recent study (R. Bateson unpublished data) indicated little difference between the study reefs in terms of vertical relief, percent live coral cover, and percent algal cover. The Barbados Marine Reserve is closed to all fishing except cast netting for clupeids. On exploited reefs, the most common gear used is the Antillean Z-trap (Miller & Hunte 1987), although some spearfishing also occurs. Based on interviews with fishers, Rakitin & Kramer (1996) estimated that 40–60 traps are set and hauled twice weekly within each of the exploited study areas to the north and south of the reserve.

Census techniques

A pilot study indicated that four species of piscivorous fish commonly preyed on juvenile grunts. These were the trumpetfish, *Aulostomus maculatus*, the spotted moray, *Gymnothorax moringa*, the coney, *Epinephelus fulvus*, and the mahogany snapper, *Lutjanus mahogani*. On each reef, the densities of these piscivores and of grunts (*Haemulon flavolineatum*, *H. aurolineatum* and *H. chrysargyreum*) were estimated by 17 weekly visual censuses from May through August 1995. Censuses were conducted in the spur-and-groove zone of each reef. The spur-and-groove zone lies at the seaward edge of the reef, with the tops of the reef spurs 2–3 m deep and the sand bottom of the grooves 4–6 m deep (Lewis 1960, Stearn et al. 1977). On each reef, four 20 m ropes were laid out parallel to each other, 1 m apart and perpendicular to shore. At each census, a diver swam slowly along each transect line, counting target species within 50 cm of either side of the transect line. All census data were collected by the same diver (MT). The total area covered by the census was 80 m^2.

Grunts and their predators were enumerated by species and size class (visually estimated as fork length (FL) $<$ 2, 2–5, 5–10, 10–15, 15–20, 20–25, 25–30 and $>$30 cm). Numbers of all species of predators were pooled, then divided into trappable and non-trappable size classes based on minimum trappable fork lengths for each species (see Rakitin & Kramer 1996). Due to the extreme difficulty of in situ species identification of individuals $<$ 5 cm FL, all species of grunts were also pooled. Grunts were grouped into four broader size classes for demographic analysis (newly settled $<$ 2 cm FL, early juvenile 2–5 cm FL, late juvenile 5–15 cm FL, trappable adults $>$15 cm FL). For the purposes of this study, recruitment is defined as the process whereby a planktonic larva metamorphoses into juvenile and settles to the substrate and assumes a benthic or demersal existence. Based on size at settlement and subsequent growth rates of settlers (M. Tupper unpublished data), it was determined that most grunts $<$2 cm FL would have settled within the past week, i.e., since the previous census. Density of newly settled grunts was therefore used as a measure of recruitment strength. This measure probably greatly underestimated the actual cumulative settlement over the one-week interval between censuses, since predation would have had ample time

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[3] Hunte, W. 1987. Derelict vehicles as artificial reef in Barbados. Report of the Bellairs Research Institute of McGill University, Barbados. 44 pp. plus appendices.

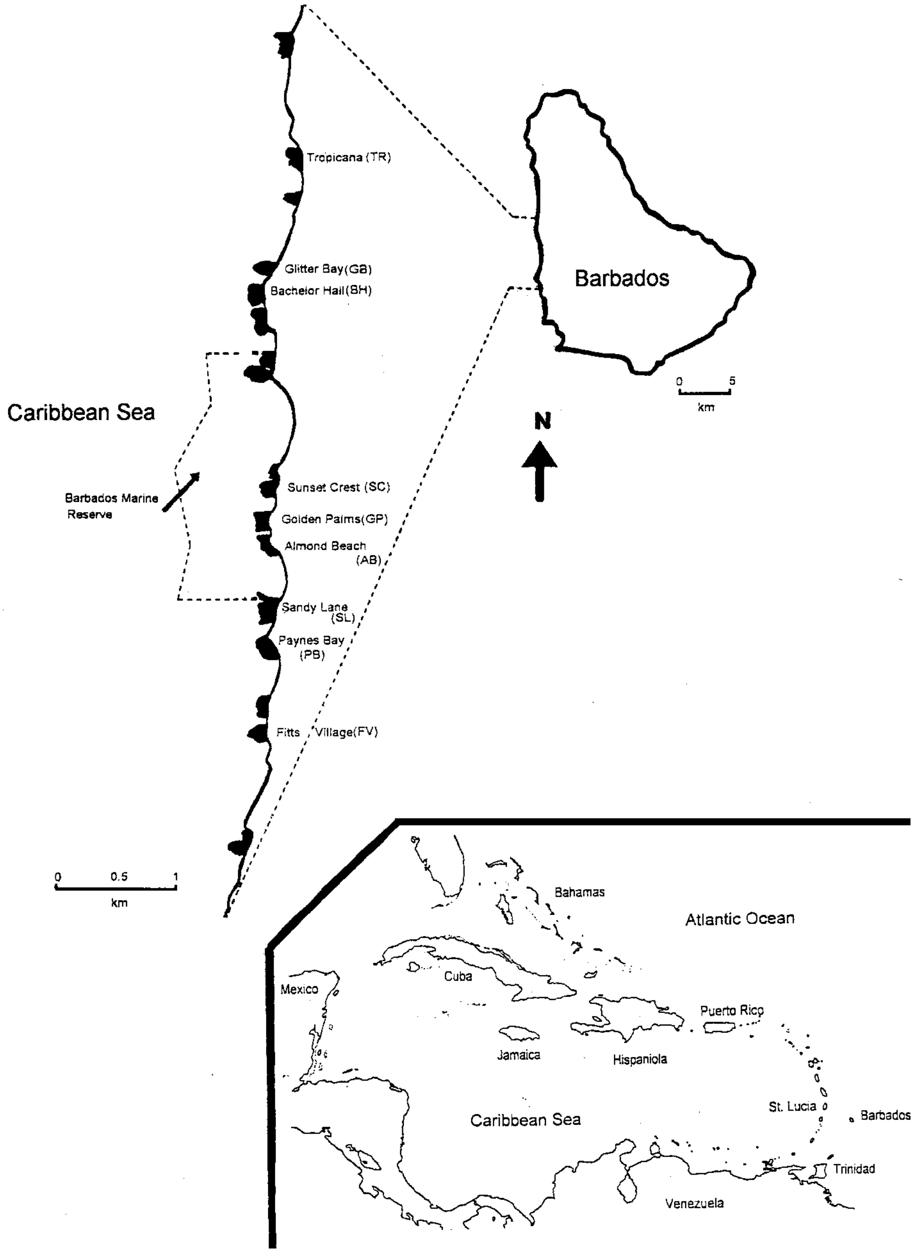

Figure 1. Upper right: island of Barbados; dashed lines indicate study area. Upper left: map of the central west coast illustrating the position of the nine study reefs. Reefs within the dashed area are protected from fishing. Lower right: map of the Caribbean Sea showing the location of Barbados. Modified from Rakitin & Kramer (1996).

to considerably reduce the number of surviving settlers (e.g. Shulman & Ogden 1987). We define colonization as the immigration of older (juvenile or adult) fishes from nearby habitats.

In Barbados, grunts tend to settle in large groups over specific points on a reef (Tupper 1989). Newly settled and early juvenile grunts (1.5–3.5 cm FL) were captured from four selected sites on each study reef using a 10% solution of the anesthetic Quinaldine (Sigma). At each site, 20–50 grunts were marked in situ with subcutaneous injections of non-toxic, waterproof acrylic paint, using a different mark for each capture site. Our original intent was to mark newly settled grunts at their smallest sizes (0.7–1.1 cm FL), i.e., immediately after settlement. In a control experiment, 200 newly settled grunts were captured, held in aquaria, then subjected to the marking procedure. The results of this experiment indicated that mortality due to handling for grunts 0.7–1.1 cm and 1.1–1.5 cm FL was 42% and 28% respectively over one week, a figure we considered unacceptable. Mortality due to handling of grunts 1.5–2.5 cm and 2.5–3.5 cm FL was considerably lower, 14% and 8% respectively, and we therefore limited marking to these larger size classes. A total of 997 fish was marked and released. The mortality due to handling was added to mortalities calculated from field data.

We investigated mortality and emigration of early juvenile grunts by 12 successive censuses of marked individuals, performed twice each week for six weeks. During each census, divers searched for marked individuals by swimming concentric circles of increasing radius (0 m, 1 m, 2 m, 5 m, 10 m, 20 m, 30 m, and 50 m) around each capture point. In most cases this represented the entire area of the study reef. The aim of this survey was to identify whether postsettlement mortality or emigration was primarily responsible for loss of grunts from their settlement sites. Marked grunts found at some distance from the original settlement site would be evidence for emigration, whereas a complete disappearance of marked fish would be more indicative of mortality. We considered it highly unlikely that such small fish would emigrate between fringing reefs separated by several hundred meters of bare sand. Cumulative percent mortality of released grunts was estimated as: $(1 - (\text{number in census}/\text{total number released})) \times 100\%$. Individuals not found within the 50 m search radius were presumed eaten. Data on juvenile grunt demographics were analyzed in relation to the density of conspecifics and/or predators on each study reef.

Statistical analyses

All numeric data were subjected to Bartlett's test for homogeneity of variance and square root transformed where necessary to meet the assumptions of parametric analyses (Sokal & Rohlf 1981). The effects of reef location on demographic variables (predator density, density of grunts within each size class, and postsettlement mortality of grunts) were tested using analysis of variance (ANOVA); transects were considered replicate units and reefs were considered a fixed treatment effect. T-tests were used to detect differences in demographic variables between protected vs. exploited reefs. For these analyses, censuses on each reef were pooled and reefs were considered replicate units. Only predators of trappable size (i.e. greater than the minimum trappable fork length for the species, see Rakitin & Kramer 1996) were included in the analysis, as smaller fish would not be directly affected by fishing mortality.

Results

Predator density

Abundance of the four predator species varied widely among reefs (ANOVA, $p < 0.0001$; Figure 2a). Predator density was significantly higher within the reserve than on exploited reefs (t-test, $p < 0.001$). Predator density did not vary among reefs within the reserve (Tukey's HSD, $p = 0.44$). Among exploited reefs, Bachelor Hall and Tropicana, both to the north of the reserve, supported significantly lower predator densities. Mean predator size was also significantly higher within than outside the reserve (t-test, $p < 0.01$; Figure 2b).

Adult and juvenile grunt density

Density of trappable adult grunts also varied widely among reefs (ANOVA, $p < 0.0001$; Figure 3a). Adult grunt density did not vary among reefs within the reserve (Tukey's HSD, $p = 0.25$) or among exploited reefs (Tukey's HSD, $p = 0.40$), but was significantly higher within the reserve than on exploited reefs (t-test, $p < 0.001$). Density of juvenile fishes (i.e. grunts 5–15 cm FL), which are not subject to fishing pressure, did not vary among reefs (ANOVA, $p = 0.6$). On all but one reef (Bachelor Hall), density of grunts $\geq$ 15 cm FL was higher than that of grunts 5–15 cm FL. The density difference between juveniles and adults was much more pronounced within the reserve. Mean size of adult grunts varied among reefs (ANOVA, $p < 0.001$) and was significantly higher within the reserve (t-test, $p < 0.001$; Figure 3b). However, mean size of older juvenile grunts did not differ among reefs (ANOVA, $p = 0.8$).

In contrast to older juvenile grunts, density of early juvenile grunts varied widely among reefs (ANOVA,

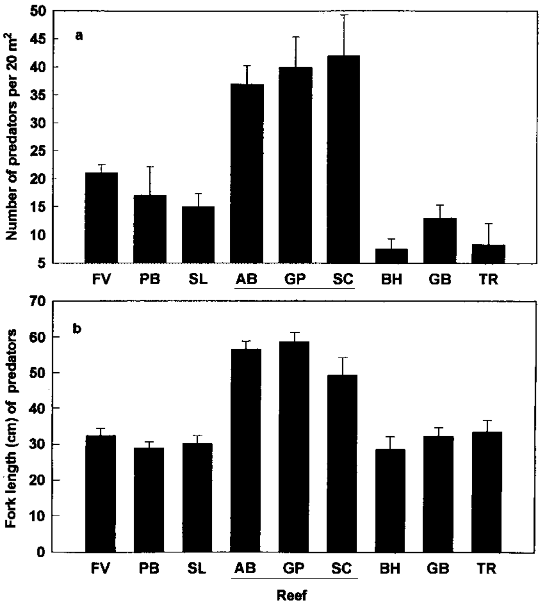

Figure 2. a – Combined population density of four large piscivorous species on nine fringing reefs on the west coast of Barbados. b – Mean size of above predators on nine fringing reefs on the west coast of Barbados. Reefs are positioned along the x axis in order of location from south to north; the three central (underlined) reefs are within the Barbados Marine Reserve. Vertical error bars indicate ±1 standard deviation from the mean.

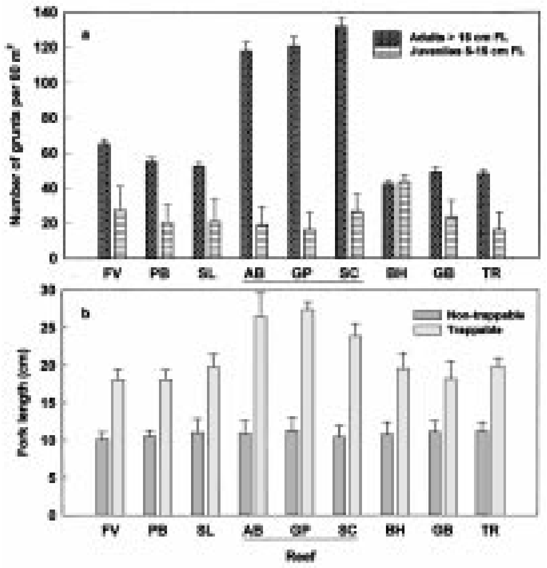

Figure 3. a – Combined stock density of trappable adults (>15 cm FL) and older juveniles (5–15 cm FL) of three species of grunts on each of the study reefs. b – Mean size of non-trappable older juvenile (5–15 cm FL) and trappable adult (>15 cm FL) grunts on nine fringing reefs on the west coast of Barbados. Reefs are positioned along the x axis in order of location from south to north; the three central (underlined) reefs are within the Barbados Marine Reserve. Vertical error bars indicate ±1 standard deviation from the mean.

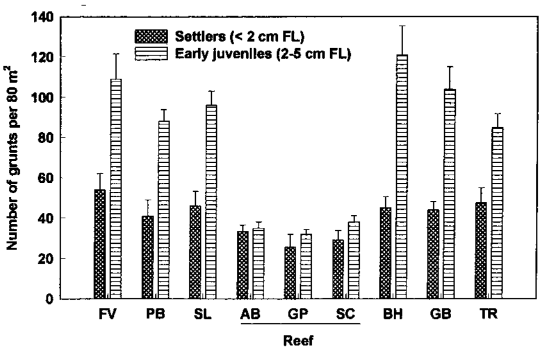

Figure 4. Combined density of newly settled (<2 cm FL) and early juvenile grunts (2–5 cm FL) of three species of grunts on nine fringing reefs on the west coast of Barbados. Reefs are positioned along the x axis in order of location from south to north; the three central (underlined) reefs are within the Barbados Marine Reserve. Vertical error bars indicate ±1 standard deviation from the mean.

$p < 0.0001$; Figure 4). Early juveniles were most abundant at Bachelor Hall, north of the reserve; the difference between Bachelor Hall and all other reefs was significant (Tukey's HSD, $p < 0.05$ for all pairwise comparisons). Density of early juveniles was much lower on protected reefs than exploited reefs (t-test, $p < 0.0001$), but did not differ among reefs within the reserve (Tukey's HSD, $p = 0.9$). Apart from Bachelor Hall, density of early juveniles did not differ among exploited reefs (Tukey's HSD, $p > 0.1$ for all pairwise comparisons).

Recruitment and post-recruitment mortality

Density of newly-settled grunts varied significantly among study reefs (ANOVA, $p < 0.01$; Figure 4). Mean settlement was higher on exploited reefs than within the reserve (t-test, $p < 0.05$). Recruitment was highest on the southernmost exploited reef at Fitt's Village, and lowest on the most central reef at Golden Palms. Only Fitt's Village differed significantly from all three reefs within the reserve (Tukey's HSD, $p < 0.05$), although settlement on Sandy Lane (also south of the reserve) was significantly higher than on Golden Palms in the central area of the reserve (Tukey's HSD, $p < 0.05$).

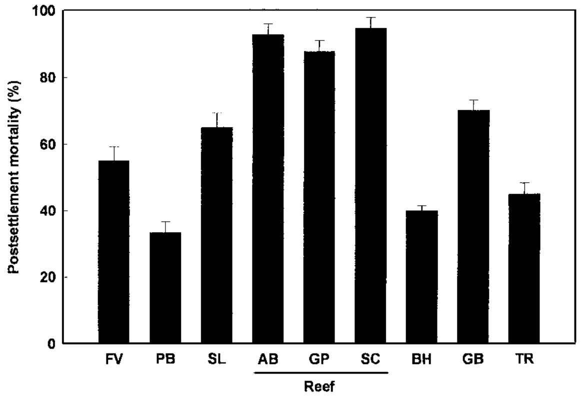

Figure 5. Percent postrecruitment mortality of early juvenile (2–5 cm FL) grunts (genus *Haemulon*) on nine fringing reefs on the west coast of Barbados. Reefs are positioned along the x axis in order of location from south to north; the three central (underlined) reefs are within the Barbados Marine Reserve. Vertical error bars indicate ±1 standard deviation from the mean.

Mortality of newly settled and early juvenile grunts (≤ 5 cm FL) varied significantly between reefs (ANOVA, $p < 0.0001$; Figure 5), ranging from 35%–93%. Mortality was higher on protected reefs than on exploited reefs (t-test, $p < 0.01$), and was positively correlated with both predator density ($r = 0.863$, $p < 0.001$; Figure 6a) and density of adult (trappable size) grunts ($r = 0.853$, $p < 0.001$; Figure 6b). Note, however, that the density of adult grunts and large predators are intercorrelated due to the effects of protection on reserve reefs and removal from exploited reefs. In repeated censuses of tagged individuals, no fishes <3 cm FL were found farther than 2 m from the point of initial capture, and no fishes ≤ 5 cm FL (the largest size reached by tagged individuals over the course of the study) were found farther than 5 m from the point of capture.

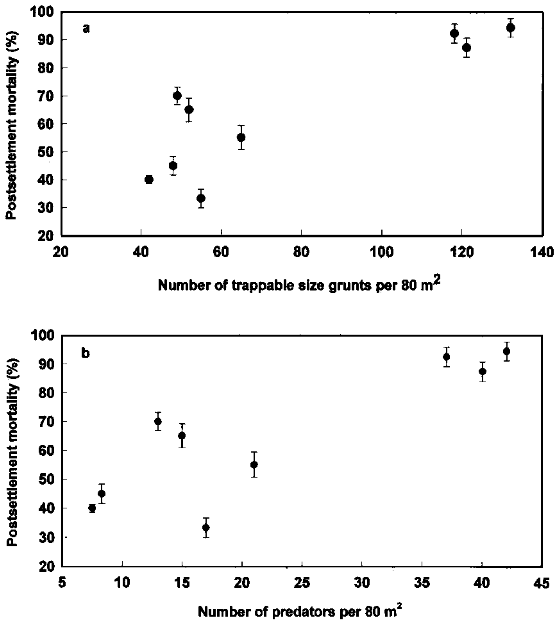

Figure 6. Percent postrecruitment mortality of early juvenile (2–5 cm FL) grunts (genus *Haemulon*) vs. a – the density of trappable-size (>15 cm FL) grunts and b – the density of large piscivorous predators other than grunts, on nine fringing reefs on the west coast of Barbados. Vertical error bars indicate ±1 standard deviation from the mean.

Discussion

One of the primary effects of protection from fishing is an increase in the numbers and size of target species (Roberts & Polunin 1991, Roberts 1995). In this study, abundance and size of trappable grunts and other piscivorous reef fishes was significantly higher within the Barbados Marine Reserve than on nearby exploited reefs. Roberts (1995) found that although individual species of grunts did not differ in biomass between unfished and fished areas around the island of Saba in the Netherlands Antilles, overall biomass of grunts was significantly greater in the unfished areas. Bell (1983) found higher densities of 11 exploited rocky-reef fishes in a reserve than in a similar fished area in the French Mediterranean. He also reported higher modal sizes within the reserve for several of these species. Buxton & Smale (1989) investigated the effects of protection on three heavily exploited species of the family Sparidae in South Africa. Two of these species occurred at significantly higher densities within the reserve, and mean size of one species was significantly larger. Several other authors have reported similar results (Russ 1985, Ayling & Ayling[4], Alcala 1988, Clark et al. 1989, Russ & Alcala 1989, McClanahan & Shafir 1990).

Increased numbers of predators and/or large conspecifics within a reserve may depress abundances of small prey species or juvenile conspecifics, either directly, by preying on smaller fishes, or indirectly,

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[4] Ayling, A.M. & A.L. Ayling. 1986. A biological survey of selected reefs in the Capricorn section of the Great Barrier Reef Marine Park. Unpublished report to the Great Barrier Reef Marine Park Authority, Townsville. 61 pp.

by density-dependent emigration. For example, Lock[5] reported that increases in fishing intensity led to increased abundance of small prey species in Papua New Guinea. In our study, recruitment of juvenile grunts was significantly lower within the Barbados Marine Reserve. There was a general inverse relationship between predator density and recruitment. For example, Bachelor Hall supported the lowest absolute number of predators, but the highest overall number of early juveniles and older juveniles. Furthermore, postrecruitment mortality of grunts was positively correlated with the density of predators and large conspecifics.

It is unlikely that the disappearance of newly settled and early juvenile grunts from our study reefs could have resulted from emigration, since all recaptures of tagged individuals were made within a 5 m radius of their capture/release point (i.e., none were observed between 5 and 50 m from the release point). We therefore attributed disappearance of newly settled grunts to predation. While many newly settled and early juvenile grunts may have attempted emigration from reefs with high densities of predators and/or conspecifics, it seems unlikely that these individuals would have survived a migration of 200–300 m across open sand to the nearest neighbouring reef. Several studies have shown fish to be more vulnerable to predation on sand and other structurally simple habitats (Shulman 1985, Lough et al. 1989, Connell & Jones 1991, Tupper & Boutilier 1995c).

Numbers of older juvenile grunts did not differ between unfished and fished reefs. This pattern might suggest that larger juveniles are immigrating to the reserve from fished areas, since recruitment to the reserve was probably not sufficient to maintain stocks of older juveniles at levels similar to fished reefs. Why then are these older juveniles not subject to the same density-dependent predation as early juvenile settlers? First, the majority of piscivores are size-selective, concentrating on smaller size classes (Juanes 1994). Older juveniles may have reached a size at which they are less susceptible to predation. However, we saw no evidence of immigration of grunts <5 cm FL, and movement of older fish was not studied. An alternative and perhaps more parsimonious explanation of the similarity among reefs in older juvenile densities, is that larger size classes include more ages and cumulatively include more recruitment events, thus compensating for higher mortality. Mathematically, if there are fewer juveniles and more adults (or vice versa) on one reef than another, then at some size class the density on each reef will be roughly equal.

A marine reserve or reserves should be designed and situated with two primary goals in mind (e.g. Plan Development Team[1], Roberts & Polunin 1991). Reserves can be employed as fisheries enhancement tools, in which the primary objective is to provide an increased yield to the surrounding area. Alternatively, reserves can be employed as a conservation tool, in which the goal is to preserve or improve local stock size and structure, and to maintain or increase local biodiversity. If the primary goal is enhancement, then the reserve should be situated such that it provides a source of recruits to fished areas. If the primary goal is conservation, then the reserve should be situated in an area that receives an adequate supply of recruits, and where appropriate nursery habitat is available to ensure the survival of such recruits. Note that a reserve may have both goals as its mandate, in which case the reserve may cover a large area, or may be separated into several smaller sections (e.g., St. Lucia; B. Hatcher personal communication).

The usefulness of reserves in supplying or receiving recruits will depend to a large extent on oceanographic processes and their effects on the transport of eggs, embryos and larvae. Reef fish almost universally possess pelagic larvae which may last several weeks (Wellington & Victor 1989, Hunt von Herbing & Hunte 1991). Reef fish larvae can thus be transported hundreds of kilometres from their natal reefs (Williams et al. 1984, Frith et al. 1986). However, spatial scales of that transport vary greatly among regions, depending on local current patterns (Roberts & Polunin 1991). For example, studies around Hawaii and Lizard Island (Australia) have illustrated that larvae may be retained close to natal reefs (Lobel & Robinson 1986, Leis & Goldman 1987, Kobayashi 1989, Black et al. 1991). Isolated oceanic islands such as Barbados are more likely to be self-recruiting units, while coastal reefs and those of island chains may depend almost entirely on upstream populations as a source of recruits (Roberts & Polunin 1991). In Barbados, evidence has been found for self-recruiting populations of *Stegastes partitus* (Tupper 1989) and *Thalassoma bifasciatum* (Hunt von Herbing & Hunte 1991).

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[5] Lock, J.M. 1986. Effects of fishing pressure on the fish resources of the Port Moresby barrier and fringing reefs. Tech. Rep. 86/3, Department of Primary Industry, Fish. Div., Port Moresby. 31 pp.

In our study, mean recruitment was higher outside the reserve than within it, although density of newly settled (<2 cm FL) grunts was significantly higher than the overall mean only on specific reefs to the south of the reserve. Since we could find no evidence of postrecruitment emigration of very small fish, lower recruitment within the reserve was attributed to predation mortality. Although no other mechanism is needed to explain these results, the observed pattern of recruitment may be reinforced to some extent by local oceanographic conditions. Specifically, it is possible that reefs south of the Barbados Marine Reserve receive a greater supply of larvae than reefs within the reserve. Cowen & Castro (1994) reported the existence of an offshore current off the mid west coast of Barbados. According to their data, current flowing south from the northern tip and north from the southern tip of the west coast converge in the vicinity of the reserve and head offshore. This pattern may contribute further to the lower recruitment rates within the reserve. Ichthyoplankton samples taken over some of our study reefs suggest that settlement-ready larvae of several other families of reef fishes (Acanthuridae, Balistidae, Carangidae) share the same distribution as grunts, i.e., most abundant south of the reserve, least abundant within the reserve, and moderately abundant north of the reserve (I. Hunt von Herbing unpublished data).

Although differences in supply of larvae caused by local oceanographic conditions may well exist on the west coast of Barbados, they may or may not affect recruitment of grunts on the study reefs. The pattern of lower recruitment to the reserve, coupled with higher post-recruitment mortality within the reserve, indicates that the Barbados Marine Reserve likely acts as a sink for early juvenile grunts. Interestingly, the fact that reefs within the reserve may have been recruitment-limited, i.e. were undersaturated with larvae (sensu Doherty & Fowler 1994), did not prevent density-dependent predatory processes from occurring.

In summary, carnivorous fishes were larger and more common in the Barbados Marine Reserve than on exploited reefs. However, recruitment of grunts was much lower within the reserve than on nearby exploited reefs. Postrecruitment mortality was positively correlated with abundance of predators, including adult conspecifics. Thus, the lower density of juveniles within the reserve was attributed to predation, although settlement may also have been lower on reefs within the reserve due to local oceanographic conditions affecting supply of larvae. Abundance of older juvenile grunts did not differ between fished and unfished reefs. It appears that at some size/age, cumulative recruitment due to lower size-specific predation mortality results in higher densities of adult grunts within the reserve. Despite protecting the spawning biomass of large, carnivorous fishes, the Barbados Marine Reserve may act as a sink for early juvenile fishes. What began as a useful tool for conserving or improving the size and structure of local fish stocks, may now depress recruitment of reef fishes to the central west coast of Barbados.

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