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CORAL REEF FISH MOVEMENTS AND THE EFFECTIVENESS OF THE BARBADOS MARINE RESERVE

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Abstract

This study examined whether movements of fishes across reserve boundaries reduced the difference in density and size of fish between reserve and non-reserve areas. Visual censuses, experimental trapping, habitat measurements and tagging were performed at 10 sites on two nearly contiguous fringing coral reefs at the northern edge of the Barbados Marine Reserve and at 10 sites on the two fringing reefs closest to the boundary in the non-reserve. The visual censuses showed that overall density and size of fishes large enough to be caught in Antillean fish traps were higher on reserve reefs than on non-reserve reefs. The differences in density and size varied considerably among species and were not statistically significant for individual species. In contrast to a previous study, experimental trap catches were not higher in the reserve than in the non-reserve. Visual censuses, trap catches, and their ratio (trappability) were affected by habitat variables. Species mobility, estimated by the maximum distance between locations at which an individual was captured, corrected for the sampling effort at that distance, was highly variable among species (medians 0 - 116 m). For the more mobile species, movements within fringing reefs and between the nearly contiguous reserve reefs was high but extremely rare among reefs separated by expanses of sand and rubble. For this discrete fringing reef system, there is no evidence that movement across the reserve boundary influences the relative density or size of fish between the reserve and non-reserve.

Résumé

J'ai examiné dans cette étude si les mouvements des poissons entre les frontières des réserves diminuent la différence de densité et de taille des poissons entre des aires situées à l'intérieur et à l'extérieur des réserves. Des recensements visuels, un trappage expérimental, des mesures de qualité d'habitat ainsi que du marquage ont été effectués sur 10 sites de deux récifs coraliens presque contigus à limite nord de la Réserve Marine des Barbades ainsi que sur 10 sites de deux récifs coraliens situés près de la frontière, mais à l'extérieur de la réserve. Les recensements visuels ont démontré que la densité et la taille des poissons suffisamment gros pour être capturés à l'aide de trappes Antillaises étaient plus élevées à l'intérieur qu'à l'extérieur de la réserve. La différence de densité et de taille ont varié considérablement entre les espèces et n'étaient pas significatives pour les espèces prises individuellement. Contrairement à une étude antérieure, les captures dans les trappes expérimentales n'ont pas été plus élevées à l'intérieur qu'à l'extérieur de la réserve. Les recensements visuels, les captures des trappes, et leur rapport ont été influencées par des variables reliées à l'habitat. La mobilité des espèces, estimée par la distance maximale entre deux endroits où un poisson a été capturé, a été très variable entre les espèces (médianes 0 – 116 m). Pour les espèces les plus mobiles, les mouvements à l'intérieur des récifs ainsi qu'entre les récifs presque contigus de la réserve ont été élevés mais ont été rares entre les récifs séparés par des étendues de sable et de gravier. Pour ce système, il n'y a pas eu d'évidences que les mouvements entre les frontières de la réserve ont influencé la densité et la taille relative entre les aires situées à l'intérieur et à l'extérieur de la réserve.

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Preface

Data were collected by M.R. Chapman, with the help of D. Robichaud, D. Haggarty, I. Popple, J. Bauman, T. Bell, and H. Maggs. All data were analyzed by M.R. Chapman. D.L. Kramer made significant contributions in the development of hypotheses, planning of the field study, analysis of the data, interpretation of the results, and revisions of the manuscript. Sections of this thesis will be submitted for publication with D.L. Kramer as co-author.

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INTRODUCTION

Marine reserves provide a valuable tool for the conservation of coral reef ecosystems and the management of coral reef fisheries (Roberts & Polunin 1991, Dugan & Davis 1993, Rowley 1994). Coral reef fisheries are socially and economically important in many tropical countries, but are usually unregulated, and reef fish communities are often subject to severe over-exploitation (e.g., Munro 1983, Koslow et al. 1988, Mahon & Drayton 1990). The need to develop management strategies for such fisheries is critical. The multi-species, multi-gear, and decentralized nature of tropical coral reef fisheries, as well as the limited resources available for research, monitoring, and enforcement, render conventional approaches to fishery management impractical. The use of "no-take" marine reserves - i.e., the exclusion of all harvesting in defined areas of habitat - provides a more effective means for conserving and managing exploited reef fish assemblages (Plan Development Team [PDT] 1990, Hatcher 1995, Bohnsack 1996, Polunin et al. 1996).

Protection of fish stocks

By reducing fishing mortality, coral reef marine reserves can increase the density, mean size, biomass, and diversity of fishes relative to exploited areas. Many studies have documented significantly higher density, size, and biomass of fish populations and communities in coral reef marine reserves compared to adjacent fished areas (Roberts & Polunin 1991). Some studies comparing fish populations and communities at the same sites with and without reserve protection have also demonstrated the ability of coral reef marine reserves to maintain increased fish density, size, and biomass (e.g., Alcala & Russ 1990). In this study, we define the effectiveness of a reserve as its ability to maintain a higher density, mean size, or biomass of exploited taxa than surrounding fished areas. Here, reserve effectiveness is a measure of the effect of protective management on fish distribution or size-structure, and should not be equated with the success of the reserve in ecological or socio-economic terms.

Yield enhancement

By preventing growth, recruitment, and ecosystem overfishing (PDT 1990) within their boundaries, no-take marine reserves also have the potential to increase the yield of neighbouring coral reef fisheries, despite the reduction in fished area due to the establishment of the reserve (e.g., PDT 1990, DeMartini 1993, Nowlis & Roberts in press). Such yield enhancement may occur through two mechanisms: the export of larvae and the export of post-settlement fishes.

Coral reef marine reserves may contribute to the yield of adjacent fisheries by producing larvae that settle outside reserve boundaries. In reef fishes, like most marine fishes, fecundity increases geometrically with body size, and eggs and larvae are usually highly dispersive; after a pelagic stage, juvenile reef fish may settle onto reefs far from the site of spawning (Doherty & Williams 1988, Leis 1991). The increased density and size of fish within a reserve may lead to enhanced larval settlement over a much wider area. The life history characteristics of reef fishes (e.g., long life, slow growth, iteroparity, and the possibility for recruitment limitation) may render them especially vulnerable to recruitment overfishing (PDT 1990, Russ 1991).

Through the export of larvae, reserves may address recruitment overfishing over the spatial scale of larval dispersal (PDT 1990, Nowlis & Roberts in press, Bohnsack 1996).

Another proposed benefit is the net emigration, or spillover, of post-settlement reef fish to adjacent fished areas (Russ 1985, Polacheck 1990, Roberts & Polunin 1991, Russ et al. 1992). As fish density and size increase inside a reserve, the movements of post-settlement fish should result in net emigration from the reserve to the surrounding fishery. If population density is higher inside a reserve, random movement will result in the net flow of fish to the non-reserve area (Rakitin & Kramer 1996). Furthermore, habitat selection theory predicts that individuals will move from areas of high population density to low density if their fitness exhibits negative density-dependence (Fretwell & Lucas 1970, MacCall 1990). Thus, as population density increases inside a reserve, the per capita rate of emigration may increase (Schonewald-Cox & Bayless 1986). The increased body size of fishes within a reserve may also promote emigration (Russ et al. 1992) if the scale of fish movements increases with body size (Sale 1978).

Spillover of reef fish from marine reserves may address growth overfishing in reef fisheries by acting as a growth refuge, thus increasing fish yields (Russ 1985, PDT 1990, Russ et al. 1992). Modeling suggests that this will occur only under relatively narrow conditions of fish mobility and fishing mortality, and that yield enhancement will be slight compared to potential increases in yield from larval output (Polacheck 1990, DeMartini 1993, Nowlis & Roberts in press). Nevertheless, by exporting fish biomass directly to the adjacent fishery, spillover may provide local benefits and reduce the local socio-economic costs of reserve implementation (Russ & Alcala 1989, PDT 1990, Roberts & Polunin 1991). Spillover is sometimes cited as a benefit of reserves in order to persuade fishers that reserve implementation will enhance the yields of local fisheries despite forfeiture of access to fished areas (e.g., Hatcher 1995). Demonstration of the emigration of adult coral reef fishes from a reserve to an adjacent fishery could therefore be useful for proponents of reserve-based fishery management (Roberts & Polunin 1993, Rowley 1994). However, there is an inherent trade-off between the benefits of enhanced reproductive output and spillover (PDT 1990, Rakitin & Kramer 1996). Enhanced reproductive output requires a resident population of fish that stays inside a reserve and is thus protected from fishing mortality, such that higher density and a more natural population size-structure can develop. Conversely, the emigration of post-settlement fish requires movement of fishes from the reserve to the surrounding fishery.

Mobility of coral reef fishes

The degree to which the proposed benefits of reproductive output and spillover will be realized depends on the rate of post-settlement fish movements across the reserve boundaries. For highly sedentary fish (i.e., those with small home ranges and which relocate home ranges infrequently), a reserve will provide protection from fishing mortality, maintain high spawner biomass, and may provide enhanced reproductive output, but will provide little spillover of post-settlement fish to an adjacent fishery. For fish with intermediate movement rates across a reserve boundary, reserves should be moderately effective at maintaining a higher density and size of fish, and spillover may enhance local yield in the adjacent fishery. For highly mobile fishes, movement of fish across reserve boundaries may prevent the increase in fish density and size required in order for spillover to occur (Rakitin & Kramer 1996; Figure 1). Yield enhancement by the reserve is the sum of spillover and reproductive output; thus, spillover may reduce the fisheries benefits of marine reserves – especially over larger spatial scales – by compromising reproductive output. Where growth overfishing predominates and fishery yield is not limited by larval supply, spillover will provide a net benefit to the adjacent fishery. Movements of post-settlement fishes will therefore affect both the ability of reserves to protect stocks within their boundaries and the spatial scale and magnitude of benefits to reef fisheries (Figure 2).

Many exploited coral reef fishes have the potential to move across marine reserve boundaries. Post-settlement coral reef fishes are generally considered highly sedentary (e.g., Bardach 1958, Ehrlich 1975, Sale 1991), and many reef fishes remain within very limited home ranges or territories, sometimes as small as 1 m^2 (Low 1971, Sale 1971, Luckhurst & Luckhurst 1978a, Bartels 1984). Tagging studies and direct observations reveal, however, that reef fish home ranges actually vary in size by four orders of magnitude (Kramer & Chapman submitted) and many exploited reef fishes have home ranges that are large relative to the size of coral reef marine reserves (e.g., PDT 1990, Holland et al. 1996, Corless et al. in press). The home ranges of some reef fishes consist of two or more disjunct areas, necessitating diel migrations between feeding and sleeping sites (e.g., Hobson 1973, Ogden & Ehrlich 1977, Holland et al. 1993, Tulevech & Recksiek 1994), and some undertake spawning migrations far beyond their daily home ranges (e.g., Johannes 1981, Colin et al. 1987, Myrberg et al. 1988). As resource levels and requirements change, fish may benefit by relocating home ranges, and may thus move outside of their daily home ranges for the purpose of habitat assessment and home range relocation (Kramer et al. 1997). For example, many exploited reef fishes exhibit evidence of ontogenetic habitat shifts (e.g., Robertson et al. 1979, Shulman & Ogden 1987, Roberts & Ormond 1992, Sluka et al. 1994, McAfee & Morgan 1996), and some fishes have demonstrated an ability to relocate in response to changes in resource levels or the competitive environment (e.g., Bartels 1984, Wellington & Victor 1988).

The distribution of reef habitat relative to reserve boundaries will affect the movement of fishes across the boundaries of marine reserves. Expanses of unsuitable habitat (e.g., sand or deep water) between protected and exploited reef habitats may constitute natural barriers to movement and decrease spillover (Robertson 1988, Roberts & Polunin 1991). Reserve shape may also influence spillover; spillover is likely to be higher for reserve shapes with high edge:area ratios and higher for several small reserves than from a single large reserve. Reserve shape should have less of an effect where reserve boundaries coincide with natural barriers to movement (Buechner 1987, Stamps et al. 1987, DeMartini 1993).

Evidence of spillover from coral reef marine reserves

There have been few direct estimates of the spillover of coral reef fishes from marine reserves. Fishers recaptured 7% of goatfish (Mulloidichthys flavolineatus) tagged inside a 137 ha no-take reserve in Hawaii (Holland et al. 1993). One third of marked omilu (Caranx melampygus) recaptured after a mean of five months emigrated from the same reserve (Holland et al. 1996). At the Soufriere Marine Management Area in St.Lucia, W.I., marked jacks (Carangidae) and Creole wrasse (Clepticus parrae, Labridae), as well as a small proportion of surgeonfish (Acanthuridae), filefish (Balistidae), goatfish

(Mullidae), and parrotfish (Scaridae), moved across marine reserve boundaries (200 m from tagging sites) in an area of continuous reef habitat (Corless et al. in press). Direct evidence of emigration from reserves has been reported for fishes in estuarine (e.g., Funicelli et al. 1988) and temperate surf-zone (e.g., Attwood & Bennett 1994) habitats, and for invertebrates (e.g., Gitschlag 1986; reviews by Rowley 1994 and Bohnsack 1996).

There has also been indirect evidence of spillover of coral reef fishes from marine reserves, and fish movements have been hypothesized as a factor influencing reserve effectiveness in several studies (Buxton & Smale 1989, Cole et al. 1990, Alcala & Russ 1990, Watson & Ormond 1994, Polunin & Roberts 1993). Alcala & Russ (1990) measured an increase in the yield of reef fishes outside the Sumilon reserve, Philippines, and hypothesized that this was the result of emigration from the reserve. Russ & Alcala (1996) demonstrated a gradient of abundance of large, predatory fishes outside a coral reef marine reserve boundary at Apo Island, Philippines, which they interpreted as evidence of export of adult fish biomass from the reserve.

Rakitin & Kramer (1996) investigated the distribution of reef fishes in and around the Barbados Marine Reserve (BMR), a no-take reserve on the fringing coral reefs on the west coast of Barbados, West Indies. They found a significant increase in the density and catch rate of fish inside the BMR. Furthermore, they showed that the catch rate did not change suddenly at the reserve boundary. Rather, there was a gradual decline in catch with increasing distance from the centre of the BMR, which they hypothesized was a result of movement of fishes from the area of higher density to the fished area. This trend was not evident in visual censuses or in the catch rate of individual species, however. Rakitin & Kramer (1996) hypothesized that, if fish movements were causing this gradual decline, reserve effectiveness should be higher for sedentary species. Their preliminary test of this hypothesis (in which species were classified as either "mobile" or "sedentary" based on literature reports) showed no effect of mobility on reserve effectiveness.

Direct measures of the movement of coral reef fishes relative to marine reserve boundaries are needed in order to assess the importance of post-settlement movements on the ability of coral reef marine reserves to conserve fishes and supply emigrants to adjacent reef fisheries (PDT 1990, Roberts & Polunin 1991, Rakitin & Kramer 1996, Roberts 1996).

Goals

The principal goal of this study is to test the hypothesis that reserve effectiveness is negatively correlated with the mobility of species. The mobility of exploited reef fishes and their rate of movement across the BMR boundary were assessed through a mark-recapture study at two reefs in the BMR and two reefs in the non-reserve (NR). Direct behavioural observations of short-term movements were also performed to provide an independent measure of the mobility of diurnally active species. The effectiveness of reserve protection from fishing mortality was measured over the same spatial scale by comparing the density and size of exploited fishes between BMR and NR study sites.

Evaluations of reserve effectiveness which compare fish communities in reserves with those in adjacent fished areas may be confounded by differences in habitat quality between the two areas (e.g., Polunin & Roberts 1993, Grigg 1994). The spatial distribution of many reef fishes is correlated with variation in characteristics of the reef habitat such as topographic complexity (e.g., Luckhurst & Luckhurst 1978b) and coral cover (e.g., Bell & Galzin 1984). Reserve sites are often chosen for their high initial habitat quality or fish abundance (e.g., Russ 1985). Thus, measures of reserve effectiveness based on spatial comparisons of reserves with unprotected fished areas should account for differences in habitat correlates of fish density and size (e.g., Grigg 1994, Jennings et al. 1996). Rakitin and Kramer (1996) did not test for the effects of habitat variables on fish density or catch rate; the spatial gradient in catch rate observed may have been due to spatial gradients in habitat correlates of density or catch rate. In this study, the effects of habitat correlates of fish density and size are controlled for statistically when assessing reserve effectiveness.

The vulnerability of exploited taxa to fishing gear will also affect reserve effectiveness. Fishes subject to higher fishing mortality in the NR are expected to exhibit a greater differential in density and size between the BMR and NR. In this study, the catch rate of exploited taxa in Antillean fish traps (the principal gear type of the Barbados reef fishery) is measured in the BMR and in the NR in order to (i) provide an alternative measure of reserve effectiveness, (ii) estimate the vulnerability of species to capture in traps, and (iii) investigate how this measure of vulnerability varies with behavioural and ecological factors.

METHODS

Study sites

The study took place on the west (leeward) coast of Barbados, W.I. from November 1995 to June 1996. Along this coast, a series of fringing coral reefs extends up to 300 m from shore, to a depth of about 10 m. The physiography of the coast has been described by Stearn et al. (1977) and the zonation of fringing reefs by Lewis (1960) and Rakitin (1994). The study sites were located on four fringing reefs along the west coast, two reefs inside the BMR (South Bellairs and North Bellairs reefs) and two reefs in the adjacent NR (Heron Bay and Bachelor Hall reefs). These fringing reefs are separated by extensive (20–100 and 150–300 m) patches of sand, rubble and small patches of rocky reef (< 10 m^2), except the two reserve reefs, which are essentially contiguous, separated by a narrow sand channel as little as 10 m across (Figure 3).

The BMR consists of 2.2 km of protected waters along the central west coast of Barbados and includes 5 fringing reefs. The reserve extends seaward 500-750 m to include portions of an offshore bank reef system. The BMR was established in 1981 and legislation prohibits the dynamiting of reefs and the harvesting of corals, invertebrates and fishes, with the exception of cast-netting for clupeids (St.Hill 1987). Illegal fishing, including spearfishing and line-fishing from boats and shore, occurs to some extent in the BMR (Rakitin 1994, pers. obs.).

Fringing reefs in the adjacent NR experience light exploitation from spearfishing, line-fishing, and from an artisanal trap fishery (Miller & Hunte 1987, Mahon & Drayton 1990, Rakitin 1994, pers. obs.). The principal gear-type of the Barbados demersal reef fishery is the Antillean fish trap (Miller & Hunte 1987), described in detail by Munro et al. (1971). In Barbados, traps are built of wire mesh supported by a wooden frame with a single entrance funnel through which fish enter and, less frequently, exit. Traps are set baited or unbaited on reef, rubble or sandy substrates for several days before hauling and emptying. Mahon & Drayton (1990) estimated there were approximately 200 full- and part-time trap fishers on the West and South coasts of Barbados. Based on interviews with local fishers, Rakitin (1994) estimated that 40 - 60 traps were set and hauled twice per week on the 7 fringing reefs to the north of the BMR. During the present study, fishing effort outside the northern BMR boundary appeared to be low; we observed occasional spearfishing and line fishing, and only 2 trap sets on our 2 non-reserve study reefs over a period of 12 weeks. Several instances of illegal line-fishing within the BMR were also observed, mainly at night and in the early morning.

Measurement of fish distribution (trapping and visual censuses) and of habitat variables took place at 20 study sites, five on each of the four study reefs. An additional three sites were included in the mark-recapture study, for a total of 23 sites (Figure 3). Sites were 20 x 20 m in planar area and included reef, rubble and sandy substrate. All sites were located seaward of the reef crest, in the spurs-and-grooves zone of the fringing reefs (Lewis 1960). Site depth ranged from 1.9 to 8.2 m (mean depth = 4.9 m).

The distance between the centres of sites on the same reef was measured using a 50-m measuring tape and an underwater compass. Site maps for each reef were then superimposed on an aerial photograph of the fringing reefs. The resultant composite map was scanned and the distance between the centres of sites on separate reefs was calculated using MapInfo (MapInfo Corporation). The distance between site centres ranged from 22 to 1086 m.

The position of each site was defined as the distance (m) from the centre of the site to the northern BMR-NR boundary; BMR sites have negative values and NR sites have positive values (Figure 3).

The field study consisted of three components: (i) sampling of fish distribution and size structure by visual censuses and trap catches, in order to assess the effectiveness of the BMR and the vulnerability of species to fish traps, (ii) measurement of habitat variables in order to determine and control for habitat correlates of fish density and size, and (iii) measurement of the mobility of reef fishes in order to measure spillover from the BMR and to test the hypothesis that the reserve is less effective for more mobile species.

I. Fish distribution and size

Visual censuses

The density and size structure of the reef fish assemblage in the BMR and NR were sampled by visual census at twenty sites, five on each of the four study reefs (Figure 3). Using SCUBA, an observer (MRC) performed three replicate censuses at each site. Censuses at the same site were approximately one lunar quarter apart. All censuses took place between 10:00 and 17:00 AST from February to June 1996. The order of visual censuses was selected randomly, with the constraint that an equal number of reserve and non-reserve sites were sampled each lunar quarter. Visual censuses were performed on days when the experimental traps used to measure catch rate and fish movements (see below) were not fishing.

During visual censuses, the observer counted the number of individuals (≥ 5 cm FL) of 47 species of fish which are large enough to be caught in commercial Antillean fish traps (trappable species). The perimeter of each census area was marked with flagging tape, and counts were made along a series of contiguous unmarked transects (~ 3 m wide), approximately parallel to shore, within the census area. To decrease the time required for visual censuses, we excluded the 5 abundant and marginally trappable species of Stegastes (Pomacentridae) from our counts. These fish rarely enter traps and are probably subject to very low fishing mortality, so their distribution is unlikely to be directly affected by reserve status (Rakitin & Kramer 1996, Robichaud 1996). Thirty-eight of the 47 trappable species were recorded in visual censuses.

During censuses, the fork lengths of all fish were estimated to the nearest centimetre. Training for underwater length estimation occurred two ways. First, the length of measured sections of PVC piping along an underwater line were estimated. Second, the fork lengths of fish in traps were estimated immediately prior to hauling and measurement. In both cases, observers subsequently compared their estimates to measured values, and continued training until the mean of the absolute value of estimation error was consistently below 10%. Underwater length estimation of tagged fish during surveys (see Visual recaptures, below) indicated that estimated fork length was highly correlated with fork length measured at the time of tagging ($r^2 = 0.92$, $p < 0.0001$, mean (± SD) estimation error = 3.6 (± 4.0) %, N = 896).

Visual census data were subsequently divided into trappable and non-trappable fish based on estimated fork lengths using body depth - fork length relationships from catch data from traps at the study sites (Robichaud 1996). Fish with a predicted body depth greater than the 4.1 cm maximum mesh aperture of the commercial Antillean fish traps were considered trappable. Using this estimate of minimum trappable fork length is likely to underestimate the actual minimum length of captured fish because many fish appear to be able to squeeze through the mesh (Robichaud et al. in prep.). This should make our comparison of the size and density of fish in the BMR and NR conservative; i.e., it will tend to include non-trappable fish which should not be directly affected by the reduction of trap-fishing mortality in the BMR. Conversely, a small number fish shorter than the estimated minimum fork length are sometimes retained in traps, although this contributes little to the total catch.

For three species, there were too few captures to estimate the minimum trappable FL so visual census data for these species were excluded from analysis (glasseye snapper, Priacanthus cruentatus, $N_{BMR} = 7$, $N_{NR} = 3$; whitespotted filefish, Cantherhines macrocerus, $N_{BMR} = 2$ $N_{NR} = 0$; greater soapfish, Rypticus saponaceus, $N_{BMR} = 6$, $N_{NR} = 11$). Therefore, 35 of the 38 species observed were included in analyses of visual census data.

To quantify the effectiveness of the reserve in maintaining increased fish density relative to the non-reserve, and to compare reserve effectiveness among species, we calculated the relative difference in fish density (RDD) between the BMR and NR for 26 species counted in the BMR and NR,

$$RDD = (N_{BMR} - N_{NR}) / (N_{BMR} + N_{NR}),$$

where N_{BMR} and N_{NR} are the mean densities in the BMR and NR, respectively. This index of effectiveness ranges from -1 to +1, where positive values indicate higher reserve density, and scales symmetrically about zero (equal density).

Similarly, the relative difference in size (RDS) between the BMR and NR was calculated for 26 species recorded in visual censuses in the BMR and NR,

$$RDS = (FL_{BMR} - FL_{NR}) / FL_{MAX},$$

where FL_{BMR} and FL_{NR} are the median fork lengths of fish in the BMR and NR, respectively, and FL_{MAX} is the maximum recorded length of the species according to Humann (1994).

Trap catches

The density and size distribution of fishes was also assessed by experimental trapping. Commercial Antillean fish traps were placed at the centre of each of the 20 400 m^2 visual census areas. Traps were placed on sand or rubble substrate no farther than 2 m from a reef spur. Each trap was modified by the addition of a hinged door which could be opened to allow fish to exit easily. Thus, traps could be opened underwater at the end of a bout of fishing, and left open until the next soak, when they could be closed underwater and set in the fishing position (Robichaud 1996).

On the first day of a quarter-lunar cycle, experimental traps were closed and set in the fishing position. After four days, the number and fork length of fish of each species in each trap was noted underwater. Traps were either opened underwater on the fourth day, or were hauled on the following day for fish measurement, tagging of fish for the mark-recapture study, or verification of the tag codes of recaptured fish (see Mark-recapture study, below). Traps were left open until the beginning of the next trap set. From three to eleven trap sets were made at each of the 20 study sites (total N = 126).

Mean catch rate at a site was defined as the mean number of individuals caught per trap set. We also calculated the relative difference in catch rate (RDC) between the BMR and NR,

$$RDC = (C_{BMR} - C_{NR}) / (C_{BMR} + C_{NR}),$$

where C_{BMR} and C_{NR} are the mean catch rates in the BMR and NR (i.e., mean of 10 site means), respectively. RDC was calculated for the total catch and separately for each species caught in both the BMR and NR.

Trappability

Trapping provides a non-destructive method of sampling cryptic and nocturnal fishes and those which avoid divers. However, the exact relationship between catch rates and local density, and how this relationship may vary among species, is unknown. It will depend on fish behaviour and may vary with habitat characteristics (Munro 1974, Robichaud 1996, Wolff 1997). Trappability is defined as the ratio of catch rate (mean number of fish caught per trap set) to fish density (estimated by the mean visual census density of trappable-size fish) and provides a measure of the vulnerability of species to Antillean fish traps. Estimates of trappability are therefore dependent on the sampling efficiency of visual censuses: trappability may be overestimated for diurnally cryptic fishes, for fishes that avoid divers, and in sites where habitat features reduce the visibility of fishes. Trappability at each site, as well as for all BMR sites pooled, all NR sites pooled, and for all 20 sites pooled, was estimated for 24 species for which there were adequate catch and visual census data. The estimated trappability of a species at all NR sites pooled was considered an index of the vulnerability of that species to trap-fishing mortality in the NR.

The epinepheline serranids (*Epinephelus cruentatus* and *E. fulvus*), *Kyphosus sectatrix*, *Lutjanus mahogani*, and the larger scarids (*Scarus vetula* and *Sparisoma viride*) are targetted by spearfishers on fringing reefs on the west coast o Barbados (Rakitin 1994, pers. obs.), and were thus classified as spearfishing target taxa.

ii. Habitat characteristics

To control for potential habitat correlates of fish distribution, we measured abiotic and biotic substrate composition, habitat structural complexity (rugosity), and depth at each of the 20 census areas, during June 1996. Habitat variables were measured by performing three point-count transects within each census area (CARICOMP 1994). For each transect, a 14-m chain was placed on the substrate parallel to shore at a randomly selected distance from the inshore edge of the census area. The abiotic and biotic substrate type under the transect chain was sampled at points 20 cm apart (N = 210 observations per site). Abiotic substrate was classified as reef (solid rock), rubble (loose fragments of rock 1 – 100 cm long), or sand (loose particulate sediment; ≤ 1 cm maximum dimension) and percent reef, percent rubble, and percent sand cover were calculated for each site. Biotic substrate was classified as turf algae (≤ 1 cm height; CARICOMP 1994), encrusting coralline algae, fleshy macroalgae, live coral (all species), other live cover (anemones, hydroids, and encrusting and erect gorgonians and sponges), or bare (uncovered sand, rubble or reef). Percent live coral was defined as the number of observations of live coral at a site divided by the sum of reef and rubble observations at a site (since live coral was never observed on sand). Percent algal cover was defined as the number of observations of turf algae and fleshy macroalgae at a site divided by the total number of observations at a site. Turf algae accounted for 99.3% of algal cover, and was present on reef, rubble, and sand. Rugosity was defined as the length of the three transects (42 m) divided by sum of the horizontal distances covered by the three transects (Luckhurst & Luckhurst 1978). To measure the horizontal distance between the endpoints of each transect, divers raised the transect chain above the substrate and pulled it taut. The minimum and maximum substrate depth were measured along each of the three transects. Site depth was defined as the mean of these six depth measurements.

If habitat quality is higher in the reserve, collinearity between reserve status and habitat variables could result in spurious significant effects of reserve status on fish density and size. We therefore tested for significant effects of habitat characteristics on fish density by performing backwards stepwise multiple regressions (Zar 1996), excluding reserve status from the set of potential independent variables. We subsequently examined residual variation in density and size to test for an effect of reserve status. This is a more conservative test of the reserve effect than including reserve status in the multiple regression model, since it may attribute an actual reserve effect to habitat variables, but it will not attribute an effect of habitat variables to reserve protection. Residual variation in density and size was used to calculate the predicted BMR and NR density and size for a hypothetical site with mean (or geometric mean) values of all habitat variables.

III. Fish movements

Mark-recapture study

In order to measure the movements of trappable reef fishes, we performed a mark-recapture study at the four study reefs. Fish were captured in traps at 23 sites in the BMR and NR (the 20 visual census sites, plus three additional sites on North Bellairs reef in the BMR; Figure 3). Traps were hauled and the fish placed in a cooler of fresh seawater. Fish were then removed from the holding cooler in haphazard order and measured (fork and total lengths to the nearest 0.5 cm). Fish 13 cm FL and longer were tagged using modified Floy™ FD-68B anchor tags (Floy Mfg. Co.) and immediately released within 20 m of the capture site. Tags measured 25.4 mm long from tip to anchor, with 12.5 mm of 1.5 mm diameter tubing at the free end. Tags were inserted in the dorsal musculature below the dorsal fin. The total time required to measure and tag each fish was less than 30 s, and the total handling time at a site was usually less than 30 min. Tags were colour-coded, and the insertion position of the tag (left- or right-hand-side) and the two-colour combination indicated the site and date of tagging ("tag code"). Tags were also individually numbered ("tag number").

A total of 1443 fish from 35 species was tagged over 6 tagging bouts from February to March 1996, in addition to a preliminary tagging bout in November 1995. Fish captured at all 23 BMR and NR sites were tagged in each 2-day tagging bout, and the order in which sites were tagged (North-to-South or South-to-North) was reversed each bout.

The movements of tagged fish were assessed by trap recaptures and visual recaptures, over a period of three lunar months from February to May, 1996.

Trap recaptures

On the first day of each quarter-lunar cycle, traps at all 23 capture sites were closed underwater and set in fishing position. Observers inspected each trap daily, noting the species, tag code and tag number, and estimated fork length of all tagged fish in each trap. Traps were opened underwater after four days or hauled on the following day and all tagged fish recorded and released at that site. Traps were left open until the first day of the following quarter-lunar cycle.

Visual recaptures

The 400 m^2 area around each of the 23 release sites was surveyed for tagged fish once each quarter-lunar cycle for 10 quarter-lunar cycles over the three lunar month period. Using SCUBA, an observer swam slowly over the survey area, carefully checking recesses and overhangs, and noting the species, tag code, and estimated fork length of all tagged fish observed within the survey area. "Visual recaptures" (Matthews & Reavis 1990) did not allow for the identification of individuals within a species, since it was difficult to read the tag numbers of freely swimming fish.

Analysis of recapture data

For both trap and visual recaptures, the position of each recaptured fish was defined as the position of the trap; i.e., the centre of each 400 m^2 area. Thus, fish visually recaptured at the site of initial release were considered to have moved 0 m, and fish which moved to adjacent sites were considered to have moved the inter-trap distance. The distribution of possible recapture distances was thus identical for visual and trap recapture data.

Correction for bias due to the distribution of recapture effort

Due to the distribution of recapture points within the study area, the proportion of reef area sampled decreases with the distance from each release point, for both traps and visual recapture surveys (Barrowclough 1978, Baker et al. 1995). As the distance moved by a fish increases, the probability of detecting such movement decreases, reaching zero beyond the maximum inter-trap distance. Thus, mark-recapture data will tend to underestimate the relative frequency of longer movements. This will in turn affect estimates of the central tendency of species' movement distances.

To correct for this bias, we calculated a series of correction factors at successive 20 m distance intervals from each release point. For each release point and distance interval, the correction factor (c) is defined as:

$$c = a_r / a_s ,$$

where a_r is the planar area of reef habitat and a_s is the planar area sampled in that distance interval (Baker et al. 1995). The correction factor, c, is thus the inverse of the proportion of reef habitat sampled in each distance interval.

The area sampled at each site (a_s) was considered to be 400 m^2 for both trap and visual recaptures. Reef area (a_r) was calculated from the scanned site map using MapInfo (MapInfo Corporation). Although there are patches of sand and rubble within the boundaries of the fringing reefs, any area within the outer reef boundary was considered reef habitat (shaded areas in Figure 3). Small patches of reef and rubble between the study reefs were not clearly discernible in the aerial photographs and were not included in calculation of reef area. The analysis assumed that all between-reef habitat was unsuitable; i.e., fish could move among reefs but would not be recaptured there. Measurement of reef area also excluded habitat seaward of the fringing reefs (e.g., the offshore bank reef). An additional fringing reef to the north of the study reefs was included in the calculation of reef area (not shown in Figure 3) since it was within the range of observed movement distances (616 m). The nearest fringing reef to the south of the BMR study reefs was outside the range of observed movements (approximately 1 km away). The correction factors ranged from 1.4 to 18.6 and generally increased with increasing distance from a given release point. In analyses of fish movements, observed movement distances are weighted by their respective correction factors when calculating measures of central tendency.

Measures of species mobility

Since the tag numbers of fish in traps could be read underwater (and verified in trap hauls), trap recaptures provided data on the movements of individual fish. There were too few recaptures (max = 11 per fish) and recapture locations (max = 5 per fish) to calculate home range areas for individual fish. For each recaptured individual, we calculated the linear distance between the two farthest capture locations (including the site of tagging), subsequently referred to as the "maximum inter-trap distance" (MTD) of that individual.

For some species, the MTD tended to increase with the number of recaptures. In order to standardize for the number of recaptures, a weighted regression of MTD against number of recaptures was performed for the thirteen species with adequate sample size (≥ 10 recaptured individuals) and range in the dependent variable (5 or more recaptures of at least one individual). The data points were weighted by the correction factors (c) corresponding to the MTD of each individual. For the 6 species where the slope of the weighted linear regression was significant ($p_{slope} < 0.05$), the MTD predicted after five recaptures was used as the trap recapture-based mobility estimate (the "standardized MTD") for the species. For the remaining 7 species, the linear regression was not significant ($p_{slope} > 0.05$), so the weighted median of the MTDs was used as the trap recapture-based mobility estimate (standardized MTD) for the species.

For visual recaptures, all recaptures of a given species were pooled, and the weighted median distance between the site of tagging and the site of visual recapture (the weighted "median visual recapture distance", or "MVD") was calculated for each species. Median visual recapture distances (MVDs) should be less than maximum inter-trap distances (MTDs) since the former are based on the distance from the point of initial capture to subsequent recaptures, whereas the latter are based on the maximum distance between any two captures of an individual.

Tag loss

A subset of tagged fish from 11 species was double-tagged in order to estimate rates of tag loss. Appendix 1 describes the methods used and provides the resultant estimates of the rate of tag loss for three families (Acanthuridae, Haemulidae, and Serranidae).

Homing experiment

In order to assess whether common trappable fishes were capable of homing across the large expanse of sand between the BMR and NR, 152 fish from 9 families were captured in the BMR and NR, tagged, displaced across the BMR boundary, and released. Displaced fish were recaptured over a period of five days. Appendix 2 describes the methods and results of the homing experiment.

Short-term mobility

In order to provide an alternative estimate of reef fish mobility, the short-term mobility of 22 diurnally active reef fish species was assessed by following randomly selected focal individuals in the field ($N \geq 8$ individuals per species). Selected fish were followed for two minutes when possible ($N = 201$). Otherwise ($N = 40$), the duration of the observation period was recorded. Care was taken not to influence fish movements; if it was suspected that the fish was avoiding or attracted to the observer, the observation period was discontinued and a new fish selected. A weighted marker was dropped at the beginning and end of the observation period and whenever fish changed directions. At the end of the observation period, the total distance between successive markers and the net displacement were measured. Distance and displacement data were divided by the duration of the observation period and expressed as speed and velocity, respectively.

Data analysis

Fish density, size, catch, and habitat data were tested for normality (Shapiro-Wilk test; Zar 1996), and were $\log_{10}$-transformed if significantly non-normal. Where transformation did not result in normality, non-parametric tests were used. Regression analyses were tested for normality of residuals using the Shapiro-Wilk test and for excessive leverage ($D > 0.5$) using Cook's test. Where the same hypothesis was tested for several species, α was adjusted using the sequential Bonferroni procedure (Rice 1989); adjusted significance levels are given. Multiple regressions of habitat correlates of fish density and size were performed using the backwards stepwise procedure (Zar 1996) of JMP (SAS Institute). Multiple regression models were considered significant for $p < 0.05$; however, adjusted significance levels (sequential Bonferroni procedure) are given as well.

RESULTS

Fish density and size

The density of trappable fish in visual censuses was significantly higher in the BMR than in the NR (ANOVA $F = 10.84$, $p < 0.005$, $df = 1, 18$; $\log_{10}$-transformed density). There was a geometric mean density of 94.6 fish per

400 m^2 in the BMR and 54.4 fish per 400 m^2 in the NR, giving a relative difference in total fish density (RDD) of 0.27. Figure 4 shows the pattern of fish density as a function of site position. The linear regression of density against position is highly significant ($r^2 = 0.44$, $F = 14.02$, df = 1, 18; $p < 0.005$), although the ANOVA (i.e., a step-function split at the reserve boundary) explains a similar amount of the among-site variance ($r^2 = 0.38$). There was no significant linear relationship between density and position within the BMR ($r^2 = 0.08$, $F = 0.69$, df = 1, 8; n.s.) or the NR ($r^2 = 0.23$, $F = 2.43$, df = 1, 8; n.s.).

There was no significant difference in the density of non-trappable size fish between the BMR and NR (ANOVA $\log_{10}$-transformed density $r^2 = 0.00$, $F = 0.07$, df = 1, 18; n.s.).

Of the 26 species counted in both the BMR and NR, trappable fish from 24 species had a higher mean density in the reserve (sign test, $p < 0.001$); however, the difference in density between the BMR and NR was statistically significant for only 1 species (Scarus iserti; Wilcoxon test, Bonferroni-adjusted $\alpha = 0.002$; Table 1). The relative difference in the density (RDD) of individual species ranged from -0.10 (Myripristis jacobus) to 0.89 (Kyphosus sectatrix). The density of each species at each site is given in Appendix 3.

Five species (Acanthurus bahianus, A. coeruleus, Haemulon chrysargyreum, H. flavolineatum, and Microspathodon chrysurus) accounted for 77 % of the total visual census density of trappable fish (Appendix 3). None of these species had a significantly higher density in the BMR than in the NR.

The mean size of trappable fish was significantly higher in the BMR than in the NR (ANOVA $F = 30.83$, df = 1, 18; $p < 0.0001$). Mean fork length was 15.3 cm in the BMR and 13.8 cm in the NR – a relative difference in size

(RDS) of 0.05. There was a significant negative correlation between mean size and position relative to the reserve boundary ($r^2 = 0.64$, $F = 32.2$, df = 1, 18; $p < 0.0001$; Figure 5) although reserve status explained as much of the among-site variance in fish size ($r^2 = 0.63$) as did position. There was no significant effect of position on mean fish size within the BMR ($r^2 = 0.07$, $F = 0.59$, df = 1, 8; n.s.) or within the NR ($r^2 = 0.14$, $F = 1.26$, df = 1, 8; n.s.).

Twenty-three of 26 species had a greater mean length in the BMR than in the NR (sign test $p < 0.001$), and this difference was significant for 5 species (Wilcoxon test, Bonferroni $\alpha = 0.002$; Table 2). The relative difference in size (RDS) ranged from -0.16 (Caranx ruber, N = 31) to 0.14 (Epinephelus cruentatus, N = 27). The larger scarids, the epinepheline serranids, the lutjanid Lutjanus mahogani, and the kyphosid Kyphosus sectatrix exhibited the largest relative differences in size between the BMR and NR (Figure 6). Appendix 4 contains size frequency distributions for the BMR and NR for the 20 most abundant species.

Habitat correlates of fish density

There was no significant difference in site depth, rugosity, live coral cover, algal cover, percent sand, percent reef, or $\log_{10}$-transformed percent rubble between the BMR and the NR (ANOVA, df = 1, 18; $p \geq 0.16$); however, the five most rugose sites, the four deepest sites, and the three sites with the highest coral cover were in the BMR (Figure 7). Percent rubble and percent reef were slightly, but not significantly, lower in the reserve than the non-reserve (Figure 8) and showed no clear trend with respect to position. Appendix 5 lists the value of each habitat variable at each site.

Deeper sites and sites with greater proportion of reef and rubble substrate had higher total densities of trappable fish. Multiple linear regression of total visual census density against habitat variables showed significant effects of both percent sand ($F = 10.28$, $p < 0.01$) and site depth ($F = 6.77$, $p < 0.05$) on $\log_{10}$-transformed visual census density (whole model: $r^2 = 0.41$, $F = 5.79$, $df = 2, 17$; $p < 0.05$).

There was a significant relationship between the visual census density of 18 of 26 species and one or more habitat variables (Table 3). Table 4 lists the predicted BMR and NR density of these 18 species at a hypothetical site with mean values for all measured habitat values. After controlling for habitat correlates of density, 14 of 18 species had a higher predicted density in the BMR (sign test, $p < 0.05$), but there was no significant effect of reserve status on fish density for any of the 18 species individually (Wilcoxon test, Bonferroni $\alpha = 0.0027$; Table 4). The predicted relative difference in density of these species ranged from -0.21 to 0.43 (Table 4). All eight species for which there was no significant relationship between visual census density and any habitat variable had a non-significantly higher density in the BMR than in the NR (Table 1). Thus, 22 of 26 species had a non-significantly higher density in the BMR after correcting for habitat correlates of fish density (sign test, $p < 0.001$).

For a site with mean values for all habitat variables, the predicted total BMR density is 70.5 trappable fish per 400 m^2 and the predicted total NR density is 49.8 trappable fish per 400 m^2 (Table 4). The predicted total density was significantly higher in the BMR than in the NR ($r^2 = 0.23$, $t = 2.34$, $df = 1, 18$; $p < 0.05$) but not significantly correlated with position relative to the reserve boundary ($r^2 = 0.20$, $df = 1, 18$; $p < 0.10$) (Figure 9). After correcting for habitat correlates of species density, the predicted relative difference in total fish density (predicted RDD) is 0.17. The variance in fish density among sites was therefore only partially accounted for by measured habitat variables; after controlling for habitat correlates of density, there is a significant effect of reserve status on total fish density.

Habitat correlates of fish size

There was a significant linear relationship between mean fork length at a site and one or more habitat variables for 14 of 26 species (Table 5). After controlling for habitat correlates of size, there was no significant effect of reserve status on residual variation in size for any of these 14 species (Wilcoxon test, Bonferroni adjusted $\alpha = 0.0036$). Table 6 lists the predicted mean BMR and mean NR fork lengths for a site with mean values of measured habitat variables. Eleven of 14 species had a higher predicted mean fork length in the BMR (sign test, $p < 0.05$), although the differences were slight. The corresponding predicted relative difference in size (predicted RDS) for these 14 species ranges from -0.02 (Chaetodon striatus and Sparisoma rubripinne) to 0.17 (Epinephelus cruentatus). Of the twelve species for which there were no significant relationships between mean fork length and any habitat variable, 10 species had a non-significantly higher mean fork length in the BMR (Table 2). Thus, after correcting for habitat correlates of fish size, 21 of 26 species had a greater mean fork length in the BMR than in the NR (sign test, $p < 0.001$).

Catch rate

A total of 3419 fish from 49 species was caught at the 20 study sites during the trapping survey. Six species (Acanthurus bahianus, A. coeruleus, Cantherhines pullus, Chaetodon striatus, H. flavolineatum, and Microspathodon chrysurus) accounted for 75 % of the total catch at all sites combined (Appendix 3).

Mean catch rate did not differ significantly between the BMR and NR (ANOVA $r^2 = 0.00$, $F = 0.01$, df = 1, 18; n.s.). Mean catch rate increased with distance from the reserve boundary in the reserve ($r^2 = 0.78$, $F = 27.62$, df = 1, 8; $p < 0.001$), but also increased with distance from the reserve boundary in the non-reserve ($r^2 = 0.56$, $F = 10.35$, df = 1, 8; $p < 0.05$) (Figure 10). Mean catch rate differed significantly among reefs (ANOVA $r^2 = 0.66$, $F = 10.48$, df = 3, 16; $p < 0.001$): mean catch rate on South Bellairs Reef was significantly higher than on North Bellairs and Heron Bay reefs, and mean catch rate on Bachelor Hall reef was significantly higher than on North Bellairs reef (Tukey-Kramer HSD tests, $p < 0.05$). In terms of catch rate, reserve effectiveness was negligible (RDC = 0.01).

Thirteen of thirty species had a higher mean catch rate in the BMR than in the NR, although none were significantly higher (Wilcoxon test, Bonferroni $\alpha = 0.0017$; Table 7). Seventeen species had a non-significantly higher mean catch rate in the NR.

The mean catch rate (of all species combined) was not significantly correlated with total fish density as estimated in visual censuses for all 20 sites ($\log_{10}$catch vs. $\log_{10}$density: $r = -0.01$; n.s.), or for the 10 BMR ($r = 0.18$; n.s.) or 10 NR sites separately ($r = -0.37$; n.s.) (Figure 11). However, catch generally increased with visual census density for individual species. There was a positive correlation between catch and visual census density for 21 of 24 species (sign test $p < 0.001$), although this correlation was significant for only 2 species (Epinephelus fulvus and Holocanthus tricolor; Pearson correlation, Bonferroni $\alpha = 0.002$). The three negative correlations were slight (slope ≥ -0.04 fish per trap/fish per $400 m^2$), non-significant ($p \geq 0.40$), and occurred in three species rare in visual censuses, catches, or both (Abudefduf saxatilis: mean visual census density = 0.43 fish / 400 m^2, Mulloidichthys martinicus: mean catch rate = 0.03 fish / trap set, Sparisoma rubripinne: mean visual census density = 0.27 fish / 400 m^2 and mean catch rate = 0.04 fish / trap set).

Trappability

The trappability of fish was higher in the NR than the BMR for 20 of 24 species (sign test, $p < 0.005$) but this difference was not significant for any individual species (Wilcoxon test, Bonferroni-adjusted $\alpha = 0.0021$; Table 8). The trappability of all species combined (total catch divided by total visual census density) was significantly higher in the NR than in the BMR (Wilcoxon $Z = -2.33$, df = 18; $p < 0.05$) and generally increased with position relative to the reserve boundary (linear regression $r^2 = 0.34$, $F = 9.29$, df = 1, 18; $p < 0.01$; Figure 12). Since there was no relationship between total catch rate and total visual census density, trappability was negatively correlated with total visual census density (linear regression $r^2 = 0.59$, $F = 26.08$, df = 1, 18; $p < 0.0001$).

The difference in trappability between the BMR and NR was relatively smaller for more trappable species, and trappability was actually lower in the NR for some of the most trappable species (Appendix 3); the relative difference in trappability between the BMR and NR (RDT = $(T_{BMR} - T_{NR}) / (T_{BMR} + T_{NR})$) was correlated with the trappability of species for all sites combined ($\rho = 0.4965$, $p < 0.05$, N = 24) and trappability for BMR sites only ($\rho = 0.6416$, $p < 0.001$, N = 24).

Multiple regression analysis of total trappability against habitat parameters showed a significant negative relationship between $\log_{10}$-transformed trappability and both rugosity and depth (whole model: $r^2 = 0.42$, F = 6.24, df = 2, 17; $p < 0.01$; rugosity: F = 11.85, $p < 0.005$; depth: F = 5.79, $p < 0.05$). There were non-significant trends of decreasing trappability with increasing rugosity and depth for many individual species, although the sample size and the range in trappabilities were often small for individual species (Appendix 3), reducing the power of such tests. After controlling for the effects of depth and rugosity on trappability, there is no significant effect of reserve status (ANOVA $r^2 = 0.12$, F = 2.47, df = 1, 18; n.s.) or position ($r^2 = 0.12$, F = 2.42, df = 1,18; n.s.) on residual trappability.

Partial correlation analysis of trappability, rugosity, and density revealed significant negative partial correlations between trappability and rugosity (r = -0.48, $p < 0.05$) and between trappability and visual census density (r = -0.77, $p < 0.001$), which suggest that trappability decreases with increasing habitat quality and with increasing fish density.

Since there is high interspecific variation in trappability (Table 8), the species composition at a site may greatly influence total trappability. Thus, an inverse correlation between trappability and visual census density may be due to a high proportion of low-trappability species at the highest density sites.

Five species (Haemulon chrysargyreum, H. flavolineatum, Kyphosus sectatrix, Lutjanus mahogani, and Mulloidichthys martinicus) with low trappabilities (< 0.1) together account for 6.0 to 63.3 % (median = 29.3 %) of the visual census density at a site, but constitute only 0 – 24.5 % (median = 5.8 %) of the total catch at a site (Appendix 3). There is a significant negative correlation between trappability and the proportion of the visual census density accounted for by these five species (Pearson $r = -0.60$, $p < 0.01$). If we exclude these five species from our visual census density and catch data, total catch rate is positively correlated with visual census density (Pearson $r = 0.56$, $p < 0.01$). However, trappability and visual census density are still negatively correlated ($r = -0.51$, $p < 0.05$), and the regression of trappability against rugosity and depth is still significant (whole model: $r^2 = 0.38$, $F = 5.08$, df = 2, 17; $p < 0.05$; rugosity: $F = 8.93$, $p < 0.01$; depth: $F = 6.00$, $p < 0.05$).

The residuals of the multiple regression of trappability against depth and rugosity allow calculation of the predicted catch rate at each site after controlling for the effects of habitat correlates of trappability (predicted catch rate = $(T + \Delta T_i)^* VCD_i$, where T = trappability at a hypothetical site with mean depth and rugosity, ΔT_i = residual of the multiple regression of trappability against depth and rugosity for site i, and VCD_i = the visual census density at site i). Predicted catch rate was not correlated with reserve status (ANOVA $r^2 = 0.08$, $F = 1.54$, df = 1, 18; n.s.) or position relative to the reserve boundary (linear regression $r^2 = 0.05$, $F = 0.92$, df = 1, 18; n.s.). After correcting for habitat correlates of trappability, there were non-significant trends towards increasing catch away from the BMR boundary within the BMR ($r^2 = 0.38$, $F = 5.00$, df = 1, 8; $p < 0.10$) and within the NR ($r^2 = 0.24$, $F = 2.52$, df = 1, 8; n.s.).

Fish movements

Trap recaptures

A total of 666 identified individuals from 28 species was recaptured at least once in our experimental traps. The number of fish tagged, their fork lengths, the number of fish recaptured, and the longest observed maximum inter-trap distances (MTDs) for each species are presented in Table 9. Forty-six percent of all tagged fish were recaptured in traps, although the recapture rate varied greatly among species (median = 38%, range 0–100%). Two species of jacks (Carangidae) were never recaptured in traps, possibly due to emigration from the study area (Table 9). The median total time-at-liberty (excluding the number of days which fish spent in traps) for all species combined was 24 days (maximum = 194 days).

Only two fish recaptured in traps moved across the BMR boundary: two schoolmaster snappers (Lutjanus apodus, 37 cm and 47 cm FL) moved from the NR to the BMR. No fish tagged in the BMR was recaptured in a trap in the NR; i.e., we measured no spillover from the BMR to the adjacent fishery (Figure 13).

We observed little movement of tagged fish among reefs separated by extensive areas of sand and rubble. In addition to the two snappers which moved across Heron Bay to the BMR, one surgeonfish (FL = 14.5 cm) moved between the two NR reefs (from Bachelor Hall to Heron Bay reef), which are separated by 20 – 100 m of sand and small patches of reef or rubble (Figure 13).

There was considerable movement of fish between the two BMR reefs. A total of 84 individuals (67 acanthurids, five chaetodontids, four pomacanthids, three scarids, three balistids, one kyphosid and one lutjanid) moved between North Bellairs reef and South Bellairs reef at least once (Figure 13).

To test the effect of between-reef habitat discontinuities on fish movements, we compared the number of observed movements among sites separated by a potential barrier with the number of movements among sites separated by a similar distance of contiguous reef. A pair of NR sites on Heron Bay reef (HE4, HE5) are 245 – 292 m from a pair of NR sites on Bachelor Hall reef (BA1, BA2), and these reefs are separated by an expanse of sand and rubble 20 – 100 m across. A pair of BMR sites on South Bellairs reef (SB4 & SB5) are 245 – 289 m from a pair of BMR sites on North Bellairs reef (NB7 & NB8), but these reefs are separated only by an expanse of sand as narrow as 10 m across (Figure 3). Of 130 fish released from these four NR sites and recaptured at least once, none moved across the large sandy area between the non-reserve reefs. Of 192 fish released from these four BMR sites and recaptured in traps at least once, four fish (two *Acanthurus bahianus*, one *Chaetodon striatus*, and one *Lutjanus apodus*) moved 240 - 290 m between site pairs (Fisher exact test; $p < 0.10$).

Appendix 6 shows the frequency distributions of the MTDs of individuals from the 13 species with a sample size of at least 10 recaptured individuals, and 5 or more recaptures of at least one individual. The median MTD varied from 0 m (for 10 species) to 62 m (*Chaetodon striatus*, N = 22) (Table 10). Correcting for bias due to the distribution of recapture effort had a strong effect on some estimates of species mobility. Weighting each MTD by its correction factor increased the median MTD of species by up to 88 m (median = 3 m). Weighted median MTDs varied from 0 m (for 6 species) to 88 m (*Acanthurus bahianus*) (Table 10). The standardized MTD (the predicted MTD after five recaptures; see Methods) for the 13 species ranged from 0 m (Holocentrus rufus) to 116 m (Acanthurus bahianus). There was no significant correlation between standardized MTD and the median fork length of a species (ρ = -0.48, n.s) although the range of median fork length was small (13.5 - 26.25 cm). There was a non-significant positive correlation between the standardized MTD and the number of individuals recaptured ($\rho = 0.45$, $p < 0.20$; N = 13 species; range in number of individuals: 11 - 261), although this was mainly due to the large sample size and high mobility of Acanthurus spp.; the correlation is not apparent when A. bahianus and A. coeruleus are excluded ($\rho = 0.13$, $p > 0.70$).

Visual recaptures

A total of 989 visual recaptures of fish from 24 species was recorded (Table 9). Ocean surgeons (Acanthurus bahianus) accounted for almost half of all visual recaptures (N = 494). The median time between release and visual recapture was 13 days (maximum = 182 days).

The visual recapture data provide evidence of only one fish crossing the BMR boundary. An ocean surgeon tagged in the NR (on Heron Bay reef) was visually recaptured at two BMR sites, 498 m and 538 m from the site of tagging, on successive dates by separate observers. (Although individual tag numbers were not recorded during visual recapture surveys, only one ocean surgeon was tagged with that tag code, allowing individual identification in this case.)

The median visual recapture distance (MVD) was 0 m for 18 of the 24 species visually recaptured. The six species with non-zero MVDs had few visual recaptures (Mulloidichthys martinicus median = 123 m, N = 4;

Acanthurus chirurgus median = 39 m, N = 3; *Kyphosus sectatrix* median = 50 m, N=2; *Caranx ruber* distance = 39 m, N = 1; *Scarus vetula* distance = 57 m, N=1; *Sparisoma rubripinne* distance = 161 m, N = 1). Weighted MVDs varied from 0 m (for 9 species) up to 44 m (*Acanthurus coeruleus*) for the 14 species with at least 8 recaptures (Table 11).

For *A. bahianus*, recapture distance was affected by schooling behaviour. Of 494 visual recaptures of ocean surgeonfish, 179 (36%) were of ocean surgeonfish in large (≥ 50 individuals) mono- or heterotypic foraging schools (Lawson *et al.* submitted) at the time of visual recapture. The MVD of *A. bahianus* visually recaptured while in schools was 63 m, whereas the MVD for non-schooling individuals was 0 m (Wilcoxon $Z = 13.57$, $p < 0.0001$). Of the 59 *A. bahianus* recaptured farther than 100 m from the site of release, 43 (73%) were members of schools.

Comparison of trap and visual recapture based mobility

Estimates of mobility based on trap and visual recaptures were highly correlated (Spearman $\rho = 0.8270$, $p < 0.005$) for the 11 species with adequate sample size in both data sets. Trap recapture-based estimates of mobility (standardized MTDs) were approximately twice as high as visual recapture-based estimates of mobility (weighted MVDs) (Figure 14).

Estimates of mobility were significantly correlated with trappability, for both trap recapture-based mobility (Spearman $\rho = 0.8364$, $p < 0.001$, $N = 12$) and visual recapture-based mobility (Spearman $\rho = 0.6334$, $p < 0.05$, $N = 14$). Partial correlation analysis indicates that trap recapture-based mobility is positively correlated with trappability when visual recapture-based mobility is held constant (Kendall partial rank-order correlation, $T = 0.50$; $p < 0.05$, N =

11). Thus, mobile species tend to be more trappable, and there is a significant tendency for trap recapture-based mobility to increase relative to visual recapture-based mobility as trappability increases.

Estimates of short-term mobility

The median swimming speed and velocities recorded for 22 diurnally active species are presented in Table 12. Fish swimming speed and velocity were not significantly correlated with trap- or visual recapture-based mobility estimates (Table 13). Movement rates over very short time scales (i.e., minutes) were therefore not good indicators of longer-term movements (i.e., at the scale of weeks), although these correlations were limited to species with adequate sample sizes in the mark-recapture study (species listed in Tables 10 and 11). Unlike trap- and visual recapture-based mobility, neither measure of short-term mobility was correlated with trappability (speed: Spearman rank correlation: $\rho = 0.15$, n.s.; velocity: $\rho = 0.17$, n.s.; $N = 18$).

Reserve effectiveness, mobility, and trappability

No measure of reserve effectiveness (RDD, RDS, or RDC) was significantly correlated with any measure of species mobility (Table 14). Thus, our hypothesis that the reserve effectiveness should be lower for more mobile fishes was not supported.

Reserve effectiveness in terms of density or size was not positively correlated with trappability in the NR (RDD: $\rho = 0.12$, RDS: $\rho = 0.12$, predicted RDD: $\rho = 0.21$, predicted RDS: $\rho = -0.02$; $p \geq 0.30$) or with trappability for all sites combined (RDD: $\rho = -0.32$, RDS: $\rho = -0.15$, predicted RDD: $\rho = -0.19$, predicted RDS: $\rho = 0.05$; $p \geq 0.10$). Thus, our hypothesis that reserve effectiveness will be higher for species that are more vulnerable to trap-fishing mortality in the non-reserve was not supported.

Partial rank-order correlation analysis did not reveal any partial correlations between reserve effectiveness and trappability or mobility (Kendall $T \leq 0.35$, $p > 0.05$).

There was no significant correlation between the relative difference in catch rate between the BMR and NR (RDC) and trappability in the NR ($\rho = 0.03$, n.s.). There was a non-significant positive correlation between RDC of species and their trappability for all sites combined ($\rho = 0.31$, $p < 0.20$) and a significant correlation between RDC of species and their trappability at BMR sites ($\rho = 0.42$, $p < 0.05$). This is consistent with the result that more trappable species tended to have a smaller difference in trappability between the BMR and NR than less trappable species (see Trappability, above).

The five species with the lowest trappability (< 0.1) account for a large proportion of the difference in total visual census density between the BMR and NR, which suggests that the difference in total density is not primarily due to a difference in trap-fishing mortality. If we exclude these 5 species (Mulloidichthys martinicus, Haemulon chrysargyreum, H. flavolineatum, Lutjanus mahogani, and Kyphosus sectatrix) from our visual census density estimates, the differences in density and in predicted density between the BMR and NR are less pronounced and non-significant (RDD = 0.20; $F = 3.98$, df = 1, 18, $p < 0.10$; predicted RDD = 0.05, $F = 0.62$, df = 1, 18; n.s.).

Spearfishing target taxa (Epinephelus cruentatus, E. fulvus, Kyphosus sectatrix, Lutjanus mahogani, Scarus vetula, and Sparisoma viride; Rakitin 1994, pers. obs.) had a significantly higher relative difference in size (RDS;

Wilcoxon Z = 3.34, $p < 0.001$) and predicted RDS (Z = 1.99, $p < 0.05$) than non-target taxa. These taxa also had a slightly, but not significantly, higher RDD (Z = 0.67, n.s.) and predicted RDD (Z = 0.41, n.s.) than non-target taxa.

DISCUSSION

The effectiveness of reserve protection: fish density and size

The total density of trappable fishes as measured by visual census was significantly higher on two reefs in the Barbados Marine Reserve than on two reefs in the adjacent non-reserve area. Much of the difference in fish density and size between the BMR and NR, however, was attributable to differences in habitat characteristics among sites; after correcting for habitat correlates of density, the relative difference in total density (RDD) between the BMR and NR decreased from 0.27 to 0.17. After correcting for habitat correlates of density and size, twenty-two of 26 species had a higher density in the BMR than in the NR, and 21 of 26 had a greater predicted mean fork length, but none of these differences were significant. The visual census data suggest a slight but consistent effect of reserve protection on distribution and size structure of trappable fishes.

Spatial variation in recruitment, survival, competition, and habitat structure result in high spatial variability in fish density (Williams 1991). The patchy distributions and/or low densities of many species reduce the accuracy and power of statistical comparisons between the reserve and non-reserve density of individual species over the small spatial scale (1 km) studied. If edge effects are important, the difference in density between reserve and non-reserve sites should be lower near the reserve boundary;

comparing sites farther from the reserve boundary should result in higher estimates of reserve effectiveness.

Surprisingly, the relative difference in the density, size, or catch rate of species between the BMR and NR was not correlated with the trappability of species in the NR. Moreover, there was no significant reserve effect on fish density when the five least trappable species were excluded. This suggests that the elimination of trap-fishing mortality within the BMR may have little effect on fish distribution and size. Little trap-fishing pressure was observed on the two NR study reefs, and trap-fishing appears to be declining in importance as older fishers leave the fishery and are not replaced by younger fishers; the average age of trap-fishers in Barbados is over 50 y (Mahon & Drayton 1990). There was some evidence that taxa that are likely to be subject to spearfishing mortality benefited more from reserve protection: spearfishing target taxa exhibited a significantly higher relative difference in size than non-target taxa. This pattern is consistent with the high size-selectivity of spearfishing.

The observed patterns of fish density and size are generally consistent with a previous survey of the BMR and adjacent NR over a broader spatial scale. In a visual census survey of all 5 fringing reefs of the BMR and 8 reefs in the NR, Rakitin & Kramer (1996) found a relative difference in fish density between the BMR and NR of 0.26, with 19 of 24 species having a higher density in the BMR, and 18 of 24 species having a higher mean estimated fork length in the BMR. The relative difference in size of species is significantly correlated between the two studies ($\rho = 0.68$, $p < 0.05$, $N = 12$); however, the relative difference in visual census density of species shows little concordance ($\rho = 0.02$, n.s.; $N = 19$). Rakitin (1994) also found non-significant trends towards higher rugosity and percent live coral cover, and lower percent sand in the BMR, but did not assess the effect of habitat variables on fish density or size.

Published values of the relative difference in fish density (RDD) between no-take coral reef marine reserves and adjacent fished areas range from -0.20 to 0.89, with a median of 0.20 (M.R. Chapman and D.L. Kramer, unpublished data). Differences among reserves in time since establishment, the degree of enforcement and observance of reserve regulations, fish community structure, fishing intensity in the adjacent area, and the status of the fish community and reef habitat before reserve establishment, make comparisons of reserve effectiveness difficult. However, the differential in fish density between the BMR and the adjacent non-reserve (predicted RDD = 0.17) appears typical of coral reef marine reserves elsewhere in the Caribbean and Indo-Pacific.

Habitat correlates of the density and size of reef fishes

The densities of most study species were correlated with habitat characteristics of the study sites (Table 3). In general, deeper sites with a higher proportion of reef and rubble (as opposed to sand) and higher rugosity had higher densities of fish; rugosity was positively correlated with the density of 10 species, and site depth was positively correlated with the density of six species. Density was positively correlated with both depth and rugosity for three of the five study species which form diurnal resting aggregations; large diurnal resting aggregations of Haemulon and Mulloidichthys species were often associated with high-relief reef spurs at the seaward edges of fringing reefs.

Percent sand cover was negatively correlated with total fish density, and the density of trappable fishes was generally at least an order of magnitude lower over sand than over reef and rubble (M. Chapman unpubl. data); however, the density of four species was positively correlated with both percent sand and rugosity. In this study, rugosity was measured across all substrate types. Since rugosity over sand is uniformly low, the multiple correlations of density percent sand and rugosity may imply that sites with the most rugose reef substrate – i.e., high rugosity despite high percent sand – tend to have a higher density of these species. However, rugosity was negatively correlated with percent sand ($r = -0.73$, $p < 0.001$) and positively correlated with percent reef ($r = 0.84$, $p < 0.001$), so the biological significance of these multiple regressions should be interpreted with caution (Zar 1996). Positive correlations between density and percent sand or percent rubble may also indicate the importance of reef habitat with adjacent rubble and sand. We suggest that future studies investigating the habitat associations of reef fishes measure habitat complexity separately for different substrate types, in order to more accurately assess the effects of the area and structural characteristics of various substrates.

The mean fork length of many species was also correlated with the habitat characteristics of study sites (Table 5). As with density, increased size was often associated with higher rugosity. Regression models often included both rugosity and percent reef (four species) or percent sand and rubble (two species), further suggesting that measurement of habitat complexity in areas of mixed substrate composition should be stratified according to substrate type.

Although there was no significant difference between the BMR and NR for any measured habitat variable, there were non-significant trends towards greater site depth, rugosity, and percent live coral cover in the BMR. This study demonstrates that the lack of a significant difference in habitat characteristics between reserve and non-reserve sites does not rule out the possibility that differences in fish density or size between the reserve and non-reserve are attributable to habitat differences. In order to exclude differences in fish distribution potentially due to habitat variables, and to reveal differences in fish distribution obscured by variation in habitat features, the effect of habitat variables on species density, size, or biomass should be tested directly, and residual variation tested against reserve status or fishing pressure.

The fixed spatial scale at which density and habitat correlates were assessed (400 m^2) is likely to reduce the accuracy of models of habitat correlates of fish density and size, and thus tests of the effect of reserve protection on fish density and size. The potential scale-dependence of correlations between species density and habitat characteristics imply that habitat correlates of density should be tested at the spatial scale of the home range of the study species (Roberts & Ormond 1987, Jennings et al. 1996).

Trap catches and trappability

Unlike visual census density, catch rate was not significantly higher in the BMR than in the NR. Variation in species composition among sites, combined with among-species and among-site variation in trappability, resulted in little concordance between visual census density and catch rate at a site.

The low catch rate at sites nearest the BMR boundary (Figure 10) appears to be due to differences in species composition and species trappability. The low catch rate near the BMR boundary was associated with a high relative abundance of haemulids near the boundary (Appendix 3), as well as the low trappability of acanthurids at the deeper sites on North Bellairs reef (Appendix 3). There was no concentration of fishing effort near the reserve boundary (e.g., McClanahan & Kaunda-Arara 1995) observed during the study period.

Trappability is the result of complex interactions among fish morphology, fish behaviour, and characteristics of traps and of the reef environment; trappability will therefore vary among species and among habitats (Munro 1971, Robichaud 1996, Wolff 1997). Similarly, the sampling efficiency of visual censuses may vary among species and habitats (e.g., Sale and Sharp 1983, Jennings & Polunin 1995), affecting estimates of trappability that assess density through visual censuses. The discordance between measures of reserve effectiveness based on the trapping and visual census surveys in this study may be due to greater trappability of fishes in the NR, increased sampling efficiency of visual censuses in the BMR, or both.

The trappability of most taxa was higher in the NR than in the BMR, and this difference in trappability was associated with differences in both density and habitat features between BMR and NR sites. The data demonstrate that individuals are less likely to be captured in Antillean fish traps at sites where habitat complexity is higher. Higher rugosity is associated with increased microhabitat diversity and greater availability of anti-predator refugia (Roberts 1996). If fish are attracted to the structure provided by traps (High & Ellis 1973), trappability should be higher where habitat complexity is lower (Robichaud 1996, Wolff 1997). Habitat complexity could also affect trappability indirectly through changes in species composition and size-structure; interactions among species in and around traps may affect catch rate, and trappability may vary intraspecifically with fish size. By reducing the probability of fishes entering traps, increased habitat complexity may reduce fishing mortality, as well as reducing natural mortality for prey fishes (Hixon & Beets 1993, Caley & St.John 1996).

Differences in trappability may also reflect differences in the sampling efficiency of visual censuses. For example, fish may be more wary of divers where habitat complexity is lower or where fish density is lower. If the availability of refuges decreases with decreasing habitat complexity, the risk of predation may increase (Godin 1997). This should increase the cost of remaining outside a refuge, which could in turn result in increased time spent in refuges. Similarly, decreases in the density of prey fishes may increase refuge use if higher conspecific density reduces predation risk (Rangeley & Kramer in press). Increases in the use of anti-predator refuges may decrease the sampling efficiency of visual censuses, and increase estimates of trappability in the NR. Lower sampling efficiency of visual censuses in the NR could also result from fish avoiding divers more where spearfishing occurs (Bell 1983, Grigg 1994, Jennings et al. 1996). However, there was no significant effect of reserve status on trappability after controlling for habitat correlates of trappability. Furthermore, there was no trend towards a greater difference in trappability between the BMR and NR for spearfishing target taxa (Wilcoxon $Z = -1.1$, n.s.). These results suggest that changes in trappability are due to differences in habitat characteristics of sites, rather than reserve status.

Rakitin & Kramer (1996) found a significant positive correlation between the relative difference in catch rate and the trappability of species. They interpreted this as evidence that the effect of the BMR was primarily due to the elimination of trap-fishing mortality. However, their result is also consistent with the hypothesis that the relative difference in catch rate is greater for more trappable species because their trappability varies less than the trappability of less trappable species in response to changes in local density and substrate rugosity. If the decrease in trappability with increasing density and rugosity is smaller for more trappable species, they will exhibit a greater difference in catch rate between low-density, low-rugosity areas (e.g., the NR) and high-density, rugose areas (e.g., the BMR). In this study, more trappable species did exhibit a smaller difference in trappability between the BMR and NR and a greater relative difference in catch rate between the BMR and NR. The behavioural bases of changes in trappability and catch rate clearly require further investigation.

The pattern of declining catch rate with increasing distance from the reserve centre found by Rakitin & Kramer (1996) was not found at the smaller spatial scale of this study. In our study, there was no effect of reserve status on mean catch rate at a site, and catch rate was highly variable among trap sets at the same site (Figure 10). The range in catch rate in this study was approximately the same as that of Rakitin & Kramer (1996). Although the lack of correlation between catch rate and visual census density in this study was largely due to the inclusion of abundant yet only slightly trappable species (notably diurnal resting aggregations of Haemulon chrysargyreum and H. flavolineatum) in visual census density estimates, the relationship between catch rate and visual census density was complex, and was affected by changes in species composition, total density, and habitat characteristics. Trap catches provide an alternative index of fish abundance which avoids some of the biases of visual census-based density estimates (e.g., Sale and Sharp 1983, Jennings & Polunin 1995) but the complex relationships between catch rate, visual census density, and habitat suggest that spatial trends in total catch rate should be interpreted with caution.

Fish movements and the effectiveness of the BMR

The movement of post-settlement fishes of trappable size appears to play a limited role in the pattern of fish distribution across reefs. Movement of fish among disjunct fringing reefs was extremely limited: only three tagged fish (two fish recaptured in traps and one fish visually recaptured in census surveys) were known to have crossed the northern BMR boundary during the study period. The mobility of species was not negatively correlated with reserve effectiveness as indicated by the relative difference in the density or size of species. Since the measures of species mobility obtained are based almost exclusively on within-reef movements (and movements between the two nearly contiguous BMR reefs), species mobility does not affect the distribution of fishes among reefs or indices of reserve effectiveness.

The data suggest that sandy areas between reefs constitute natural boundaries to fish movement, preventing extensive transfer of fishes from reserve to non-reserve reefs. Several species showed extensive within-reef movements (e.g., Acanthurus, Chaetodon, Cantherhines, and Holocanthus spp.). If reef edges constitute a boundary to their movements, these species may have even larger ranges on larger patches of continuous reef. Significant spillover of these taxa is likely to occur across reserve boundaries which intersect continuous reef habitat (e.g., Corless et al. in press). In order to enhance the local yields of species reluctant to disperse across foreign habitat, no-take marine reserves should be located within a larger patch of similar habitat. Conversely, in order to create and maintain a differential of fish density and size between a reserve and adjacent fished habitat, reserve boundaries should coincide with habitat discontinuities (Rowley 1994, Barrett 1995).

Density-dependent habitat selection theory suggests that emigration from marine reserves should increase as the differential in density between the reserve and non-reserve increases. If habitat discontinuities form a barrier to fish movements, however, spillover may be negligible despite pronounced gradients in density between a reserve and adjacent non-reserve. Density-dependent habitat selection theory predicts that fish will relocate from reserves when the difference in net benefits between reserve sites and non-reserve sites exceeds the cost of moving between them (Kramer and Chapman submitted). We hypothesize that future increases in the gradient in fish density and size between the BMR and NR will not result in a pronounced increase in spillover from the BMR because of the discontinuous nature of the fringing reef habitat on the West coast of Barbados.

It is notable that a homing experiment (Appendix 2) indicated that fish from at least 7 families (Acanthuridae, Balistidae, Chaetodontidae, Haemulidae, Holocentridae, Pomacanthidae, and Scaridae) can relocate to their home reefs following displacement from the BMR to the NR or vice versa, which demonstrates that they are capable of relocating across fairly large (150–300 m) areas of sand and rubble. On the other hand, homing behaviour suggests that reef fish are extremely philopatric and reluctant to relocate home ranges. Thus, demonstration of the ability or inability to return to a home reef following displacement provides no information regarding the actual transfer rate of fishes among reefs.

Although the common taxa in this study displayed little movement among fringing reefs, many exploited reef fishes are more mobile and may relocate among reefs despite habitat discontinuities of several hundred metres. For example, although only two individuals were recaptured, Lutjanus apodus appears to be highly mobile. Only one of twelve tagged bar jacks (Caranx ruber) was recaptured (Table 9), which may have been due to emigration from the study area. During the short-term mobility study, three bar jacks (Caranx ruber) were followed, with recorded swimming velocities of up to 55 $m.min^{-1}$, suggesting that this species could travel the length of the study area in as little as 20 minutes. Furthermore, no individuals from a school of 47 horse-eye jacks (Caranx latus) tagged on South Bellairs in the preliminary tagging bout (November 1995) were seen during the study period (February - May 1996); these fish may have relocated to another reef (Table 9). Several other exploited reef-associated species (e.g., Sphyraena barracuda and Scomberomorus regalis), rare in the study area, may also range widely. The relative rarity of mobile species on the fringing reefs of Barbados may not be representative of most reef fisheries.

Measures of species mobility

Estimates of mobility based on trap and visual recaptures and the rarity of observed movements between reefs are generally consistent with previous studies of the movement patterns of the study species.

The ocean surgeon, Acanthurus bahianus, and the blue tang, A. coeruleus, moved extensively within reefs, especially when schooling, and often crossed narrow channels of bare sand. One recaptured A. bahianus individual moved from the non-reserve to the reserve, and another between the two non-reserve reefs. Robertson (1988) reported extensive relocation of A. bahianus and A. coeruleus among patch reefs up to 100 m apart in the San Blas archipelago of Panama. Dense beds of seagrass and macroalgae and smaller size of reefs in the San Blas reef system may encourage greater rates of movement among reefs (Robertson 1988). In general, differences in the type of habitat among reefs will affect the permeability of reserve boundaries to fish movements (Robertson 1988, Rowley 1994).

The butterflyfish Chaetodon striatus also displayed relatively extensive within-reef movements; Roberts & Ormond (1992) report that chaetodontid home ranges may be up to several hundred square metres.

Grunts (Haemulidae) also showed little movement; non-reef habitat was not sampled, and the off-reef nocturnal foraging migrations of grunts were not included in the mobility estimates for these species. The data are consistent with earlier reports that individuals do not relocate their diurnal resting locations (e.g., Ogden & Quinn 1984, Burke 1995). Tulevech & Recksiek (1994), however, report migration of an adult white grunt (H. plumieri, 23 cm TL) between patch reefs separated by 560 m of sand and seagrass.

The three holocentrid species showed little movement, consistent with earlier reports (Luckhurst & Luckhurst 1978, Corless et al. in press), as did the pomacentrid Microspathodon chrysurus, and the two epinepheline serranids (Epinephelus cruentatus and E. fulvus); maximum observed movement distances for these taxa were less than 70 m.

Parrotfishes (Scaridae) showed relatively little movement in this study; however, small sample sizes, high rates of tag loss, and diver avoidance, especially by large terminal phase parrotfishes (pers. obs.) suggest that mobility was underestimated for parrotfishes. Diel migrations of larger Scarus spp. to deeper reef habitats are known to occur (Dubin & Baker 1982), but deeper habitat was not sampled in this study.

Estimates of species mobility based on trap and visual recaptures were highly correlated. Trap recapture based mobility tended to be about twice as high as visual recapture-based mobility. This can be attributed to the fact that trap-based mobility estimates were based on the maximum distance between captures, whereas visual-recapture based mobility is based on the net displacement from the point of release. It should be noted, however, that visual recaptures did not sample crepuscular or nocturnal movements, which may result in further underestimation of mobility compared to trap recapture-based estimates.

The correlation between mobility and trappability suggests that more mobile species are more trappable. More mobile fishes have been hypothesized to have higher trappability because of their increased probability of encountering traps (Robichaud 1996). Trap-recapture based estimates of mobility were significantly higher than predicted by visual recapture-based mobility for more trappable species. For example, the most trappable species (C. striatus) had a standardized MTD based on trap-recaptures of 110 m, compared to a weighted MVD based on visual recaptures of 39 m. The probability of observing rare long distance movements in trap recaptures should be higher for more trappable species, and placement of traps on the reef could even induce longer movements by more trappable species if they are attracted to the structure provided by traps.

Short-term mobility was not correlated with mobility estimates from the mark-recapture study or with trappability. For mobile species, short-term movements are likely to considerably underestimate the actual area used, since this is expected to increase asymptotically over time (e.g., Shapiro et al. 1994).

Short-term mark-recapture studies of a subset of fish species and size-classes provide limited information about fish movements. The actual paths and habitat types traversed, and the causes of low recapture rates (i.e., low recapture efficiency, mortality, and emigration from the study area) cannot be determined without additional observations (Appeldoorn in press). Recapture rates will be lower for mobile species which emigrate beyond the study area, biasing movement data towards more sedentary species. Although we corrected for the distribution of sampling effort within our study area, the short average time-at-liberty and limited recapture area and efficiency in this study are likely to have resulted in underestimates of species mobility. Furthermore, between-reef habitat was not sampled for fish movements, preventing assessment of off-reef migrations known to occur in invertivorous species which feed over sand flats at night. Although fishing pressure in the sandy bay near the northern BMR boundary appeared low (pers. obs.), the small amount of line fishing in the bay probably results in some capture of nocturnally foraging invertivores from the BMR.

In-depth studies of exploited fishes are required in order to assess patterns of movement over various habitat types and over longer time frames. In particular, understanding of onshore-offshore movements (to the deeper bank reef; e.g., Dubin & Baker 1982) and use of between-fringing reef habitats (sand, rubble, and reef patches) by juveniles and adults are required to assess spillover from the BMR. The potential importance of juvenile movements should also be assessed, since juvenile relocation (e.g., Brock et al. 1979, Russell et al. 1974) may strongly affect the distribution of trappable fishes. Finally, rare or occasional movements – e.g., spawning migrations, and movements in response to storms and hurricanes (Lassig 1983, Walsh 1983) – may be important processes affecting reserve fishes' exposure to the fishery, and should be assessed in this and other reserve-fishery systems.

Other potential factors limiting the effectiveness of the BMR

Several factors besides the emigration of trappable fishes could limit the effectiveness of the BMR. Perhaps most importantly, the apparently low fishing pressure on non-reserve fringing reefs and observations of illegal fishing in the reserve (Rakitin 1994, pers. obs.) imply that the difference in fishing mortality between the reserve and non-reserve is likely to be small. Second, although no spillover was observed in this study, undetected fish movements may compromise the effectiveness of the BMR. Onshore-offshore movements were not assessed in this study; spillover to exploited sections of the offshore bank reef could reduce the differential in size and density between the BMR and NR fringing reefs if connectivity with offshore habitat is greater for reefs in the BMR. Movements of fish below trappable size could also reduce density and size differentials (e.g., ontogenetic habitat shifts or density-dependent relocation of juveniles and small adults), but these were not assessed in the present study. Third, recruitment rate may limit the recovery of fish stocks in the BMR. Recruitment appears to be lower in the BMR than in the non-reserve due to patterns of larval transport (Sponaugle & Cowen 1996). Finally, it should also be noted that the statistical methods of this study may have attributed effects of reserve protection to spuriously correlated habitat characteristics.

Conclusions

Study sites in the Barbados Marine Reserve (BMR) had a significantly higher total density of fishes than those in the adjacent non-reserve. The effect of the BMR on the density and size of individual species was limited, however, possibly because of the low fishing pressure in the surrounding non-reserve. The density and size of most species were correlated with measured habitat characteristics, particularly substrate rugosity. Although there were no significant differences in habitat characteristics between the BMR and non-reserve, habitat characteristics explained some of the variance in fish density and size associated with reserve status. There was no significant difference in catch rate between the BMR and non-reserve; the relationship between catch rate and local visual census density was complex and varied among species and sites. Comparisons of total catch rate should be interpreted with caution in the absence of data regarding variation in habitat characteristics and the local density and assemblage structure of reef fishes.

The rate of emigration of post-settlement reef fishes from the BMR appeared to be negligible. Movements were extensive within reefs for many taxa, but little movement among reefs was detected. The data suggest that post-settlement fish movements do not affect the ability of the BMR to maintain a differential of fish density or size, and that large expanses of sand between fringing reefs act as barriers to fish movements for many species. Spillover of the common trappable species studied is expected to be minimal where coral reef marine reserve boundaries and habitat discontinuities coincide. However, estimates of within-reef mobility suggests that spillover from small coral reef marine reserves could be significant where reserve boundaries intersect more structurally complex habitats.

In order to maximize the increase in density and size – and therefore reproductive output – of fish inside a marine reserve, spillover must be minimized. A growing number of authors have suggested that the primary fishery benefit of marine reserves is the possibility of enhanced larval output (Roberts & Polunin 1991, Russ et al. 1992, Holland et al. 1993, 1996, Nowlis & Roberts in press). Although minimizing spillover may maximize the net benefit of the reserve in terms of the enhancement of fish biomass in the fishery, the ecological and socio-economic benefits of larval export may be spatially diffuse, temporally variable and highly unpredictable, reducing the sustainability of the fishery, and may fail to engender support for the continued existence of the marine reserve.

In many reef fisheries, the provision of harvestable fish biomass to the exploited area immediately adjacent to a reserve may be necessary for the sustenance of the local reef fishery and to ensure support for the reserve. However, excessive emigration will compromise the ability of the reserve to conserve fish stocks. Designing coral reef marine reserves such that they will export harvestable fish biomass without compromising their effectiveness will require a richer understanding of the movement patterns of exploited fishes in relation to the distribution of fish and habitat.

SUMMARY

The emigration of post-settlement fishes may enhance local fisheries yields, but will compromise the ability of a reserve to conserve stocks and export larvae. Little is known of the rate of emigration of exploited coral reef fishes across reserve boundaries, and the effect of fish mobility on reserve effectiveness has never been tested directly. This study measured the mobility of exploited coral reef fishes and the effect of the Barbados Marine Reserve (BMR) on fish distribution in order to test the hypothesis that reserve protection is more effective for less mobile species.

The BMR supported a greater total density and average size of fishes than the adjacent non-reserve. The catch rate of fishes was not significantly higher in the BMR as a result of effects of habitat characteristics, species composition, and fish density on trappability. Much of the variance in the density and size of species among sites was attributable to differences in habitat characteristics among sites. After controlling for habitat correlates of density and size, the effect of reserve status on total density was still significant, but the reserve had no significant effect on the density and size of any species.

Several study species moved extensively within reefs, but little movement among reefs was detected. Fewer than 0.5% of recaptured fish moved across the BMR boundary, and there was no observed emigration from the BMR. Large expanses of sand and rubble between reefs appear to act as natural barriers to the movement of many post-settlement reef fishes. The movements of post-settlement fishes may have a greater impact on reserve function where reserve boundaries do not coincide with habitat discontinuities, and where the reef fish community includes greater numbers of highly mobile fish.

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Table 1. Mean density of species in visual census surveys in the BMR and the NR. N = total sample size (BMR+NR), RDD = $(\text{Density}_{BMR} - \text{Density}_{NR})/(\text{Density}_{BMR} + \text{Density}_{NR})$; Z= Wilcoxon test statistic, p = Wilcoxon test probability.

Species	**N**	**BMR density (400 m^{-2})**	**NR density (400 m^{-2})**	**RDD**	**Z**	**p**
Abudefduf saxatilis	26	0.77	0.10	0.77	1.97	0.0492
Acanthurus bahianus	1130	22.60	15.07	0.20	1.21	0.2261
A. coeruleus	272	6.80	2.27	0.50	3.03	0.0025
Bodianus rufus	17	0.37	0.20	0.29	0.85	0.3937
Cantherhines pullus	45	0.97	0.53	0.29	0.78	0.4377
Caranx ruber	31	0.87	0.17	0.68	1.54	0.1231
Chaetodon striatus	28	0.60	0.33	0.29	0.37	0.7146
Epinephelus cruentatus	27	0.63	0.27	0.41	2.00	0.0454
E. fulvus	48	0.97	0.63	0.21	0.31	0.7559
Haemulon carbonarium	36	1.00	0.20	0.67	1.85	0.0638
H. chrysargyreum	548	15.60	2.67	0.71	1.39	0.1641
H. flavolineatum	986	23.17	9.70	0.41	1.32	0.1854
Holocanthus tricolor	27	0.57	0.33	0.26	0.83	0.4076
Holocentrus rufus	70	1.53	0.80	0.31	0.88	0.3783
Kyphosus sectatrix	19	0.60	0.03	0.89	2.40	0.0164
Lactophrys triqueter	20	0.37	0.30	0.10	0.24	0.8102
Lutjanus mahogani	92	2.07	1.00	0.35	1.77	0.0772
Microspathodon chrysurus	801	13.20	13.50	-0.01	-0.08	0.9397
Mulloidichthys martinicus	190	4.77	1.57	0.51	2.50	0.0124
Myripristis jacobus	168	2.53	3.07	-0.10	-0.99	0.3223
Scarus iserti	77	2.37	0.20	0.84	3.49	0.0005
S. taeniopterus	75	1.43	1.07	0.15	0.15	0.8789
S. vetula	30	0.83	0.17	0.67	1.80	0.0717
Sparisoma aurofrenatum	58	1.07	0.87	0.10	0.31	0.7569
S. rubripinne	16	0.43	0.10	0.62	2.05	0.0408
S. viride	62	1.20	0.87	0.16	0.62	0.5382

Table 2. Mean fork length of species in visual census surveys in the BMR and the NR. N = total sample size in both BMR and NR, FL_{MAX} are from Humann (1994), RDS = $(FL_{BMR} - FL_{NR})/FL_{MAX}$, Z = Wilocoxon test statistic, p = Wilcoxon test probability.

Species	N	Mean FL_{BMR} (cm)	Mean FL_{NR} (cm)	FL_{MAX} (cm)	RDS	Z	p
Abudefduf saxatilis	26	12.0	11.3	18	0.04	0.74	0.4571
Acanthurus bahianus	1130	14.4	13.1	38	0.03	12.84	0.0000
A. coeruleus	272	12.5	12.4	38	0.00	0.46	0.6477
Bodianus rufus	17	21.2	21.2	76	0.00	0.36	0.7226
Cantherhines pullus	45	16.2	14.8	22	0.07	2.02	0.0436
Caranx ruber	31	19.3	28.8	61	-0.16	-1.64	0.1003
Chaetodon striatus	26	12.7	11.7	15	0.07	1.93	0.0503
Epinephelus cruentatus	27	23.3	19.1	30	0.14	1.20	0.2287
E. fulvus	50	21.8	18.3	41	0.09	1.16	0.2466
Haemulon carbonarium	36	24.0	21.2	38	0.08	1.48	0.1395
H. chrysargyreum	548	16.0	15.7	25	0.01	2.47	0.0134
H. flavolineatum	986	14.4	14.2	30	0.01	1.98	0.0479
Holocanthus tricolor	27	13.6	13.2	31	0.01	0.77	0.4431
Holocentrus rufus	67	17.4	17.7	32	-0.01	-0.12	0.9054
Kyphosus sectatrix	19	21.8	13.0	76	0.12	1.66	0.0974
Lactophrys triqueter	20	14.5	12.8	30	0.06	0.19	0.8473
Lutjanus mahogani	92	20.1	17.1	38	0.08	1.58	0.1151
Microspathodon chrysurus	813	13.2	12.2	19	0.05	8.59	0.0000
Mulloidichthys martinicus	116	20.5	18.3	39	0.06	3.15	0.0016
Myripristis jacobus	167	14.3	13.8	22	0.02	2.76	0.0058
Scarus iserti	76	17.6	15.3	28	0.08	2.90	0.0037
S. taeniopterus	76	19.2	16.5	33	0.08	4.83	0.0000
S. vetula	30	23.3	18.3	61	0.08	2.33	0.0197
Sparisoma aurofrenatum	49	17.3	15.6	28	0.06	2.96	0.0031
S. rubripinne	16	25.2	26.3	46	-0.02	-0.82	0.4144
S. viride	64	20.7	15.9	61	0.08	3.09	0.0020

Table 3. Multiple regression models of $\log_{10}$-transformed visual census density against measured habitat variables for 18 species. Adjusted α = significance level according to the sequential Bonferroni procedure (Rice 1989). * = significant at adjusted α; n.s. = not significant at adjusted α.

	Model fit			Model coefficients						
Species	r^2	p	Adjusted α	Intercept	Depth	Rugosity	Coral cover	Percent sand	Percent rubble	Percent reef
Acanthurus bahianus	0.56	0.0038	0.0033 n.s.	-2.267		2.078		1.591	3.575	
A. coeruleus	0.41	0.0325	. n.s.	-4.094		3.153		1.434	3.692	
Cantherhines pullus	0.31	0.0116	. n.s.	0.075					1.270	
Epinephelus cruentatus	0.47	0.0145	. n.s.	-1.390		1.216	-0.530	0.499		
E. fulvus	0.27	0.0201	. n.s.	0.087					1.224	
Haemulon carbonarium	0.59	0.0005	0.0021 *	-2.031	0.152	1.201				
H. chrysargyreum	0.58	0.0006	0.0023 *	-6.922	0.206	5.312				
Holocanthus tricolor	0.55	0.0012	0.0025 *	-0.242	0.060				0.870	
Holocentrus rufus	0.62	0.0000	0.0019 *	-2.121		1.984				
Lactophrys triqueter	0.40	0.0026	0.0031 *	0.027					0.850	
Microspathodon chrysurus	0.63	0.0002	0.0020 *	0.524			0.751			0.742
Mulloidichthys martinicus	0.28	0.0446	. n.s.	-3.582	0.204	2.454				
Myripristis jacobus	0.50	0.0025	0.0029 *	-0.083	0.206			-1.257		
Scarus iserti	0.61	0.0014	0.0028 *	-4.944		3.630		1.370	3.112	
S. taeniopterus	0.55	0.0012	0.0026 *	-0.429	0.128				0.979	
S. vetula	0.49	0.0006	0.0024 *	-1.427		1.296				
Sparisoma aurofrenatum	0.31	0.0108	. n.s.	0.090					1.488	
S. viride	0.59	0.0005	0.0022 *	-0.895		0.783	0.965			

Table 4. Predicted density in the BMR and NR of 18 species after correcting for habitat correlates of density. Predicted density is the density predicted for a site with mean habitat quality, based on multiple regression of $\log_{10}$density against habitat variables, plus the mean of the residual variation of the BMR or NR sites. Predicted Relative Difference in Density between the BMR and NR = (Predicted densityBMR - Predicted densityNR)/(Predicted densityBMR + Predicted densityNR). t = two-tailed t-value (df=18), p = t-test probability.

Species	**Predicted BMR density (400 m^{-2})**	**Predicted NR density (400 m^{-2})**	**Predicted RDD**	**t**	**p**
Abudefduf saxatilis	.	.	.	.	.
Acanthurus bahianus	13.26	13.49	-0.01	0.09	0.93
A. coeruleus	3.43	1.75	0.32	1.89	0.08
Bodianus rufus	.	.	.	.	.
Cantherhines pullus	0.65	0.36	0.28	1.15	0.27
Caranx ruber	.	.	.	.	.
Chaetodon striatus	.	.	.	.	.
Epinephelus cruentatus	0.47	0.32	0.18	1.16	0.26
E. fulvus	0.62	0.44	0.17	0.64	0.53
Haemulon carbonarium	0.54	0.34	0.23	1.13	0.27
H. chrysargyreum	2.06	1.98	0.02	0.06	0.95
H. flavolineatum	.	.	.	.	.
Holocanthus tricolor	0.39	0.26	0.19	0.96	0.35
Holocentrus rufus	0.89	0.84	0.03	0.16	0.87
Kyphosus sectatrix	.	.	.	.	.
Lactophrys triqueter	0.27	0.22	0.11	0.45	0.66
Lutjanus mahogani	.	.	.	.	.
Microspathodon chrysurus	12.14	12.08	0.00	0.04	0.97
Mulloidichthys martinicus	1.94	0.86	0.39	1.26	0.22
Myripristis jacobus	1.42	2.19	-0.21	1.13	0.28
Scarus iserti	0.86	0.34	0.43	2.01	0.06
S. taeniopterus	0.82	0.93	-0.06	0.37	0.72
S. vetula	0.49	0.25	0.33	1.45	0.16
Sparisoma aurofrenatum	0.67	0.56	0.09	0.33	0.74
S. rubripinne	.	.	.	.	.
S. viride	0.77	0.96	-0.11	0.82	0.42
Total[1]	**70.53**	**49.81**	**0.17**	**2.34**	**0.03**

1. Total density includes uncorrected densities (Table 1) of 8 species for which there were no significant multiple regressions ($p > 0.05$) of density against habitat variables.

Table 5. Multiple regression models of mean fork length (cm) against measured habitat variables for 14 species. Adjusted α = significance level according to the sequential Bonferroni procedure (Rice 1989). * = significant at adjusted α; n.s. = not significant at adjusted α.

	Model fit					Model coefficients							
Species	r^2	df	p	Adjusted α		Intercept	Depth	Rugosity	Algal cover	Coral cover	Percent sand	Percent rubble	Percent reef
Acanthurus bahianus	0.49	3, 16	0.0111	.	n.s.	-0.240		9.636			4.268	7.450	
Chaetodon striatus	0.65	2, 7	0.0256	.	n.s.	9.249				6.344		9.010	
Epinephelus cruentatus	0.50	1, 13	0.0031	0.0026	n.s.	12.124					22.327		
Haemulon chrysargyreum	0.66	1, 11	0.0008	0.0022	*	14.566	0.296						
H. flavolineatum	0.64	3, 16	0.0008	0.0023	*	5.795		5.492			3.413	8.267	
Lutjanus mahogani	0.91	1, 13	0.0000	0.0019	*	6.402	2.772						
Microspathodon chrysurus	0.53	3, 16	0.0065	.	n.s.	5.311		7.406	2.840				-4.969
Mulloidichthys martinicus	0.46	1, 9	0.0211	.	n.s.	30.313		-9.576					
Myripristis jacobus	0.55	1, 14	0.0010	0.0024	*	13.213						5.537	
Scarus iserti	0.68	2, 10	0.0031	.	n.s.	5.069		14.540					-11.145
S. taeniopterus	0.73	2, 13	0.0002	0.0020	*	-28.277		45.430					-15.159
S. vetula	0.84	2, 7	0.0017	0.0025	*	-23.715		39.132		-19.596			
Sparisoma rubripinne	0.71	1, 5	0.0179	.	n.s.	33.367	-1.591						
S. viride	0.66	2, 14	0.0005	0.0021	*	-47.656		64.589					-24.644

Table 6. Predicted mean fork length (cm) in the BMR and NR for 14 species after correcting for habitat correlates of mean FL. Predicted mean FL is the FL predicted for a site with mean habitat quality based on multiple regressions of mean FL against habitat variables, plus the mean of the residual variation of the BMR or NR sites. Predicted RDS = (Predicted FL_{BMR} - Predicted FL_{NR})/(Maximum FL), t = Student's t value, df = error degrees of freedom, p = t-test probability. No species is significantly longer according to the sequential Bonferroni procedure (adjusted α for *Epinephelus cruentatus* = 0.004).

Species	Predicted BMR mean FL (cm)	Predicted NR mean FL (cm)	Max FL (cm)	Predicted RDS	t	df	p
Acanthurus bahianus	13.8	13.4	38	0.01	2.13	18	0.048
Chaetodon striatus	11.3	11.6	15	-0.02	0.58	8	0.576
Epinephelus cruentatus	22.7	17.6	30	0.17	2.51	13	0.026
Haemulon chrysargyreum	16.0	16.0	25	0.00	0.15	11	0.880
H. flavolineatum	14.4	14.4	30	0.00	0.09	18	0.932
Lutjanus mahogani	20.0	19.8	38	0.01	1.25	12	0.234
Microspathodon chrysurus	12.9	12.6	19	0.01	1.55	18	0.139
Mulloidichthys martinicus	18.9	18.4	39	0.01	0.53	9	0.606
Myripristis jacobus	13.7	13.6	22	0.00	0.36	14	0.728
Scarus iserti	16.8	17.0	28	-0.01	0.34	11	0.743
S. taeniopterus	19.0	18.3	33	0.02	1.14	14	0.275
S. vetula	19.2	18.5	61	0.01	1.01	8	0.343
Sparisoma rubripinne	25.5	26.3	46	-0.02	0.43	5	0.687
S. viride	17.6	17.2	61	0.01	0.36	15	0.722

Table 7. Catch rate by species. Mean catch rates for the BMR and NR are the means of 10 site means (N = 3 to 11 trap sets per site). RDC = (Catch_{BMR} - Catch_{NR})/(Catch_{BMR} + Catch_{NR}); Z= Wilcoxon test statistic, p = Wilcoxon test probability. No difference is significant according to the sequential Bonferroni procedure (adjusted α for *Microspathodon chrysurus* = 0.0016).

Species	BMR mean catch rate	NR mean catch rate	RDC	Z	p
Abudefduf saxatilis	0.21	0.15	0.18	-0.61	0.5430
Acanthurus bahianus	8.44	9.86	-0.08	-0.45	0.6500
A. chirurgus	0.16	0.21	-0.14	-0.69	0.4918
A. coeruleus	4.70	2.97	0.23	1.59	0.1121
Bodianus rufus	0.25	0.14	0.27	0.09	0.9320
Cantherhines pullus	1.00	1.02	-0.01	-0.19	0.8498
Chaetodon striatus	1.72	1.56	0.05	-0.72	0.4717
Epinephelus adscensionis	0.09	0.07	0.15	0.40	0.6909
E. cruentatus	0.32	0.37	-0.07	-1.09	0.2736
E. fulvus	0.18	0.23	-0.11	-1.41	0.1584
Gymnothorax moringa	0.79	0.52	0.20	0.38	0.7041
H. chrysargyreum	0.29	0.30	-0.03	0.47	0.6386
H. flavolineatum	1.27	1.57	-0.10	-0.53	0.5961
Holocanthus tricolor	0.67	0.11	0.71	1.61	0.1066
Holocentrus adscensionis	0.11	0.45	-0.61	-1.44	0.1497
H. rufus	0.50	0.10	0.68	0.65	0.5180
Kyphosus sectatrix	0.03	0.01	0.49	0.00	1.0000
Lactophrys triqueter	0.17	0.04	0.65	1.17	0.2430
Lutjanus mahogani	0.06	0.07	-0.09	0.05	0.9569
Microspathodon chrysurus	0.95	2.10	-0.38	-2.19	0.0282
Mulloidichthys martinicus	0.04	0.02	0.37	0.55	0.5842
Myripristis jacobus	0.81	0.89	-0.04	-0.59	0.5522
Pomacanthus paru	0.13	0.02	0.75	1.54	0.1236
Scarus iserti	0.13	0.16	-0.11	0.00	1.0000
S. taeniopterus	0.14	0.22	-0.23	-0.83	0.4051
S. vetula	0.20	0.20	-0.01	0.12	0.9065
Sparisoma aurofrenatum	0.40	0.40	0.68	0.08	0.9388
S. chrysopterum	0.15	0.02	-0.79	1.26	0.2083
S. rubripinne	0.05	0.03	-0.04	0.05	0.9567
S. viride	0.52	0.38	-0.10	0.63	0.5257
Others[1]	0.35	0.36	5.01	-0.23	0.8168

1. "Others" includes19 species caught no more than once in the BMR or NR

Table 8. Trappability in the BMR and NR, and for all sites combined for 24 species. Trappability is defined as the sum of the catch rate at all sites (in the BMR, NR, or both) divided by the sum of the visual census density at those sites. Z= Wilcoxon test statistic, p = Wilcoxon test probability, df = 18. The difference between BMR and NR trappability is significant for all species combined, but not significant for any individual species according to the sequential Bonferroni procedure (adjusted significance level for *Acanthurus bahianus* = 0.0021).

Species	**BMR trappability**	**NR trappability**	**Total trappability**	**Z**	**p**
Abudefduf saxatilis	0.27	1.46	0.41	0.00	1.0000
Acanthurus bahianus	0.37	0.65	0.49	-2.76	0.0058
A. coeruleus	0.69	1.31	0.85	-1.51	0.1307
Bodianus rufus	0.68	0.72	0.70	-1.05	0.2923
Cantherhines pullus	1.04	1.92	1.35	-0.07	0.9431
Chaetodon striatus	2.87	4.69	3.52	-0.63	0.5309
Epinephelus cruentatus	0.15	0.26	0.18	-1.80	0.0716
E. fulvus	0.18	0.36	0.25	-1.48	0.1401
H. chrysargyreum	0.02	0.11	0.03	-0.69	0.4884
H. flavolineatum	0.05	0.16	0.09	-1.63	0.1037
Holocanthus tricolor	1.18	0.33	0.86	-2.07	0.0384
Holocentrus rufus	0.33	0.14	0.27	0.12	0.9028
Kyphosus sectatrix	0.05	0.30	0.06	0.00	1.0000
Lactophrys triqueter	0.46	0.12	0.31	0.53	0.5993
Lutjanus mahogani	0.03	0.07	0.04	-0.93	0.3536
Microspathodon chrysurus	0.07	0.15	0.11	-2.16	0.0308
Mulloidichthys martinicus	0.01	0.02	0.01	0.52	0.6000
Myripristis jacobus	0.32	0.29	0.31	-0.16	0.8694
Scarus iserti	0.05	0.80	0.11	-2.04	0.0409
S. taeniopterus	0.10	0.20	0.14	-0.49	0.6248
S. vetula	0.25	1.50	0.43	-0.11	0.9138
Sparisoma aurofrenatum	0.44	0.55	0.49	-0.32	0.7483
S. rubripinne	0.12	0.34	0.16	0.00	1.0000
S. viride	0.41	0.44	0.42	0.15	0.8811
Total	**0.24**	**0.44**	**0.31**	**-2.31**	**0.0209**

Table 9. The number and length of tagged fish, the number recaptured in trap and visual recapture surveys, and the longest observed movements in each recapture survey, for 35 species of reef fish. Taxa are in alphabetical order by family and species.

Species	Number tagged	Fork length (cm) Median	Fork length (cm) Range	Trap recaptures Number recaptured	Trap recaptures Percent recaptured	Trap recaptures Longest observed movement[1] (m)	Visual recaptures Number of visual recaptures	Visual recaptures Longest observed movement[2] (m)
Acanthuridae								
Acanthurus bahianus	522	14.5	(13.5 - 18.0)	261	50%	422	494	538
A. chirurgus	13	15.0	(13.0 - 16.0)	4	31%	80	3	215
A. coeruleus	127	14.5	(13.0 - 20.5)	78	61%	217	60	171
Balistidae								
Cantherhines pullus	74	17.0	(13.0 - 20.0)	46	62%	95	48	80
Carangidae								
Caranx latus	47	19.0	(16.5 - 33.5)	0	0%		0	
C. ruber	12	19.5	(18.0 - 22.0)	0	0%		1	39
Chaetodontidae								
Chaetodon striatus	44	13.5	(13.0 - 15.5)	22	50%	245	9	127
Haemulidae								
Haemulon carbonarium	9	23.0	(16.0 - 26.5)	4	44%	69	2	0
H. chrysargyreum	21	16.5	(15.0 - 17.5)	4	19%	36	29	0
H. flavolineatum	97	15.5	(13.5 - 17.5)	38	39%	62	86	62
H. sciurus	1	27.5		0	0%		0	
Holocentridae								
Holocentrus adscensionis	22	17.0	(15.0 - 24.0)	14	64%	66	3	0
H. rufus	24	17.5	(15.0 - 21.0)	15	63%	0	32	62
Myripristis jacobus	37	14.5	(13.5 - 17.0)	21	57%	43	6	22
Kyphosidae								
Kyphosus sectatrix	2	25.0	(22.0 - 28.5)	2	100%	217	2	100
Labridae								
Bodianus rufus	4	21.5	(20.5 - 24.0)	3	75%	37	0	

1. Longest MTD (maximum intertrap distance) of any individual
2. Maximum observed distance from tagging site of any individual

Table 9 (continued)

Species	Number tagged	Fork length (cm)		Trap recaptures			Visual recaptures	
		Median	Range	Number recaptured	Percent recaptured	Longest observed movement[1] (m)	Number of visual recaptures	Longest observed movement[2] (m)
Lutjanidae								
Lutjanus apodus	3	37.0	(34.5 - 47.0)	2	67%	616	0	
L. mahogani	8	25.0	(18.0 - 32.0)	1	13%	0	0	
Mullidae								
Mulloidichthys martinicus	3	23.5	(21.5 - 23.5)	0	0%		4	150
Pseudopeneus maculatus	1	23.0		0	0%		0	
Muraenidae								
Gymnothorax moringa	28	(not measured)		10	36%	100	0	
Pomacanthidae								
Holocanthus tricolor	26	16.0	(13.0 - 24.0)	19	73%	217	16	64
Pomacanthus paru	7	15.0	(13.0 - 18.0)	5	71%	117	3	41
Pomacentridae								
Abudefduf saxatilis	7	13.5	(13.0 - 14.5)	1	14%	127	0	
Microspathodon chrysurus	117	14.0	(13.0 - 16.0)	60	51%	62	133	43
Scaridae								
Scarus iserti	6	18.5	(17.5 - 26.0)	0	0%		0	
S. taeniopterus	27	21.0	(17.0 - 27.0)	3	11%	0	9	79
S. vetula	2	22.5	(19.5 - 26.0)	0	0%		1	57
Sparisoma aurofrenatum	27	18.5	(14.5 - 21.5)	7	26%	53	8	97
S. chrysopterum	10	21.5	(18.5 - 27.0)	1	10%	0		
S. rubripinne	2	22.0	(22.0 - 22.5)	1	50%	0	1	161
S. viride	56	18.5	(14.5 - 28.0)	20	36%	110	14	127
Serranidae								
Epinephelus adscensionis	7	38.0	(20.0 - 52.0)	2	29%	44		
E. cruentatus	29	26.5	(20.5 - 33.0)	11	38%	32	10	32
E. fulvus	21	26.0	(18.0 - 32.0)	11	52%	27	15	27
Total	**1443**			**666**	**46%**		**989**	

1. Longest MTD (maximum intertrap distance) of any individual
2. Maximum observed distance from tagging site of any individual

Table 10. Estimates of the mobility of 13 species based on trap recaptures of tagged fish. MTD is the maximum inter-trap distance of a recaptured individual (see Methods).

Species	N[1]	Median MTD (m)	Weighted median MTD[2] (m)	Standardized MTD (m)
Acanthuridae				
Acanthurus bahianus	261	0	88	116 [3]
A. coeruleus	78	0	39	88 [3]
Balistidae				
Cantherines pullus	46	11	43	42 [3]
Chaetodontidae				
Chaetodon striatus	22	62	65	110 [3]
Haemulidae				
Haemulon flavolineatum	38	0	0	0
Holocentridae				
Holocentrus adscensionis	14	0	22	22
H. rufus	15	0	0	0
Myripristis jacobus	21	0	0	26 [3]
Pomacanthidae				
Holocanthus tricolor	19	0	62	62
Pomacentridae				
Microspathodon chrysurus	60	0	0	0
Scaridae				
Sparisoma viride	20	27	43	43
Serranidae				
Epinephelus cruentatus	11	0	0	0
E. fulvus	11	0	0	8 [3]

[1] number of individuals recaptured

[2] each value weighted by a correction factor to account for bias due to the distribution of recapture locations.

[3] MTD after 5 recaptures predicted by a weighted linear regression of MTD against number of recaptures.

Table 11. Estimates of the mobility of 14 species based on visual recaptures of tagged fish.

Species	**N**[1]	**Median visual recapture distance (m)**	**Weighted median visual recapture distance**[2] **(m)**
Acanthuridae			
Acanthurus bahianus	494	0	41
A. coeruleus	60	0	44
Balistidae			
Cantherines pullus	48	0	22
Chaetodontidae			
Chaetodon striatus	9	0	39
Haemulidae			
Haemulon chrysargyreum	29	0	0
H. flavolineatum	86	0	0
Holocentridae			
Holocentrus rufus	32	0	0
Pomacanthidae			
Holocanthus tricolor	16	0	0
Pomacentridae			
Microspathodon chrysurus	133	0	0
Scaridae			
Scarus taeniopterus	9	0	0
Sparisoma aurofrenatum	8	0	0
S. viride	14	0	27
Serranidae			
Epinephelus cruentatus	10	0	0
E. fulvus	15	0	0

[1] total number of recaptures

[2] each value weighted by a correction factor to account for bias due to the distribution of recapture locations.

Table 12. The speed (distance per minute) and velocity (net displacement per minute) of 22 species of diurnally-active reef fish. Ranges (minimum – maximum) in parentheses.

Species	**N**	**Median speed ($m.min^{-1}$)**	**Median velocity ($m.min^{-1}$)**
Acanthuridae			
Acanthurus bahianus	10	6.8 (0.6 - 12.8)	2.8 (0.4 - 7.8)
A. chirurgus	8	15.0 (4.0 - 17.2)	4.9 (0.6 - 15.2)
A. coeruleus	8	7.6 (5.7 - 14.4)	3.6 (0.1 - 12.3)
Balistidae			
Cantherhines pullus	8	6.4 (4.3 - 14.8)	5.3 (3.4 - 11.8)
Chaetodontidae			
Chaetodon capistratus	9	11.7 (5.3 - 19.4)	4.4 (0.8 - 12.0)
Kyphosidae			
Kyphosus sectatrix	8	18.3 (8.6 - 23.3)	8.0 (0.3 - 17.2)
Labridae			
Bodianus rufus	8	11.4 (7.3 - 27)	4.8 (1.5 - 21.6)
Lutjanidae			
L. mahogani	9	6.2 (0.5 - 24.9)	2.0 (0.1 - 5.9)
Mullidae			
Mulloidichthys martinicus	9	8.9 (3.1 - 16.8)	6.1 (0.2 - 8.8)
Ostraciidae			
Lactophrys triqueter	8	3.4 (1.2 - 10.1)	1.8 (0.3 - 7.0)
Pomacanthidae			
Holocanthus tricolor	8	7.6 (1.5 - 12.0)	3.9 (0.7 - 9.1)
Pomacanthus paru	8	6.1 (1.9 - 9.7)	2.6 (0.0 - 5.2)
Pomacentridae			
Abudefduf saxatilis	9	17.6 (9.3 - 27.6)	8.8 (1.3 - 16.6)
Microspathodon chrysurus	9	5.6 (3.2 - 7.6)	2.4 (0.3 - 4.9)
Scaridae			
Scarus iserti	16	9.7 (5.2 - 22.8)	3.4 (0.5 - 9.4)
S. taeniopterus	20	9.2 (2.7 - 27.4)	4.8 (0.7 - 12.0)
S. vetula	16	17.9 (4.0 - 30.8)	4.1 (1.1 - 21.6)
Sparisoma aurofrenatum	16	10.5 (4.3 - 21.6)	5.2 (0.9 - 14.6)
S. rubripinne	10	30.7 (12.8 - 47.1)	12.0 (5.0 - 44.3)
S. viride	16	22.3 (5.0 - 40.0)	8.3 (2.1 - 31.6)
Serranidae			
E. cruentatus	9	2.0 (0 - 2.8)	0.5 (0.0 - 2.3)
E. fulvus	8	7.9 (0.4 - 18.8)	3.7 (0.1 - 11.3)

Table 13. Spearman rank correlations between short-term and mark-recapture based estimates of species mobility. r = correlation coefficient; sample size (number of species, N) and significance value (p) for each correlation are given in parentheses.

	Standardized Maximum Inter-trap Distance (m)	**Weighted median visua recapture distance (m)**
Median speed ($m.min^{-1}$)	$\rho = 0.49$ (N=9, p=0.18)	$\rho = 0.21$ (N=11, p=0.54)
Median velocity ($m.min^{-1}$)	$\rho = 0.34$ (N=9, p=0.37)	$\rho = -0.01$ (N=11, p=0.97)

Table 14. Spearman correlation coefficients (ρ) and significance levels (p) for correlations between indices of reserve effectiveness and indices of mobility based on the mark-recapture and short-term mobility studies. RDD = relative difference in density, RDS = relative difference in size, RDC = relative difference in catch rate. Predicted reserve effectiveness indices (from Tables 4 and 6) control for habitat correlates of density and size. Sample sizes (number of species) are in parentheses.

	Reserve effectiveness indices			**Predicted reserve effectiveness indices**	
Mobility index	**RDD**	**RDS**	**RDC**	**RDD**	**RDS**
Standardized maximum inter-trap distance (m)	$\rho = -0.10$ $p = 0.74$ (12)	$\rho = -0.01$ $p = 0.97$ (12)	$\rho = 0.38$ $p = 0.22$ (12)	$\rho = 0.04$ $p = 0.90$ (12)	$\rho = -0.13$ $p = 0.69$ (12)
Weighted median visual recapture distance (m)	$\rho = 0.17$ $p = 0.57$ (13)	$\rho = -0.20$ $p = 0.51$ (13)	$\rho = 0.46$ $p = 0.11$ (13)	$\rho = 0.12$ $p = 0.70$ (13)	$\rho = -0.38$ $p = 0.21$ (13)
Median speed ($\mathrm{m.min^{-1}}$)	$\rho = 0.43$ $p = 0.07$ (19)	$\rho = 0.07$ $p = 0.78$ (19)	$\rho = 0.25$ $p = 0.29$ (19)	$\rho = 0.35$ $p = 0.14$ (19)	$\rho = -0.30$ $p = 0.22$ (19)
Median velocity ($\mathrm{m.min^{-1}}$)	$\rho = 0.31$ $p = 0.19$ (19)	$\rho = -0.13$ $p = 0.59$ (19)	$\rho = 0.37$ $p = 0.12$ (19)	$\rho = 0.32$ $p = 0.18$ (19)	$\rho = -0.07$ $p = 0.79$ (19)

Figure 1. The mobility of exploited species should influence their distribution relative to the boundaries of a no-take marine reserve. Sedentary fishes should exhibit a sudden change in density at the reserve boundary, while more mobile fishes should exhibit a more gradual increase in density towards the centre of the reserve. Near the reserve boundary, these different gradients in abundance should be detectable as differences in the relative difference in mean density between reserve and non-reserve. Modified from Rakitin & Kramer 1996.

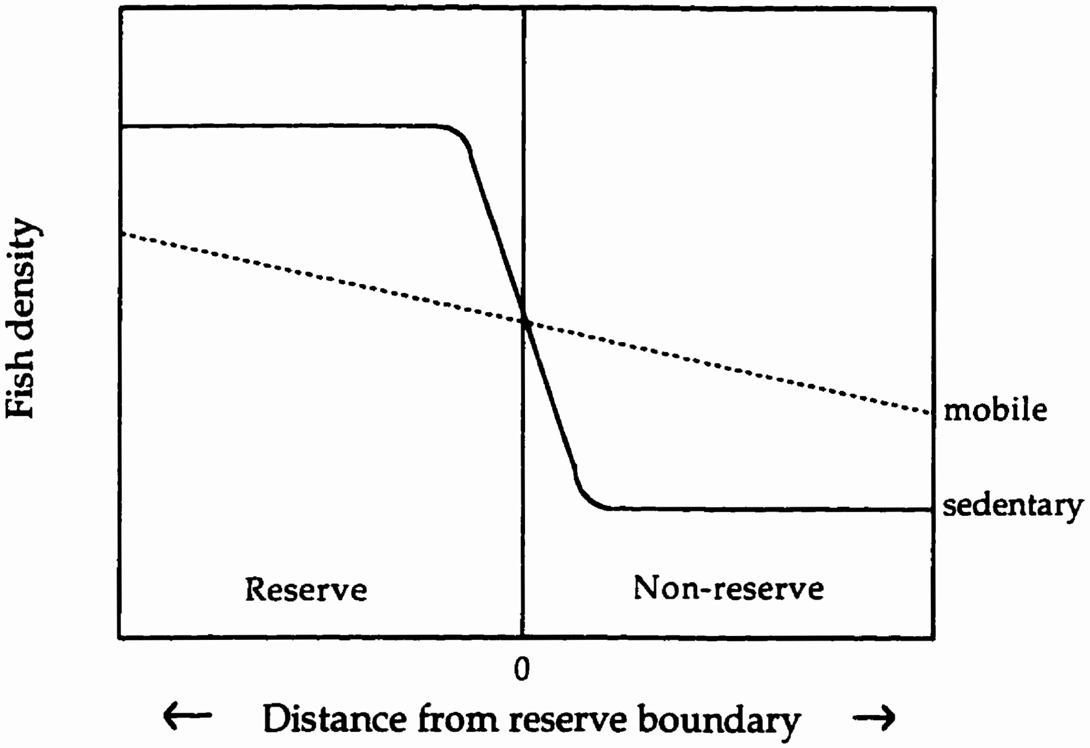

Fish density
mobile
sedentary
Reserve
Non-reserve
0
← Distance from reserve boundary →

Figure 2. Graphical model of the potential effects of fish mobility on marine reserve effectiveness, spillover, and reproductive output. **A.** Increases in mobility (the likelihood of fish crossing the reserve boundary) will reduce the ability of a marine reserve to maintain a differential of fish density, size, or biomass (effectiveness) between the reserve and adjacent exploited areas. **B.** Spillover (the net transfer of fish biomass from reserve to non-reserve) is a product of mobility and effectiveness. Thus, spillover will peak at intermediate mobility. **C.** Potential reproductive output is a geometric function of effectiveness.

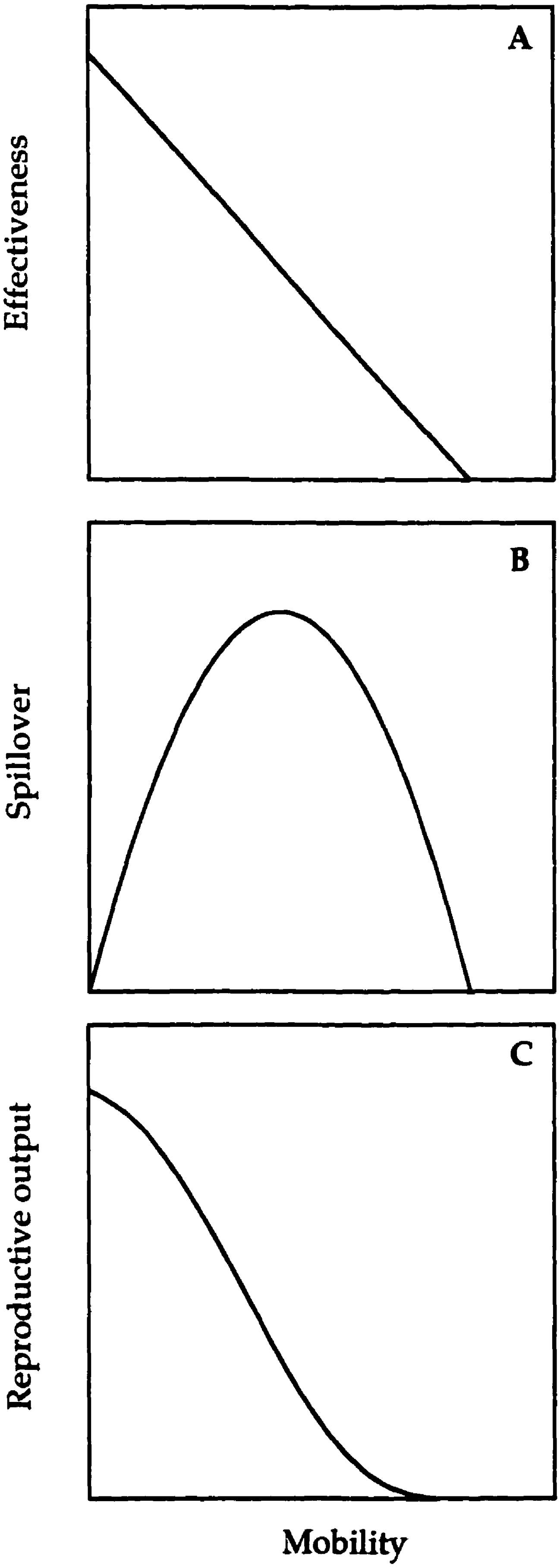

A
Effectiveness
B
Spillover
C
Reproductive output
Mobility

Figure 3. Map of the study site showing the four study reefs (stippled areas) and study sites (squares). Filled squares indicate the position of the twenty 400 m^2 sites where measures of fish density, catch rate, habitat characteristics, and tagging and recaptures were performed. Open squares indicate the position of the 3 additional sites where only tagging and recaptures were performed. The northern BMR boundary is indicated by a dotted line extending from shore. Study reef (and site) names, in order from South to North, are: South Bellairs (SB5, SB4, SB6, SB8, SB1), North Bellairs (filled: NB1, NB2, NB4, NB5, NB9, NB6, NB8, NB7), Heron Bay (HE1, HE2, HE3, HE4, HE5), and Bachelor Hall (BA1, BA2, BA3, BA5, BA4). The shaded area represents land. **Inset:** Map of Barbados showing the location of the Barbados Marine Reserve (BMR) and the study area.

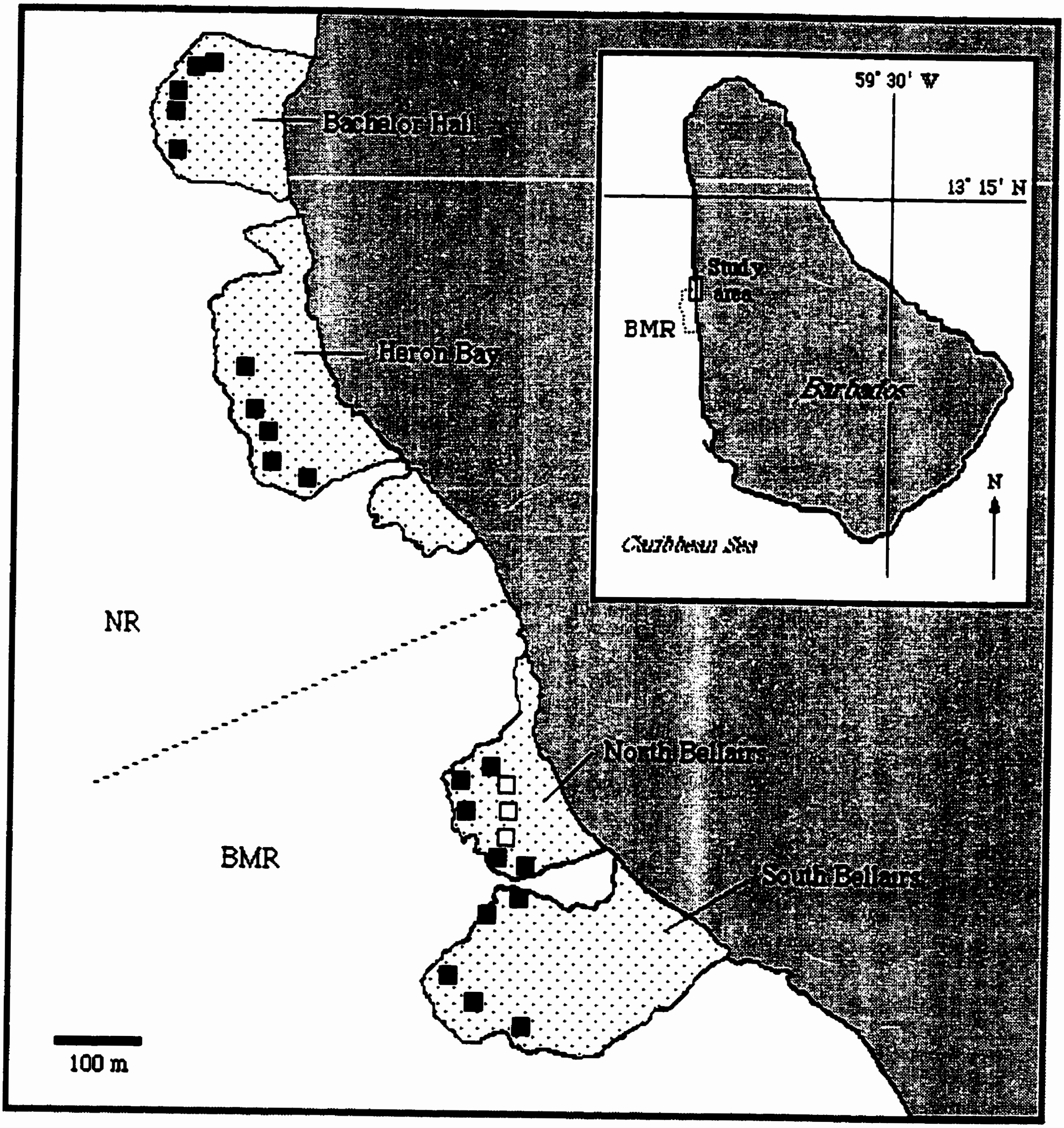

Bachelor Hall
Heron Bay
NR
BMR
North Bellairs
South Bellairs
100 m
59° 30' W
13° 15' N
Study area
BMR
Barbados
Caribbean Sea
N

Figure 4. Total density (number per 400 m^2) of fish of trappable size counted in visual censuses as a function of distance (m) from the northern Barbados Marine Reserve (BMR) boundary. Closed circles indicate BMR sites and open circles NR sites. Values are the mean (± SD) of three census counts per site. The fit of the linear regression ($r^2 = 0.439$, df = 1,18; $p < 0.005$) is similar to that of a step-function split at the reserve boundary ($r^2 = 0.375$, df = 1,18; $p < 0.0001$). Note the $\log_{10}$-scale of the ordinate axis.

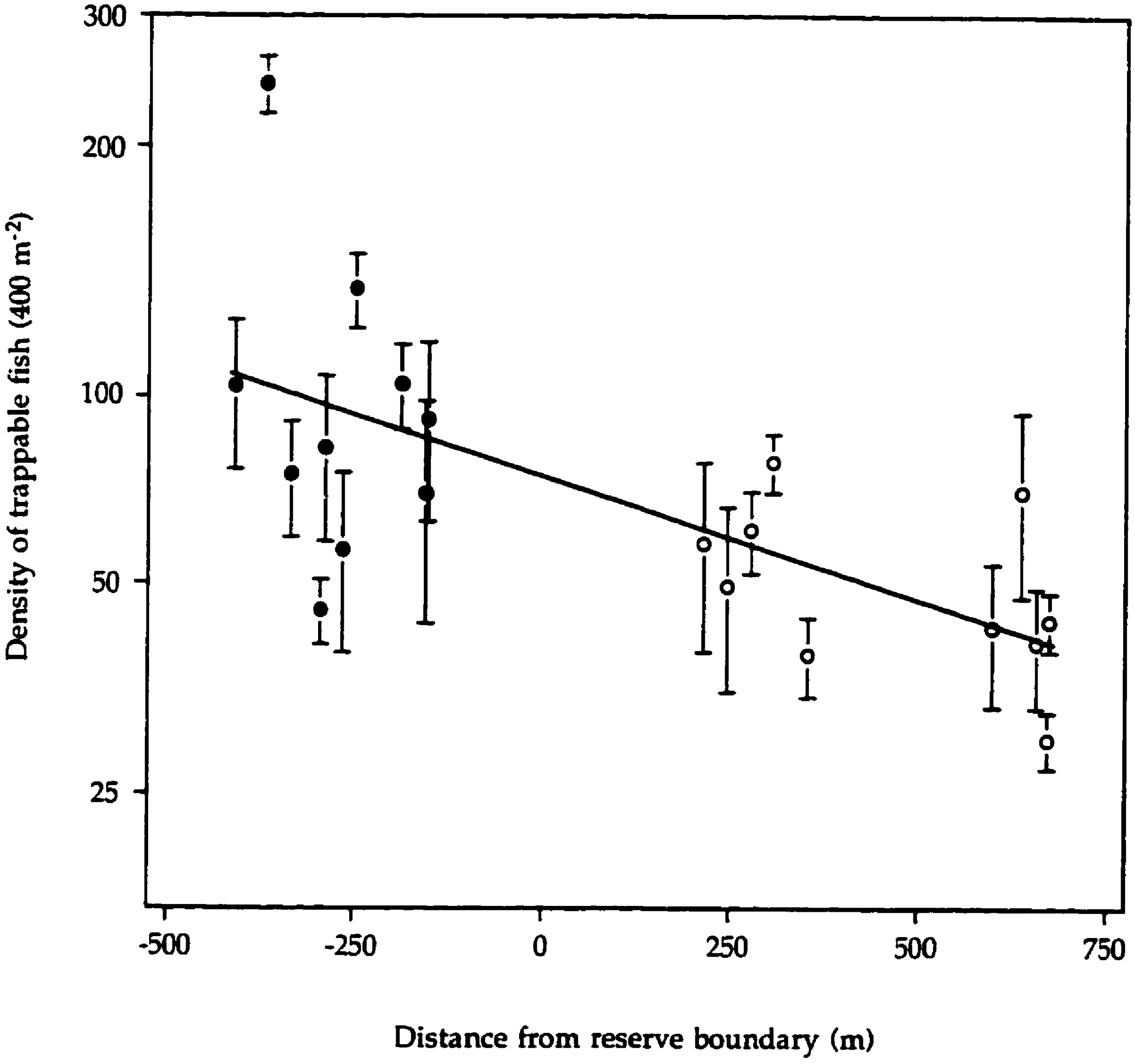

300
200
100
50
25
Density of trappable fish (400 m^{-2})
-500
-250
0
250
500
750
Distance from reserve boundary (m)

Figure 5. Mean estimated fork length (cm) of all fish of trappable size counted in visual censuses as a function of distance (m) from the northern Barbados Marine Reserve (BMR) boundary. Closed circles indicate BMR sites and open circles NR sites. The fit of the linear regression ($r^2 = 0.64$, df = 1,18; $p < 0.0001$) is similar to that of a step-function split at the reserve boundary ($r^2 = 0.63$, df = 1,18; $p < 0.0001$).

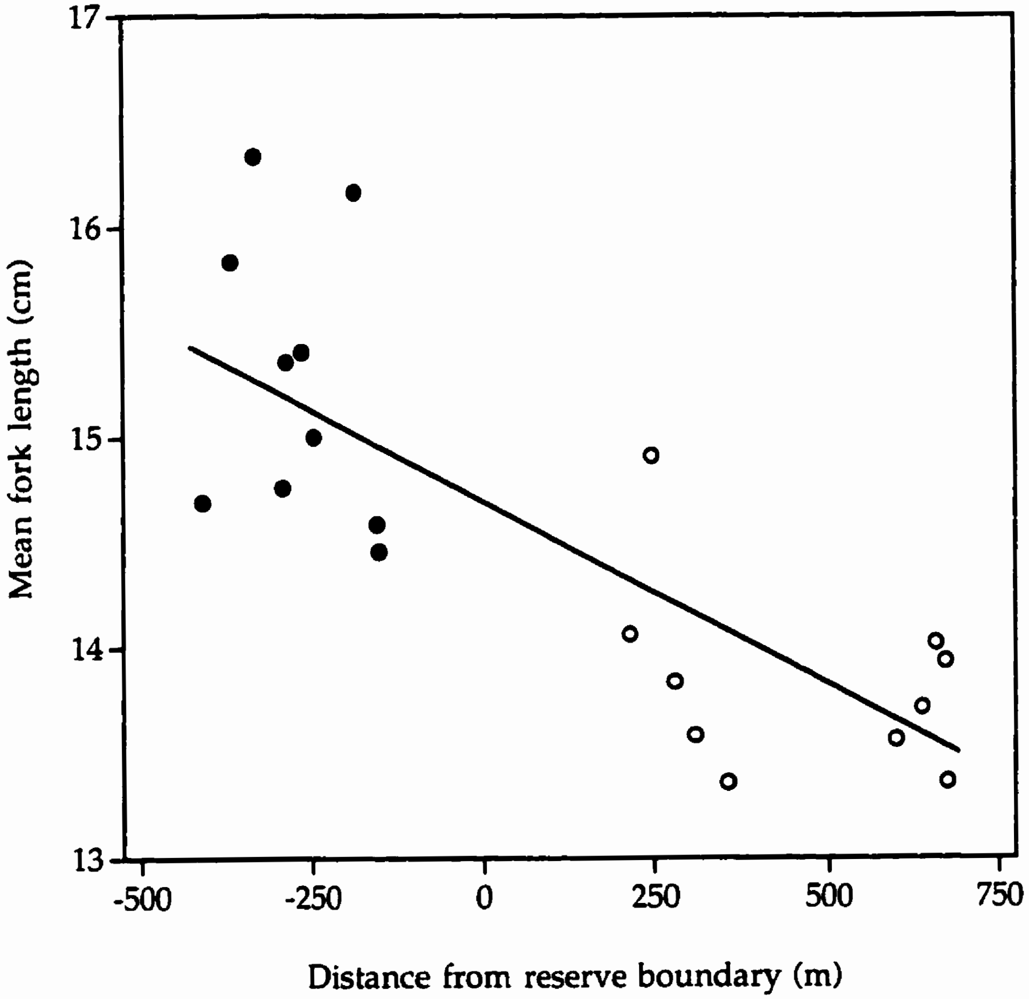
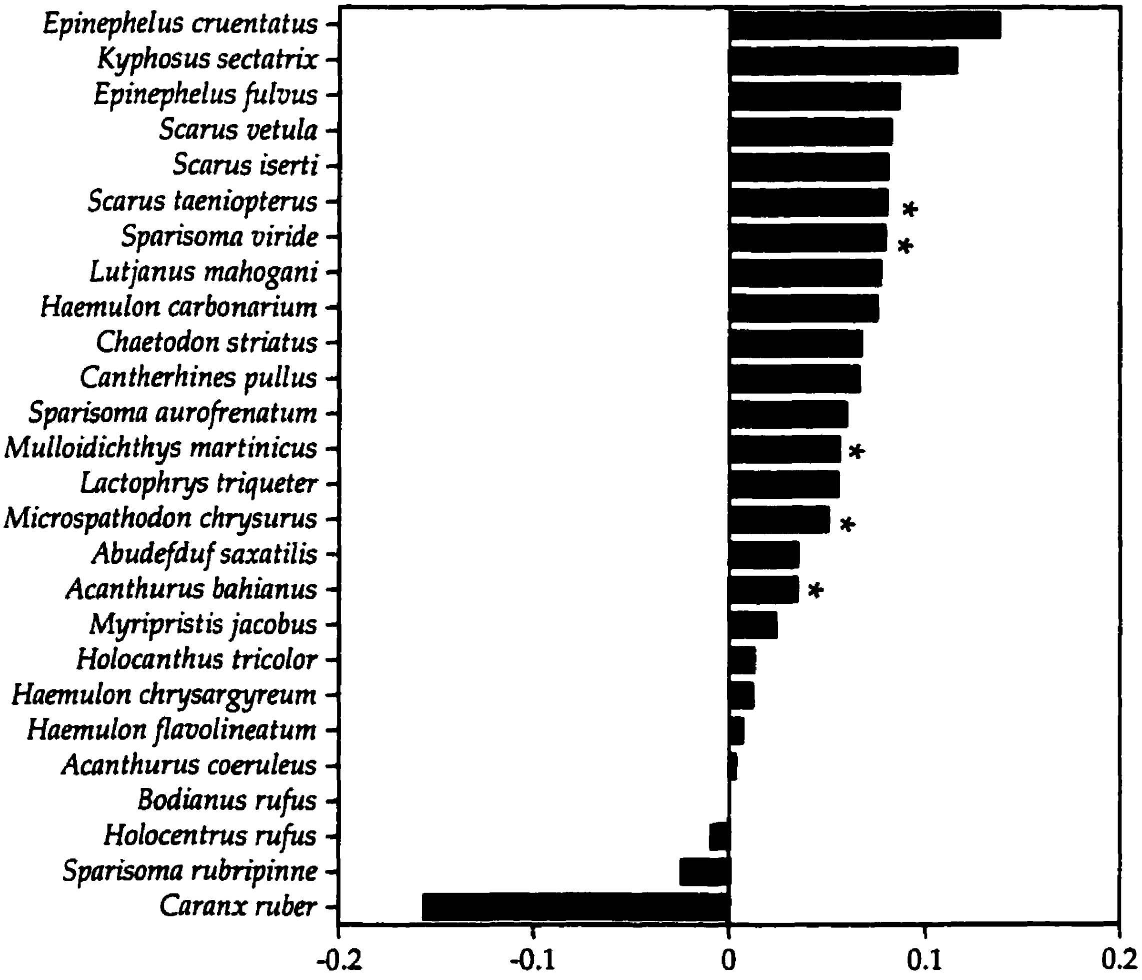
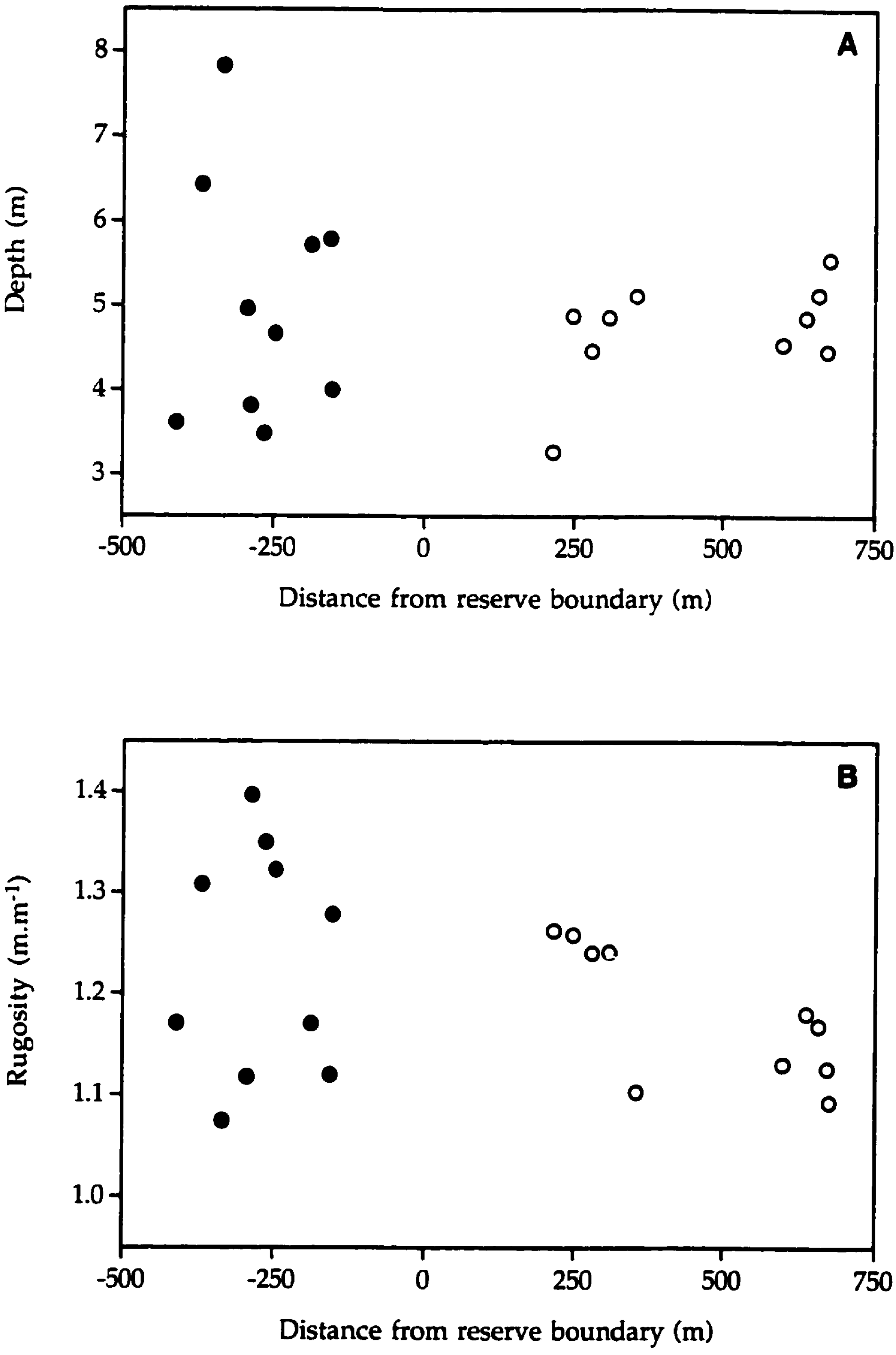

17
16
15
14
13
Mean fork length (cm)
-500
-250
0
250
500
750
Distance from reserve boundary (m)

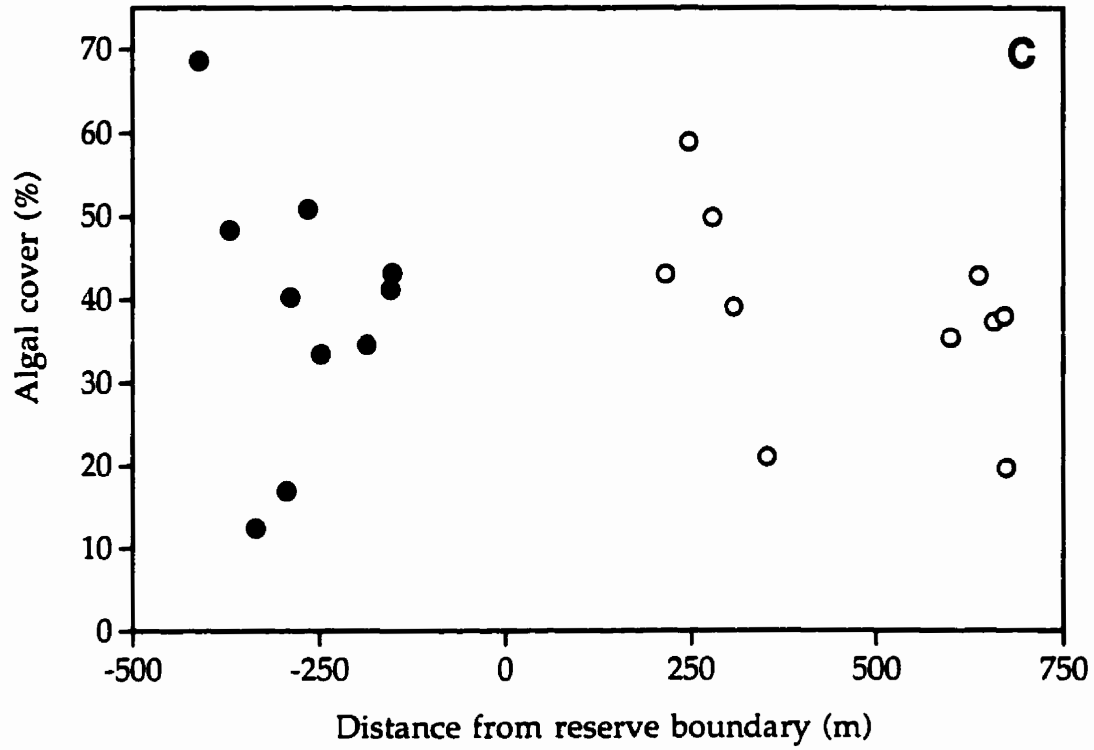
Figure 6. The relative difference in size (estimated fork length, cm) between the BMR and NR for 26 species. Asterisks indicate a significant difference in size between the BMR and NR (Wilcoxon test, sequential Bonferroni-adjusted α; sample sizes are given in Table 2).



$$\text{RDS} = \frac{\text{Mean FL (BMR) - Mean FL (NR)}}{\text{Maximum recorded length}}$$

Figure 7. Habitat characteristics of sites as a function of distance (m) from the northern Barbados Marine Reserve (BMR) boundary. Closed circles indicate BMR sites and open circles NR sites. **A.** Site depth (m). **B.** Substrate rugosity index. **C.** Percent algal cover of reef, rubble, and sand substrate. **D.** Percent live coral cover of reef and rubble substrate (excludes sand substrate).


A
Depth (m)
8
7
6
5
4
3
-500
-250
0
250
500
750
Distance from reserve boundary (m)
B
Rugosity (m.m⁻¹)
1.4
1.3
1.2
1.1
1.0
-500
-250
0
250
500
750
Distance from reserve boundary (m)


C
Algal cover (%)
0
10
20
30
40
50
60
70
-500
-250
0
250
500
750
Distance from reserve boundary (m)

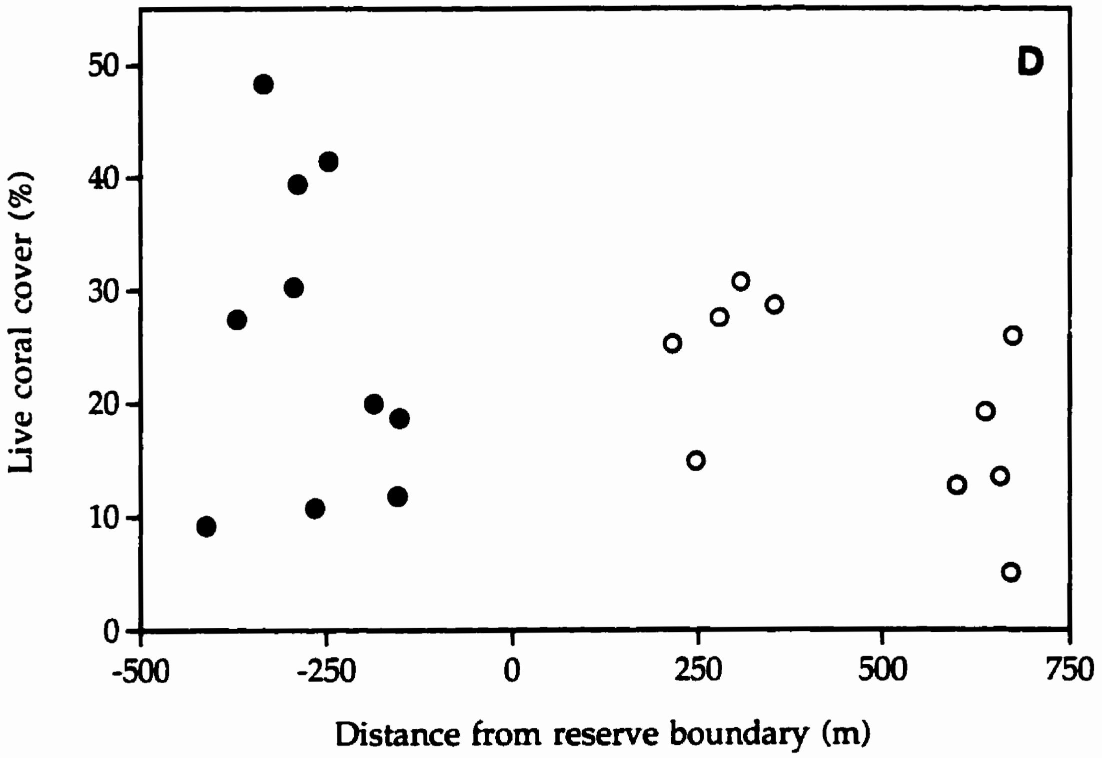

D
Live coral cover (%)
0
10
20
30
40
50
-500
-250
0
250
500
750
Distance from reserve boundary (m)

Figure 8. Abiotic substrate composition (%) by site. Solid bars indicate percent reef, stippled bars percent rubble, and open bars percent sand. Sites are listed in order from South to North.

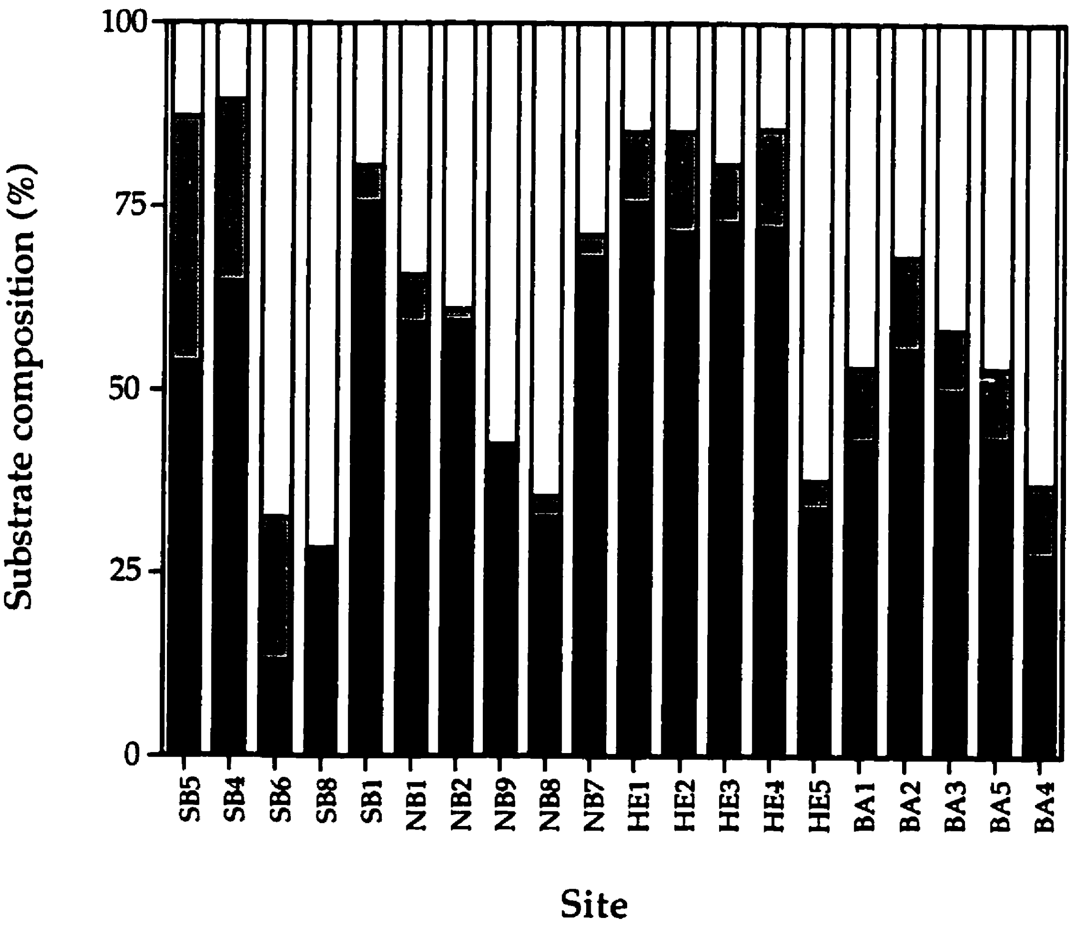

Substrate composition (%)
100
75
50
25
0
SB5
SB4
SB6
SB8
SB1
NB1
NB2
NB9
NB8
NB7
HE1
HE2
HE3
HE4
HE5
BA1
BA2
BA3
BA5
BA4
Site

Figure 9. The predicted density (number of fish per 400 m^2) at each site after controlling for habitat correlates of species density (see text) as a function of distance from the northern BMR boundary. Closed circles indicate BMR sites and open circles NR sites.

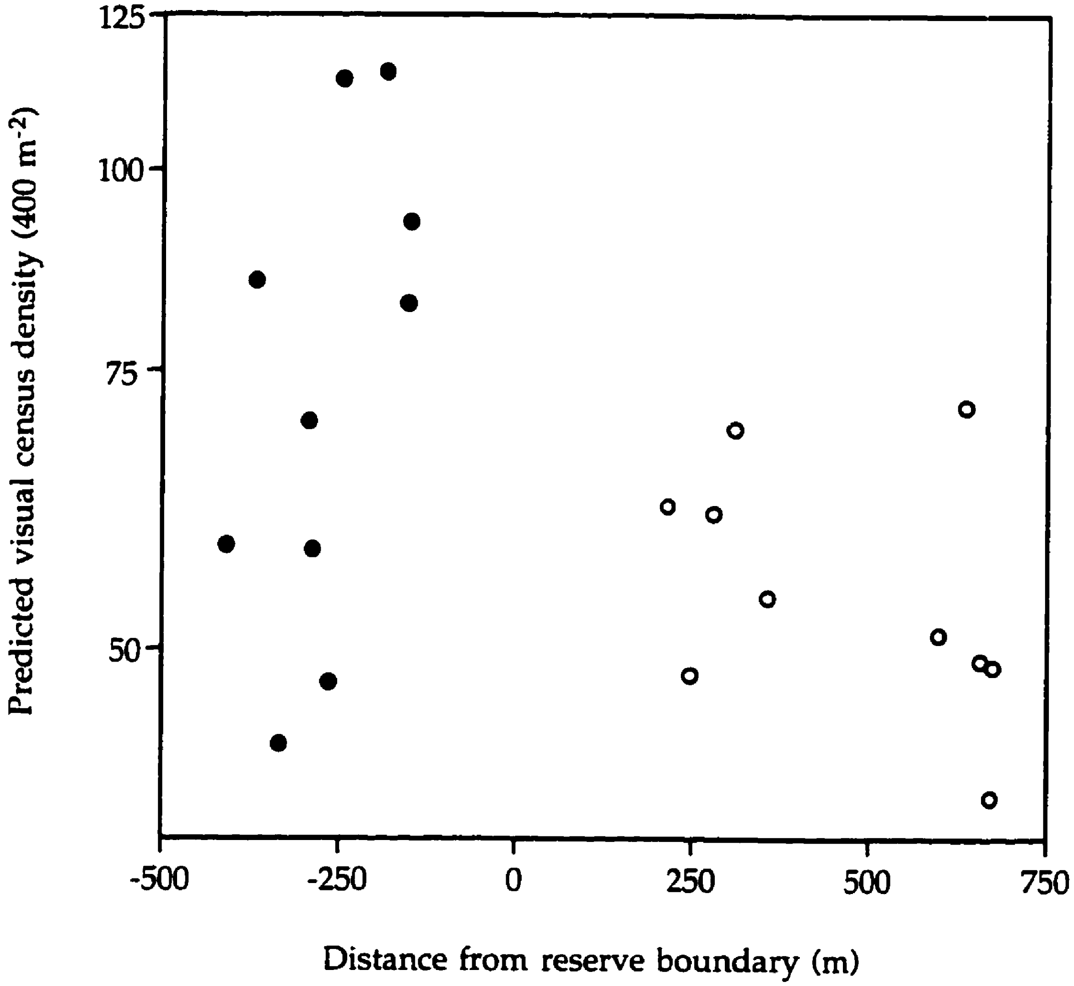

125
100
75
50
-500
-250
0
250
500
750
Predicted visual census density (400 m^{-2})
Distance from reserve boundary (m)

Figure 10. Mean (± SD) number of fish caught per trap set at each site as a function of distance from the northern BMR boundary. Closed circles indicate BMR sites and open circles NR sites. The solid line is the regression line for BMR sites ($r^2 = 0.78$, $F = 27.62$, df = 1,8; $p < 0.001$), and the broken line is the regression line for NR sites ($r^2 = 0.56$, $F = 10.35$, df = 1,8; $p < 0.05$).

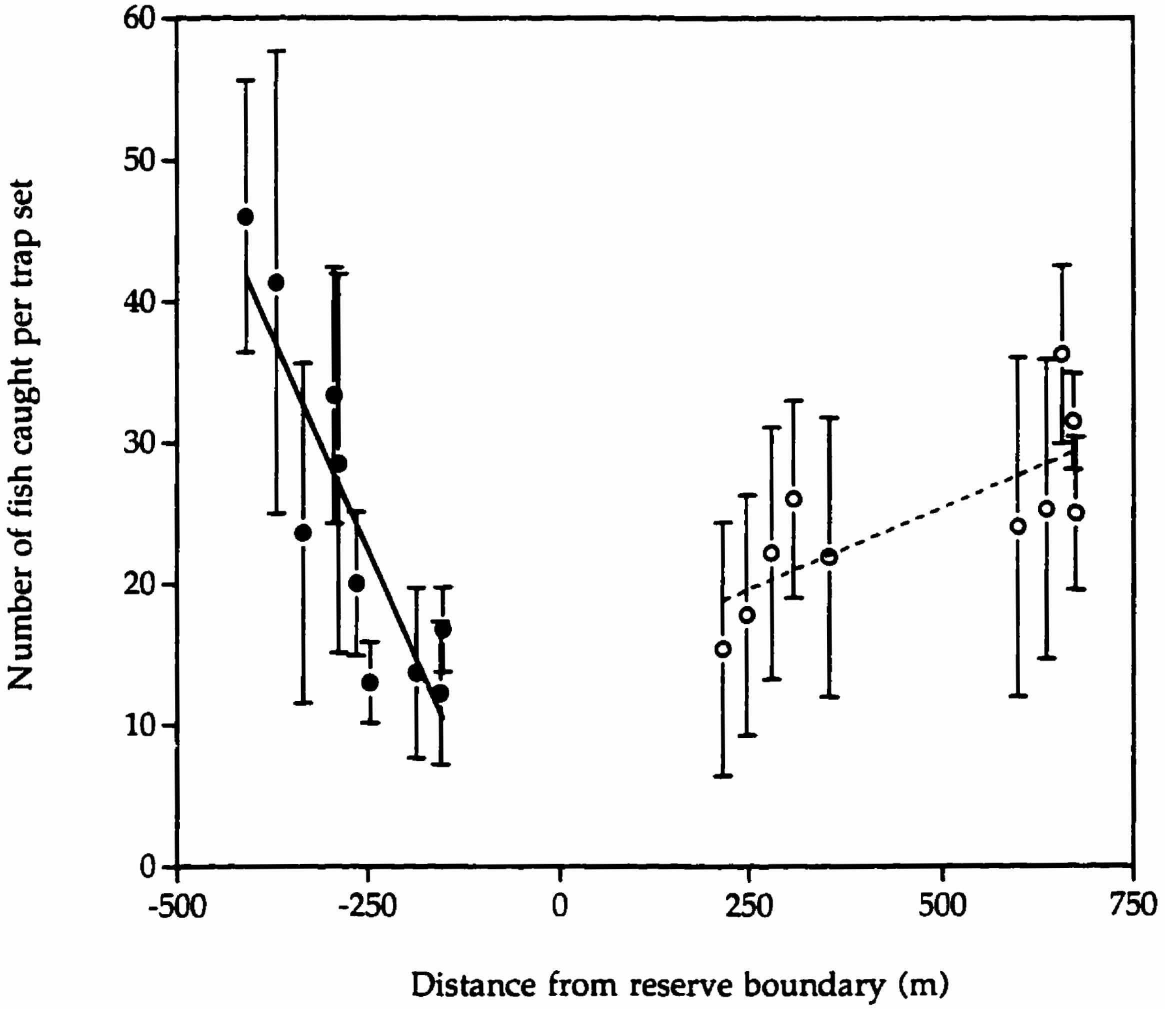
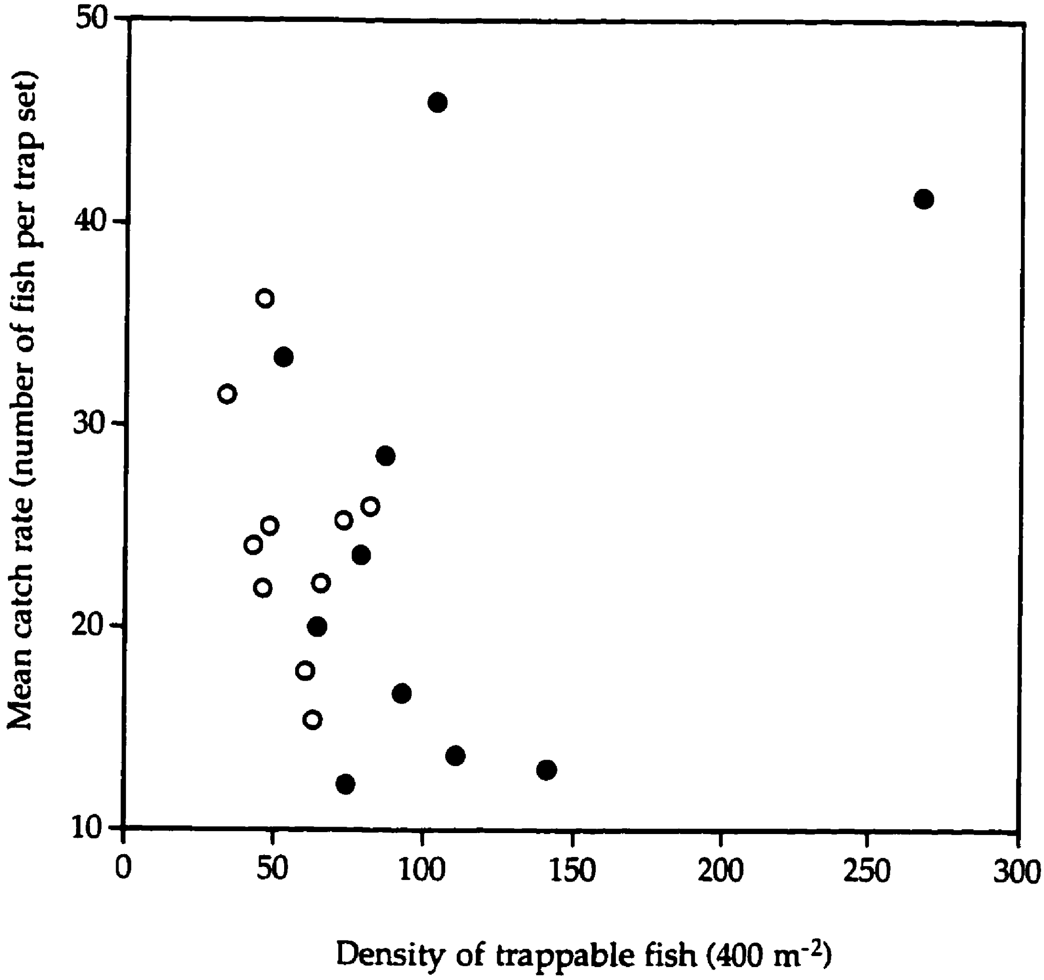

60
50
40
30
20
10
0
Number of fish caught per trap set
-500
-250
0
250
500
750
Distance from reserve boundary (m)

Figure 11. Catch rate (mean number of fish caught per trap set) at each site as a function of the visual census density of trappable fish (mean number per 400 m^2) at that site.



Mean catch rate (number of fish per trap set)
10
20
30
40
50
0
50
100
150
200
250
300
Density of trappable fish (400 m-2)

Figure 12. Trappability ($\log_{10}$-transformed) as a function of distance from the northern BMR boundary. Closed circles indicate BMR sites and open circles NR sites. Note the $\log_{10}$-scale of the both axes. Trappability is the ratio of the mean catch rate at a site to the visual census density of trappable fishes at that site; the units are (fish•400 m^{-2})• (fish•trap set^{-1})$^{-1}$, or (trap set^{-1} • 400 m^{2}).

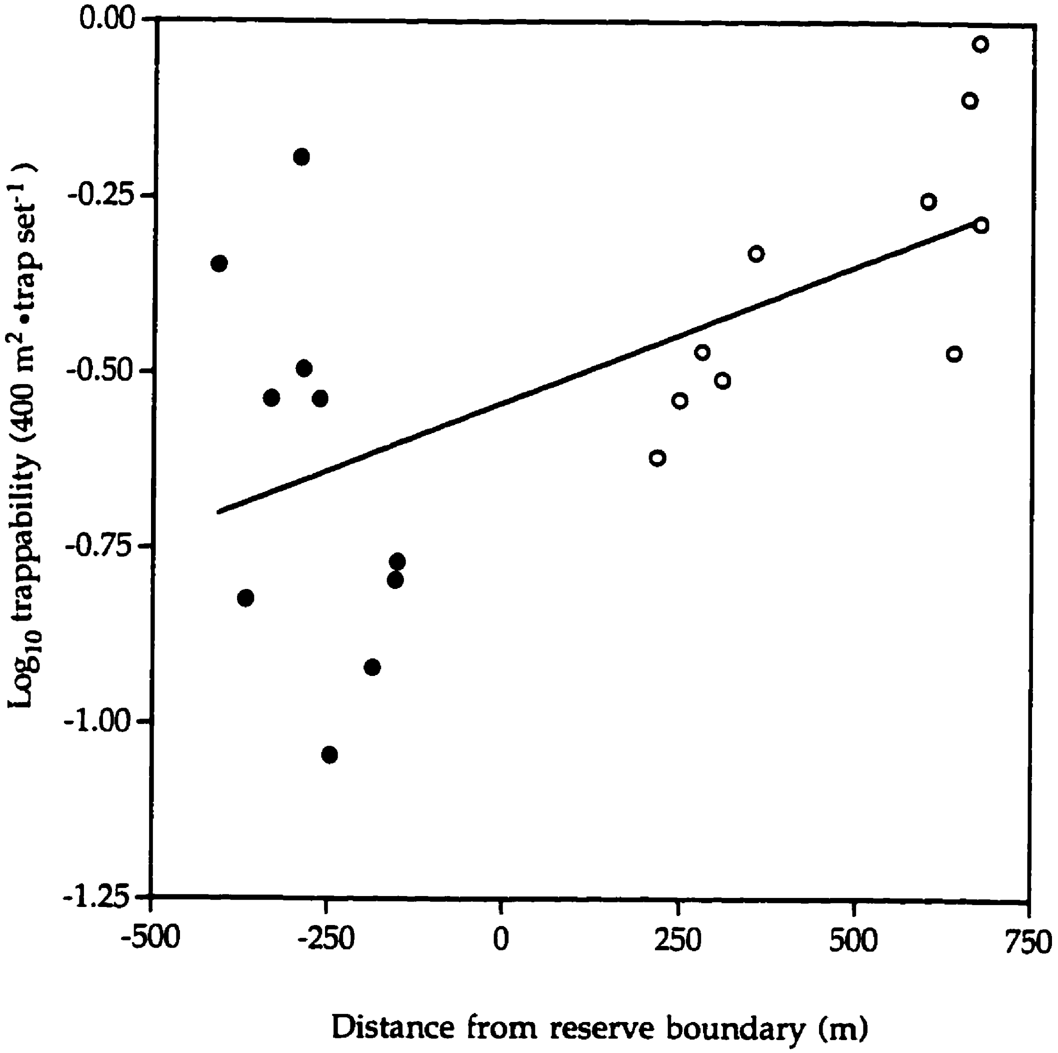

0.00
-0.25
-0.50
-0.75
-1.00
-1.25
Log$_{10}$ trappability (400 m^2 •trap set^{-1})
-500
-250
0
250
500
750
Distance from reserve boundary (m)

Figure 13. Observed movements of fish among study reefs. **1.** One ocean surgeon (Acanthurus bahianus) tagged at site BA2 was recaptured in a trap at site HE1, 422 m away. **2.** Two schoolmaster snappers (Lutjanus apodus) tagged at site HE2 were recaptured in a trap at SB4, 616 m away. **3.** One ocean surgeon (Acanthurus bahianus) tagged at site HE2 was visually recaptured at site NB2, 498 m away. **4.** 84 individuals (from 7 families) recaptured in traps moved between North and South Bellairs reefs at least once. See Figure 3 for reef and site names.

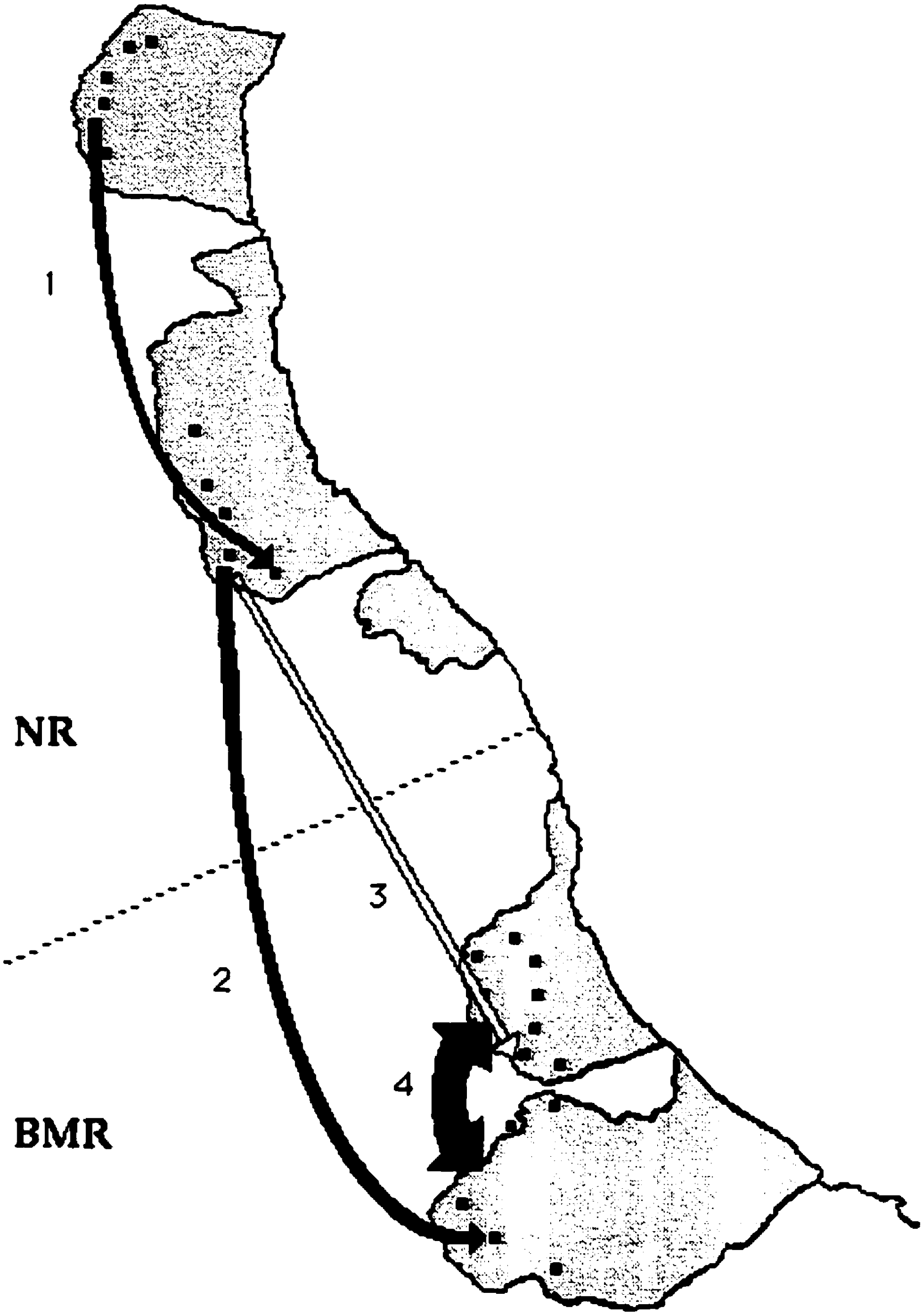
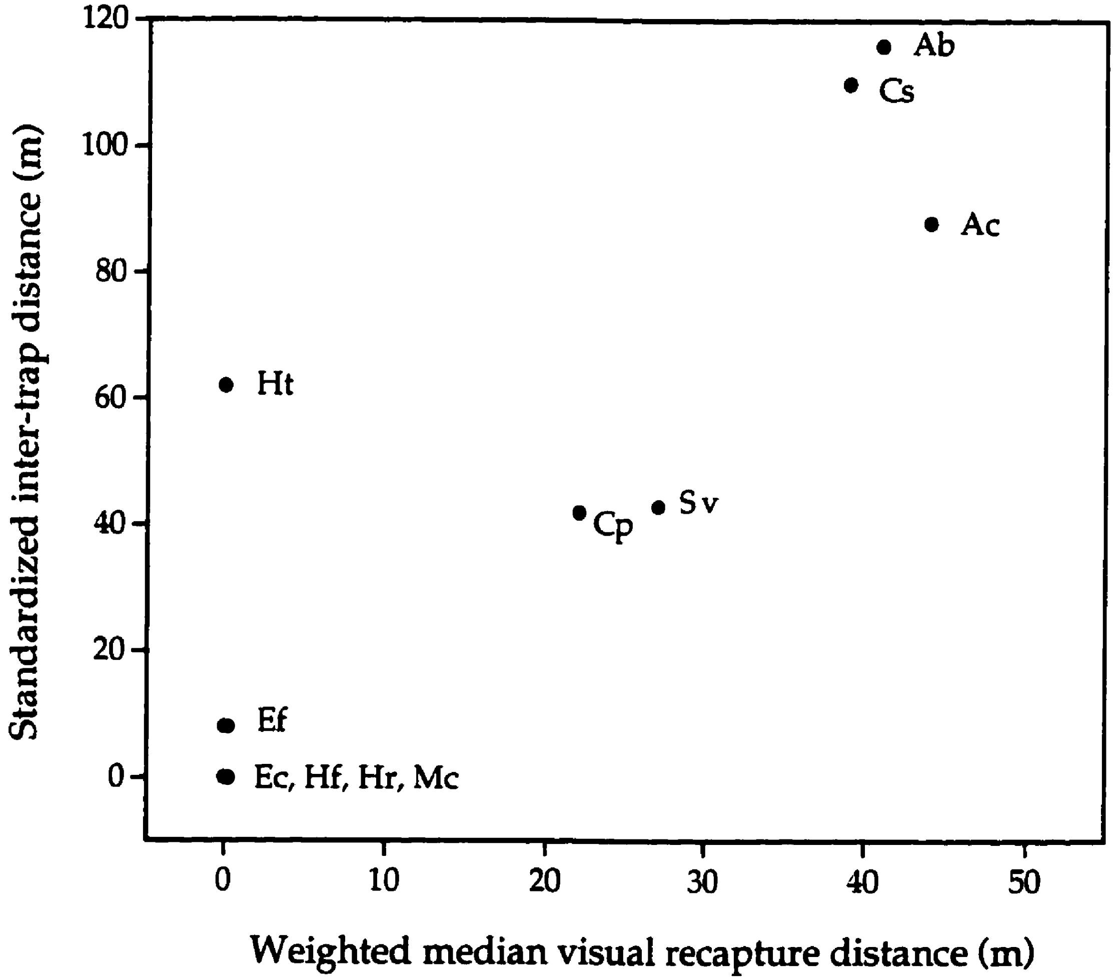

1
NR
3
2
4
BMR

Figure 14. Mobility estimates of 11 species based on trap and visual recaptures of tagged individuals. Trap recapture-based mobility is the standardized maximum intertrap distance (m) of a species after 5 recaptures. Visual recapture-based mobility is the weighted median visual recapture distance (m) of a species. **Ab** = Acanthurus bahianus, **Ac** = Acanthurus coeruleus, **Cs** = Chaetodon striatus, **Cp** = Cantherhines pullus, **Ec** = Epinephelus cruentatus, **Ef** = Epinephelus fulvus, **Hr** = Holocentrus rufus, **Hf** = Haemulon flavolineatum, **Ht** = Holocanthus tricolor, **Mc** = Microspathodon chrysurus, **Sv** = Sparisoma viride.


Ab
Cs
Ac
Ht
Cp
Sv
Ef
Ec, Hf, Hr, Mc
120
100
80
60
40
20
0
0
10
20
30
40
50
Standardized inter-trap distance (m)
Weighted median visual recapture distance (m)

Appendix 1 - Tag loss

Introduction

In order to estimate the rate at which fish lost tags, we double-tagged a subset of fish in the mark-recapture study. Over the course of the study, 169 fish (Table A1.1) were double-tagged with modified Floy™ FD-68B tags (Floy Mfg. Co.). Tags measured 25.4 mm long from tip to anchor, with 12.5 mm of 1.5 mm diameter tubing at the free end. Two tags were inserted in the dorsal musculature on the same side of the body, 1.5 - 4 cm apart. All of the fish of a given species and tag code were either single- or double-tagged. Thus, recaptures of fish bearing a single tag, but with a tag code indicating the fish had been double-tagged, provided evidence of tag loss.

Tag loss formula

If tags are lost at a rate **TL** (where **TL** is the cumulative proportion of tags lost after a time interval, **t**, since tagging), and assuming tags on the same fish are lost independently of each other, the expected proportions of recaptured double-tagged fish with one (**ST**) and two (**DT**) remaining tags are:

$$\mathbf{ST_t = 2\,(1\text{-}TL)\,TL}$$

$$\mathbf{DT_t = (1\text{-}TL)^2}$$

(The number of fish that have lost both tags (**NT** = TL^2) can not be calculated from recapture data.)

The ratio of recaptured fish with one and two remaining tags at time t,

$$DT/ST = (1-TL)^2 / 2\,(1-TL)\,TL$$

provides an estimate of the cumulative rate of tag loss (**TL**) at time t:

$$TL = 1 / (\,2\,(DT/ST) + 1\,)$$

Alternatively, tag retention (**TR = 1 - TL**), defined as the proportion of tags retained after time t, can be calculated as:

$$TR = 1 - (1 / (\,2\,(DT/ST) + 1\,)$$

Violation of the assumption of independent tag loss will result in an understimation of the rate of tag loss. Thus, **TL** can be considered a minimum estimate of the rate of tag loss.

Fish were excluded from the calculation of **DT/ST** after their date of last recapture. Thus, the number of fish included in the calculation of this ratio decreases over time. We estimated the ratio **DT/ST** as long as the sample size was greater than or equal to 10 individuals (Acanthuridae: ≤ 81 days, Haemulidae: ≤ 20 days, Serranidae: ≤ 22 days).

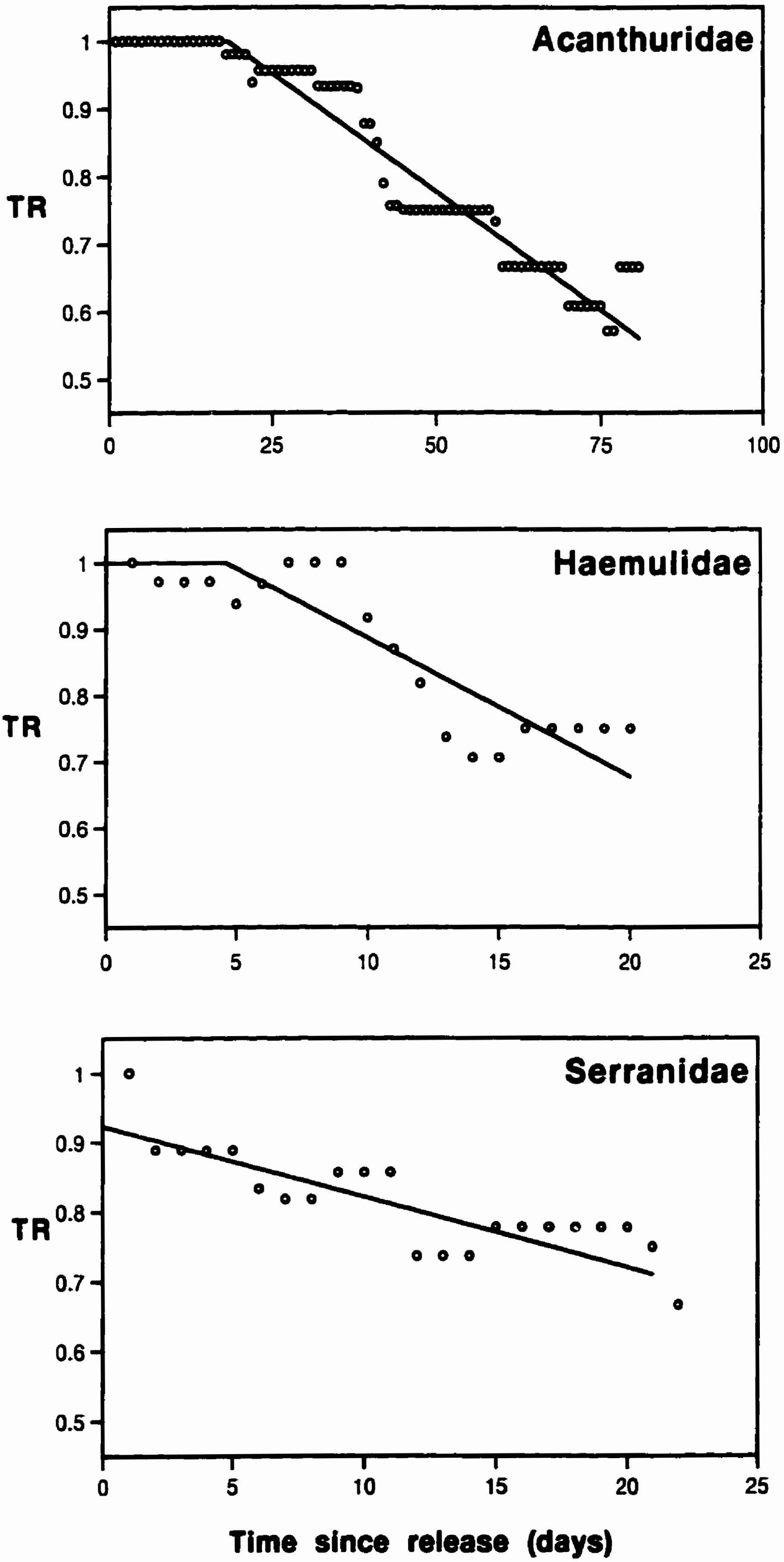
Results and discussion

Figure A1.1 shows tag retention, **TR**, over time for the three families (Acanthuridae, Haemulidae, and Serranidae) for which there were adequate recaptures of double-tagged fish. For acanthurids, the data are best described by two phase linear regression equation, suggesting an initial lag of 18.2 (15.6 - 20.8) days before tags are shed at a subsequent tag loss rate of 0.007 d^{-1} (corrected $r^2 = 0.94$). For haemulids, linear regression estimates an initial lag of about 4.6 (1.9 - 7.4) days, and a subsequent rate of tag loss of 0.021 d^{-1} (corrected $r^2 = 0.79$) -- about three times the estimated rate for acanthurids. A linear model of tag retention by serranids suggests an initially rapid period of tag loss (i.e., y-intercept < 1) and subsequent loss at a rate of 0.010 d^{-1}; constraining the y-intercept to 1 gives a slope of -0.015 ($r^2 = 0.45$). The highly laterally-compressed acanthurids appear to retain anchor tags better than haemulids and serranids. Serranids appear to have an intermediate rate of tag loss, but may lose more tags immediately after tagging; the softer muscle tissue and reduced lateral compression of serranids may decrease the probability of proper the tag becoming firmly anchored.

Table A1.1. The number of fish of each species double-tagged and the number of each species recaptured at least once.

Family	**Species**	**N tagged**	**N recaptured**
Acanthuridae	Acanthurus bahianus	63	28
	A. chirurgus	2	1
Haemulidae	Haemulon carbonarium	6	4
	Haemulon chrysargyreum	8	1
	H. flavolineatum	32	14
	H. sciurus	1	0
Muraenidae	Gymnothorax moringa	20	8
Pomacentridae	Microspathodon chrysurus	12	7
Serranidae	Epinephelus adscensionis	8	7
	E. cruentatus	17	2
	E. fulvus	10	6

Figure A1.1. Tag retention (TR) as a function of the number of days since tagging for three families of reef fishes. The solid lines represent the best fitting linear or two-phase regressions.


Acanthuridae
TR
1
0.9
0.8
0.7
0.6
0.5
0
25
50
75
100
Haemulidae
TR
1
0.9
0.8
0.7
0.6
0.5
0
5
10
15
20
25
Serranidae
TR
1
0.9
0.8
0.7
0.6
0.5
0
5
10
15
20
25
Time since release (days)

Appendix 2. Homing experiment

We displaced tagged fish across the northern BMR boundary to assess whether trappable fishes were capable of homing across the large expanse of sand between the BMR and the NR. On June 13, 1996, 68 fish were captured at five sites (NB5, NB6, NB7, NB8, NB9) on North Bellairs reef in the BMR, tagged, and released on Heron Bay reef in the NR. The same day, 84 fish were captured at five sites (HE1, HE2, HE3, HE4, HE5) on Heron Bay reef in the NR, tagged, and released on North Bellairs reef in the BMR (see Figure 3 for site locations). All fish were released in the spurs-and-grooves zone, about 25 m from the reef edge closest to the BMR boundary. Visual and trap recaptures of tagged displaced fishes were conducted at all ten sites over a period of 5 days, from June 14 to 18, 1996.

A total of 49 fish (32%) were recaptured in traps or unambiguously identified in visual recaptures during the five day recapture period (Table A2.1, below). Twenty-five fish from seven families were recaptured on the reef on which they were captured. No pomacentrids or serranids were observed on their home reefs, although the sample sizes were very small for these families (N = 3 and N = 2 recaptures, respectively). The data show that fish from at least seven families can relocate across the large expanse of sand and rubble separating the BMR reefs from NR reefs.

Table A2.1 Results of the homing experiment. See text for details.

Family	Number tagged	Number recaptured	Number recaptured on home reef
Acanthuridae	73	19	13
Balistidaae	4	5	1
Chaetodontidae	2	1	1
Haemulidae	6	3	1
Holocentridae	11	2	2
Pomacanthidae	4	4	1
Pomacentridae	10	3	0
Scaridae	32	10	6
Serranidae	10	2	0
Total	**152**	**49**	**25**

Appendix 3a. Mean visual census density by species for the 20 study sites, for the BMR and the NR, the relative difference in density (RDD) between the BMR and NR, and the mean density for all sites combined. Species are listed in alphabetical order. See Figure 3 for site locations.

Species	SB5	SB4	SB6	SB8	SB1	NB1	NB2	NB9	NB8	NB7	BMR
Abudefduf saxatilis	0.00	1.33	0.00	2.00	0.33	1.33	0.00	0.33	0.00	2.33	0.77
Acanthurus bahianus	51.33	37.33	26.33	12.67	19.00	28.00	9.00	19.33	16.00	7.00	22.60
A. coeruleus	13.00	16.00	9.00	2.67	4.67	3.67	2.67	7.33	3.67	5.33	6.80
Bodianus rufus	0.33	1.00	0.00	0.00	0.33	0.33	0.00	1.00	0.00	0.67	0.37
Cantherhines pullus	2.67	1.33	2.33	0.33	0.67	0.00	0.00	2.00	0.00	0.33	0.97
Caranx ruber	0.00	1.33	1.67	0.67	0.00	0.00	3.67	0.33	1.00	0.00	0.87
Chaetodon striatus	1.67	2.67	0.00	0.00	0.33	0.00	0.67	0.67	0.00	0.00	0.60
Epinephelus cruentatus	0.33	0.67	0.00	0.67	0.33	1.33	0.67	1.67	0.33	0.33	0.63
E. fulvus	1.67	1.33	4.33	0.00	0.00	1.33	0.00	0.33	0.67	0.67	1.03
Haemulon carbonarium	0.00	4.00	2.00	0.67	1.00	0.33	0.00	1.33	0.67	0.00	1.00
H. chrysargyreum	0.00	122.67	1.00	0.33	9.67	3.00	12.67	0.00	2.33	4.33	15.60
H. flavolineatum	7.33	16.33	5.00	9.00	13.67	6.00	65.00	22.33	38.33	48.67	23.17
Holocanthus tricolor	1.00	2.00	1.00	0.33	0.00	0.00	0.33	0.67	0.33	0.00	0.57
H. rufus	0.00	3.33	0.00	1.33	5.33	1.00	2.00	0.33	0.33	1.67	1.53
Kyphosus sectatrix	0.33	0.67	2.00	0.00	1.00	1.67	0.00	0.00	0.00	0.33	0.60
Lactophrys triqueter	1.33	0.67	0.67	0.33	0.33	0.00	0.00	0.33	0.00	0.00	0.37
Lutjanus mahogani	0.00	1.33	2.33	1.00	1.33	0.33	5.33	1.33	2.00	5.67	2.07
Microspathodon chrysurus	10.00	16.00	9.00	11.67	14.00	10.33	26.67	14.00	5.33	14.33	13.13
Mulloidichthys martinicus	0.33	0.33	1.00	3.00	2.00	0.33	2.67	19.67	0.67	0.00	3.00
Myripristis jacobus	1.00	14.67	1.33	2.33	0.67	0.00	1.00	3.33	1.00	0.00	2.53
Scarus iserti	3.00	9.00	2.00	0.67	2.33	0.67	3.00	1.33	1.00	0.33	2.33
S. taeniopterus	1.67	4.33	3.33	0.67	0.33	0.00	0.67	3.33	0.00	0.00	1.43
S. vetula	0.33	2.00	0.00	0.00	3.67	0.67	0.67	0.00	0.00	0.67	0.80
Sparisoma aurofrenatum	3.00	2.00	1.67	0.33	0.67	0.00	0.00	1.33	0.00	0.00	0.90
S. rubripinne	2.00	0.67	0.33	0.00	0.67	0.33	0.33	0.00	0.00	0.00	0.43
S. viride	1.00	1.33	2.00	0.33	2.33	1.00	3.00	1.67	0.00	0.00	1.27
Others*	0.00	2.33	0.00	0.00	0.33	0.00	0.33	0.00	0.00	0.00	0.30
Total	103.33	266.67	78.33	51.00	85.00	61.67	140.33	104.00	73.67	92.67	105.67

* includes 9 species: 5 counted only in the NR, and 4 counted only in the BMR

(continued)

Appendix 3a. (continued)

Species	**HE1**	**HE2**	**HE3**	**HE4**	**HE5**	**BA1**	**BA2**	**BA3**	**BA4**	**BA5**	**NR**	**RDD**	**Total**
Abudefduf saxatilis	0.33	0.00	0.00	0.00	0.67	0.00	0.00	0.00	0.00	0.00	0.10	0.77	0.43
Acanthurus bahianus	3.00	7.33	9.00	14.33	23.33	15.67	19.33	23.00	24.33	11.33	15.07	0.20	18.83
A. coeruleus	1.33	1.00	0.00	11.33	0.67	0.67	1.67	3.33	1.67	1.00	2.27	0.50	4.53
Bodianus rufus	0.33	0.00	0.67	0.33	0.00	0.00	0.33	0.00	0.33	0.00	0.20	0.29	0.28
Cantherhines pullus	0.00	0.33	0.67	1.33	1.00	0.00	1.33	0.00	0.67	0.00	0.53	0.29	0.75
Caranx ruber	0.00	0.00	0.00	0.00	0.33	0.00	0.33	0.67	0.33	0.00	0.17	0.68	0.52
Chaetodon striatus	0.00	0.00	0.00	0.00	1.33	0.00	0.67	0.33	0.67	0.33	0.33	0.29	0.47
Epinephelus cruentatus	0.00	0.33	0.33	0.00	0.00	0.33	0.00	1.00	0.33	0.33	0.27	0.41	0.45
E. fulvus	0.00	0.00	1.33	1.00	0.00	1.33	1.00	0.00	0.33	1.33	0.63	0.24	0.83
Haemulon carbonarium	0.67	0.33	0.33	0.33	0.00	0.00	0.00	0.33	0.00	0.00	0.20	0.67	0.60
H. chrysargyreum	13.33	2.67	9.67	0.00	0.00	0.33	0.00	0.00	0.00	0.67	2.67	0.71	9.13
H. flavolineatum	17.00	9.00	12.00	7.33	4.00	9.67	17.33	5.00	9.33	6.33	9.70	0.41	16.43
Holocanthus tricolor	0.00	0.67	1.00	0.67	0.00	0.00	0.00	0.00	0.67	0.33	0.33	0.26	0.45
H. rufus	0.33	2.33	1.67	1.00	0.00	0.67	0.67	0.00	0.00	0.33	0.70	0.37	1.12
Kyphosus sectatrix	0.33	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.03	0.89	0.32
Lactophrys triqueter	0.00	0.33	0.33	0.00	0.00	0.33	0.33	1.00	0.67	0.00	0.30	0.10	0.33
Lutjanus mahogani	5.33	1.67	0.33	1.67	0.00	0.00	0.00	0.00	0.00	1.00	1.00	0.35	1.53
Microspathodon chrysurus	17.00	13.67	17.33	26.00	9.33	15.33	21.00	6.67	5.67	7.67	13.97	-0.03	13.55
Mulloidichthys martinicus	0.00	8.00	0.00	0.67	0.00	0.00	0.00	0.00	0.00	0.00	0.87	0.55	1.93
Myripristis jacobus	2.33	4.67	6.67	6.67	0.00	0.33	4.67	2.33	0.00	2.67	3.03	-0.09	2.78
Scarus iserti	0.67	1.00	0.33	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.20	0.84	1.27
S. taeniopterus	0.00	0.33	1.00	2.33	2.00	1.33	0.67	0.67	2.33	0.33	1.10	0.13	1.27
S. vetula	0.00	0.00	0.00	0.33	0.00	0.33	0.33	0.33	0.00	0.00	0.13	0.71	0.47
Sparisoma aurofrenatum	0.00	0.00	1.33	2.33	1.33	0.00	0.33	1.00	1.00	0.00	0.73	0.10	0.82
S. rubripinne	0.00	0.00	0.00	0.00	0.00	0.00	1.00	0.00	0.00	0.00	0.10	0.63	0.27
S. viride	1.00	1.00	1.33	2.33	0.33	1.00	1.00	0.33	0.33	0.00	0.87	0.19	1.07
Others*	0.00	0.33	0.33	1.33	0.00	1.00	2.00	0.00	0.67	0.33	0.60	-0.33	0.45
Total	63.00	55.00	65.67	81.33	44.33	48.33	74.00	46.00	49.33	34.00	56.10	0.31	80.88

* includes 9 species: 5 counted only in the NR, and 4 counted only in the BMR

Appendix 3b. Mean catch rate per trap by species for the 20 study sites, for the BMR and the NR, the relative difference in catch rate (RDC) between the BMR and NR, and the mean catch rate for all sites combined. The sample size (number of trap sets) is indicated in parentheses below each site name. Species are listed in alphabetical order. See Figure 3 for site locations.

Species	**SB5 (4)**	**SB4 (11)**	**SB6 (4)**	**SB8 (3)**	**SB1 (4)**	**NB1 (4)**	**NB2 (4)**	**NB9 (3)**	**NB8 (4)**	**NB7 (4)**	**BMR**
Abudelduf saxatilis	0.00	0.09	0.00	0.00	1.50	0.25	0.00	0.00	0.25	0.00	0.21
Acanthurus bahianus	19.50	13.82	8.86	15.33	12.00	7.75	1.75	0.67	2.25	2.50	8.44
A. chirurgus	0.00	0.36	0.29	0.67	0.00	0.00	0.00	0.00	0.00	0.25	0.16
A. coeruleus	5.00	6.09	4.00	10.00	3.75	3.00	4.75	6.67	0.00	3.75	4.70
Bodianus rufus	0.25	0.09	0.00	0.00	0.00	1.50	0.00	0.67	0.00	0.00	0.25
Cantherhines pullus	2.25	1.36	1.57	0.33	0.75	0.25	0.50	0.00	1.25	1.75	1.00
Chaetodon striatus	6.00	4.36	0.71	0.67	0.50	1.75	0.75	0.00	0.50	2.00	1.72
Epinephelus adscensionis	0.00	0.09	0.00	0.00	0.00	0.00	0.50	0.33	0.00	0.00	0.09
E. cruentatus	0.00	0.36	0.00	0.67	0.00	0.00	0.25	1.67	0.00	0.25	0.32
E. fulvus	0.25	0.00	1.57	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.18
Gymnothorax moringa	3.00	1.18	0.86	0.67	1.00	0.00	0.00	0.67	0.50	0.00	0.79
Haemulon chrysargyreum	0.50	0.64	0.00	0.00	1.25	0.25	0.00	0.00	0.25	0.00	0.29
H. flavolineatum	2.75	1.45	0.29	0.00	2.00	1.00	2.00	0.00	2.75	0.50	1.27
Holocanthus tricolor	0.25	2.82	1.43	0.67	0.00	0.00	0.00	1.00	0.50	0.00	0.67
Holocentrus adscensionis	0.00	1.09	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.11
H. rufus	1.00	2.18	0.00	1.33	0.25	0.00	0.25	0.00	0.00	0.00	0.50
Kyphosus sectatrix	0.00	0.00	0.29	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.03
Lactophrys triqueter	0.75	0.18	0.00	0.00	0.00	0.50	0.00	0.00	0.00	0.25	0.17
Lutjanus mahogani	0.25	0.00	0.00	0.33	0.00	0.00	0.00	0.00	0.00	0.00	0.06
Microspathodon chrysurus	0.25	0.73	0.14	0.67	1.00	0.25	1.25	0.00	1.50	3.75	0.95
Mulloidichthys martinicus	0.25	0.00	0.14	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.04
Myripristis jacobus	3.25	2.55	2.00	0.33	0.00	0.00	0.00	0.00	0.00	0.00	0.81
Pomacanthus paru	0.25	0.36	0.14	0.00	0.00	0.00	0.50	0.00	0.00	0.00	0.13
Scarus iserti	0.00	0.27	0.00	0.00	0.25	0.50	0.00	0.00	0.25	0.00	0.13
S. taeniopterus	0.00	0.18	0.29	0.00	0.25	0.00	0.00	0.67	0.00	0.00	0.14
S. vetula	0.25	0.18	0.29	0.00	0.75	0.25	0.00	0.00	0.00	0.25	0.20
Sparisoma aurofrenatum	0.00	0.45	0.29	0.67	1.25	0.00	0.00	0.33	0.50	0.50	0.40
S. chrysopterum	0.00	0.00	0.14	0.33	0.00	0.75	0.00	0.00	0.00	0.25	0.15
S. rubripinne	0.00	0.00	0.00	0.00	0.25	0.00	0.00	0.00	0.00	0.25	0.05
S. viride	0.00	0.27	0.00	0.67	1.25	0.75	0.00	1.00	1.25	0.00	0.52
Others*	0.00	0.18	0.29	0.00	0.25	1.25	0.50	0.00	0.50	0.50	0.35
Total	46.00	41.33	23.58	33.34	28.50	20.00	13.00	13.68	12.25	16.75	24.84

* includes19 species caught no more than once in the BMR or NR

(continued)

Appendix 3b. (continued)

Species	HE1 (10)	HE2 (10)	HE3 (11)	HE4 (11)	HE5 (11)	BA1 (8)	BA2 (8)	BA3 (4)	BA4 (4)	BA5 (4)	NR	RDC	Total
Abudefduf saxatilis	0.00	0.00	0.09	0.09	0.27	0.13	0.63	0.25	0.00	0.00	0.15	0.18	0.18
Acanthurus bahianus	6.20	5.90	8.09	7.00	12.91	10.63	8.63	11.75	12.00	15.50	9.86	-0.08	9.15
A. chirurgus	0.00	0.30	0.18	0.36	0.00	0.00	0.50	0.00	0.50	0.25	0.21	-0.14	0.18
A. coeruleus	0.10	2.00	0.91	1.82	1.45	2.12	4.00	10.50	5.50	1.25	2.97	0.23	3.83
Bodianus rufus	0.10	0.00	0.09	0.00	0.00	0.00	0.00	0.50	0.00	0.75	0.14	0.27	0.20
Cantherhines pullus	0.50	0.80	1.09	0.82	0.64	0.75	2.38	1.50	0.50	1.25	1.02	-0.01	1.01
Chaetodon striatus	1.00	0.70	1.18	4.55	0.82	1.25	2.87	0.75	0.50	2.00	1.56	0.05	1.64
Epinephelus adscensionis	0.00	0.00	0.18	0.00	0.00	0.00	0.00	0.00	0.00	0.50	0.07	0.15	0.08
E. cruentatus	0.00	0.50	0.27	0.55	0.00	0.38	0.50	0.75	0.00	0.75	0.37	-0.07	0.35
E. fulvus	0.00	0.00	0.91	0.64	0.09	0.13	0.00	0.25	0.25	0.00	0.23	-0.11	0.20
Gymnothorax moringa	0.20	0.00	0.36	0.73	0.55	0.87	0.25	0.75	0.50	1.00	0.52	0.20	0.65
Haemulon chrysargyreum	0.90	0.50	1.64	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.30	-0.03	0.30
H. flavolineatum	1.70	1.20	3.45	1.09	1.00	0.88	0.38	0.25	2.50	3.25	1.57	-0.10	1.42
Holocanthus tricolor	0.00	0.00	0.00	0.09	0.27	0.00	0.00	0.00	0.75	0.00	0.11	0.71	0.39
Holocentrus adscensionis	0.10	0.00	0.00	0.00	0.00	2.25	0.38	1.75	0.00	0.00	0.45	-0.61	0.28
H. rufus	0.00	0.30	0.27	0.18	0.09	0.13	0.00	0.00	0.00	0.00	0.10	0.68	0.30
Kyphosus sectatrix	0.00	0.10	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.01	0.48	0.02
Lactophrys triqueter	0.00	0.00	0.18	0.18	0.00	0.00	0.00	0.00	0.00	0.00	0.04	0.65	0.10
Lutjanus mahogani	0.60	0.00	0.00	0.09	0.00	0.00	0.00	0.00	0.00	0.00	0.07	-0.09	0.06
Microspathodon chrysurus	2.10	2.00	0.55	3.36	1.36	1.87	1.50	5.50	0.50	2.25	2.10	-0.38	1.53
Mulloidichthys martinicus	0.00	0.00	0.00	0.00	0.18	0.00	0.00	0.00	0.00	0.00	0.02	0.37	0.03
Myripristis jacobus	0.00	1.10	0.73	0.00	1.27	0.00	1.75	1.25	0.25	2.50	0.89	-0.04	0.85
Pomacanthus paru	0.00	0.00	0.00	0.00	0.18	0.00	0.00	0.00	0.00	0.00	0.02	0.75	0.07
Scarus iserti	0.10	0.40	1.00	0.09	0.00	0.00	0.00	0.00	0.00	0.00	0.16	-0.11	0.14
S. taeniopterus	0.50	0.20	0.27	0.91	0.09	0.13	0.13	0.00	0.00	0.00	0.22	-0.23	0.18
S. vetula	0.10	0.20	0.27	0.18	0.00	0.75	0.00	0.00	0.50	0.00	0.20	-0.01	0.20
Sparisoma aurofrenatum	0.00	0.30	0.09	1.09	0.27	1.00	0.50	0.00	0.75	0.00	0.40	0.00	0.40
S. chrysopterum	0.00	0.00	0.00	0.09	0.00	0.13	0.00	0.00	0.00	0.00	0.02	0.74	0.08
S. rubripinne	0.00	0.00	0.00	0.09	0.00	0.00	0.00	0.00	0.00	0.25	0.03	0.19	0.04
S. viride	1.00	0.80	0.00	1.09	0.00	0.63	0.25	0.00	0.00	0.00	0.38	0.16	0.45
Others*	0.20	0.50	0.36	0.91	0.45	0.00	0.63	0.50	0.00	0.00	0.36	-0.01	0.35
Total	15.40	17.80	22.16	26.00	21.89	24.03	25.28	36.25	25.00	31.50	24.53	0.01	24.67

* includes19 species caught no more than once in the BMR or NR

Appendix 3c. Trappability (catch rate / census density) by species for the 20 study sites, for the BMR and the NR, the relative difference in trappability (RDT) between the BMR and NR, and trappability for all sites combined. Species are listed in alphabetical order. See Figure 3 for site locations.

Species	SB5	SB4	SB6	SB8	SB1	NB1	NB2	NB9	NB8	NB7	BMR
Abudefduf saxatilis	*	0.07	*	0.00	4.50	0.19	*	0.00	*	0.00	0.27
Acanthurus bahianus	0.38	0.37	0.34	1.21	0.63	0.28	0.19	0.03	0.14	0.36	0.37
A. coeruleus	0.38	0.38	0.44	3.75	0.80	0.82	1.78	0.91	0.00	0.70	0.69
Bodianus rufus	0.75	0.09	*	*	0.00	4.50	*	0.67	*	0.00	0.68
Cantherhines pullus	0.84	1.02	0.67	0.99	1.13	*	*	0.00	*	5.25	1.04
Chaetodon striatus	3.60	1.64	*	*	1.50	*	1.13	0.00	*	*	2.87
Epinephelus cruentatus	0.00	0.54	*	1.01	0.00	0.00	0.38	1.00	0.00	0.75	0.15
E. fulvus	0.15	0.00	0.36	*	*	0.00	*	0.00	0.00	0.00	0.18
Haemulon chrysargyreum	*	0.01	0.00	0.00	0.13	0.08	0.00	*	0.11	0.00	0.02
H. flavolineatum	0.38	0.09	0.06	0.00	0.15	0.17	0.03	0.00	0.07	0.01	0.05
Holocanthus tricolor	0.25	1.41	1.43	2.01	*	*	0.00	1.50	1.50	*	1.18
H. rufus	*	0.65	*	1.00	0.05	0.00	0.13	0.00	0.00	0.00	0.33
Kyphosus sectatrix	0.00	0.00	0.14	*	0.00	0.00	*	*	*	0.00	0.05
Lactophrys triqueter	0.56	0.27	0.00	0.00	0.00	*	*	0.00	*	*	0.46
Lutjanus mahogani	*	0.00	0.00	0.33	0.00	0.00	0.00	0.00	0.00	0.00	0.03
Microspathodon chrysurus	0.03	0.05	0.02	0.06	0.07	0.02	0.05	0.00	0.28	0.26	0.07
Mulloidichthys martinicus	0.75	0.00	0.14	0.00	0.00	0.00	0.00	0.00	0.00	*	0.01
Myripristis jacobus	3.25	0.17	1.50	0.14	0.00	*	0.00	0.00	0.00	*	0.32
Scarus iserti	0.00	0.03	0.00	0.00	0.11	0.75	0.00	0.00	0.25	0.00	0.05
S. taeniopterus	0.00	0.04	0.09	0.00	0.75	*	0.00	0.20	*	*	0.10
S. vetula	0.75	0.09	*	*	0.20	0.38	0.00	*	*	0.38	0.25
Sparisoma aurofrenatum	0.00	0.23	0.17	2.01	1.88	*	*	0.25	*	*	0.44
S. rubripinne	0.00	0.00	0.00	*	0.38	0.00	0.00	*	*	*	0.12
S. viride	0.00	0.20	0.00	2.01	0.54	0.75	0.00	0.60	*	*	0.41
Total	0.45	0.15	0.29	0.64	0.32	0.29	0.09	0.12	0.16	0.17	0.24

* indicates infinite trappability (species not observed in visual censuses at that site)

(continued)

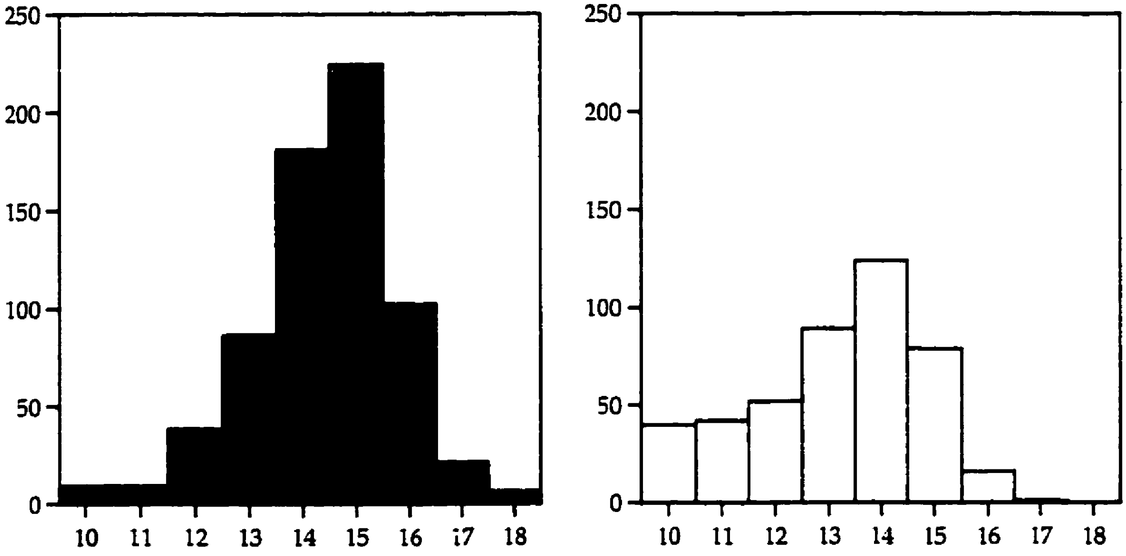
Appendix 3c. (continued)

Species	HE1	HE2	HE3	HE4	HE5	BA1	BA2	BA3	BA4	BA5	NR	RDQ	Total
Abudefduf saxatilis	0.00	*	*	*	0.41	*	*	*	*	*	1.46	-0.69	0.41
Acanthurus bahianus	2.07	0.80	0.90	0.49	0.55	0.68	0.45	0.51	0.49	1.37	0.65	-0.27	0.49
A. coeruleus	0.08	2.00	*	0.16	2.18	3.18	2.40	3.15	3.30	1.25	1.31	-0.31	0.85
Bodianus rufus	0.30	*	0.14	0.00	*	*	0.00	*	0.00	*	0.72	-0.03	0.70
Cantherhines pullus	*	2.40	1.64	0.62	0.64	*	1.79	*	0.75	*	1.92	-0.30	1.35
Chaetodon striatus	*	*	*	*	0.62	*	4.31	2.25	0.75	6.00	4.69	-0.24	3.52
Epinephelus cruentatus	*	1.50	0.81	*	*	1.14	*	0.75	0.00	2.25	0.26	-0.27	0.18
E. fulvus	*	*	0.68	0.64	*	0.10	0.00	*	0.75	0.00	0.36	-0.34	0.25
Haemulon chrysargyreum	0.07	0.19	0.17	*	*	0.00	*	*	*	0.00	0.11	-0.72	0.03
H. flavolineatum	0.10	0.13	0.29	0.15	0.25	0.09	0.02	0.05	0.27	0.51	0.16	-0.49	0.09
Holocanthus tricolor	*	0.00	0.00	0.14	*	*	*	*	1.13	0.00	0.33	0.56	0.86
H. rufus	0.00	0.13	0.16	0.18	*	0.20	0.00	*	*	0.00	0.14	0.40	0.27
Kyphosus sectatrix	0.00	*	*	*	*	*	*	*	*	*	0.30	-0.73	0.06
Lactophrys triqueter	*	0.00	0.54	*	*	0.00	0.00	0.00	0.00	*	0.12	0.58	0.31
Lutjanus mahogani	0.11	0.00	0.00	0.05	*	*	*	*	*	0.00	0.07	-0.42	0.04
Microspathodon chrysurus	0.12	0.15	0.03	0.13	0.15	0.12	0.07	0.83	0.09	0.29	0.15	-0.35	0.11
Mulloidichthys martinicus	*	0.00	*	0.00	*	*	*	*	*	*	0.02	-0.23	0.01
Myripristis jacobus	0.00	0.24	0.11	0.00	*	0.00	0.38	0.54	*	0.94	0.29	0.05	0.31
Scarus iserti	0.15	0.40	3.00	*	*	*	*	*	*	*	0.80	-0.87	0.11
S. taeniopterus	*	0.60	0.27	0.39	0.05	0.10	0.13	0.00	0.00	0.00	0.20	-0.35	0.14
S. vetula	*	*	*	0.54	*	2.25	0.00	0.00	*	*	1.50	-0.72	0.43
Sparisoma aurofrenatum	*	*	0.07	0.47	0.20	*	1.50	0.00	0.75	*	0.55	-0.10	0.49
S. rubripinne	*	*	*	*	*	*	0.00	*	*	*	0.34	-0.49	0.16
S. viride	1.00	0.80	0.00	0.47	0.00	0.63	0.25	0.00	0.00	*	0.44	-0.03	0.42
Total	0.24	0.29	0.34	0.31	0.47	0.56	0.34	0.78	0.52	0.94	0.44	-0.30	0.31

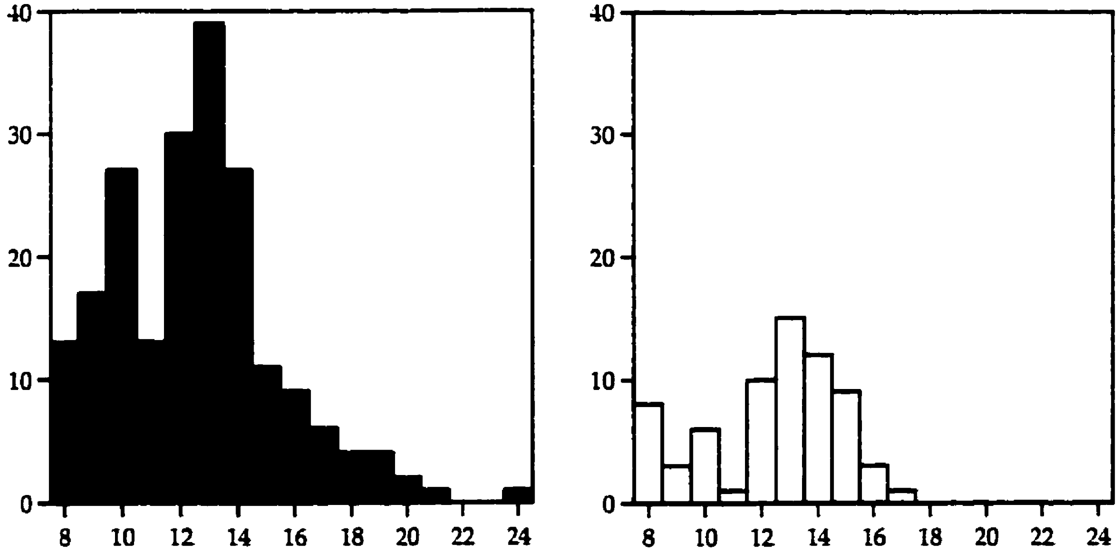
* indicates infinite trappability (species not observed in visual censuses at that site)

Appendix 4. Frequency distributions of the estimated fork length (cm) for the 20 most common species in visual censuses in the BMR (filled bars) and NR (open bars). Species are listed in alphabetical order. Sample sizes (total number of individuals per species) are given in Table 2.

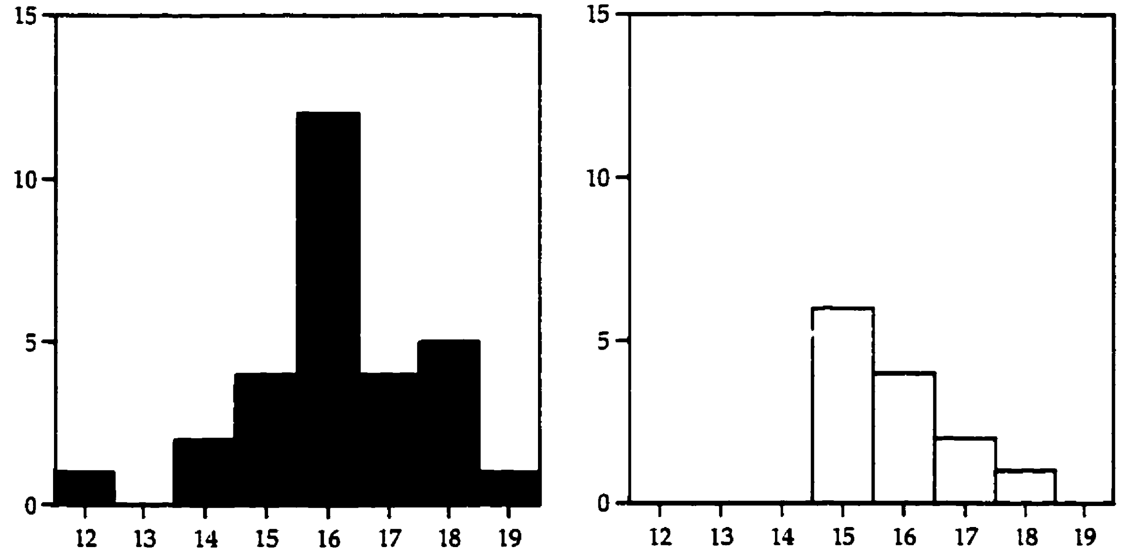
Acanthurus bahianus



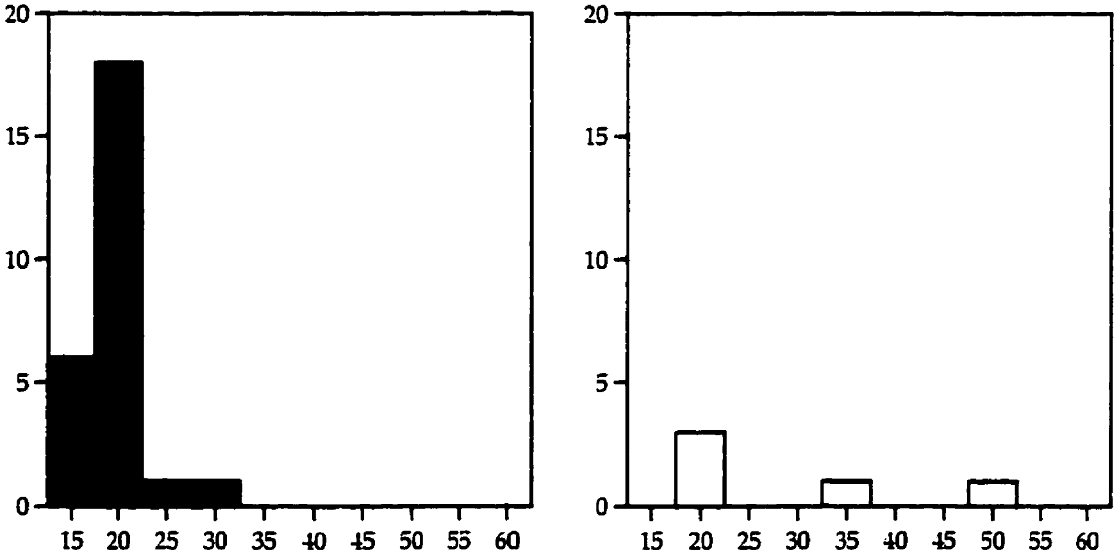
A. coeruleus



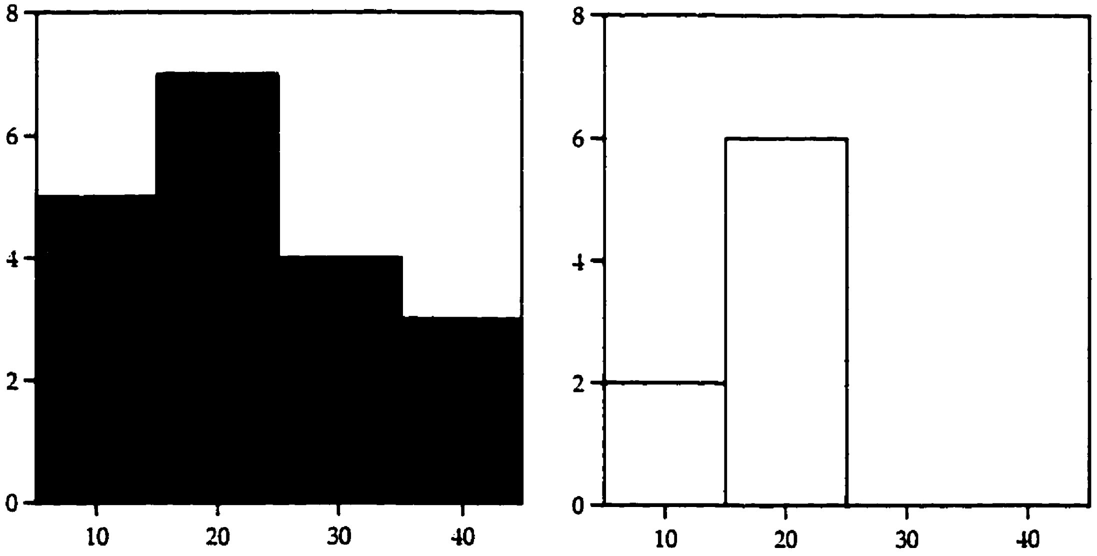
Cantherines pullus



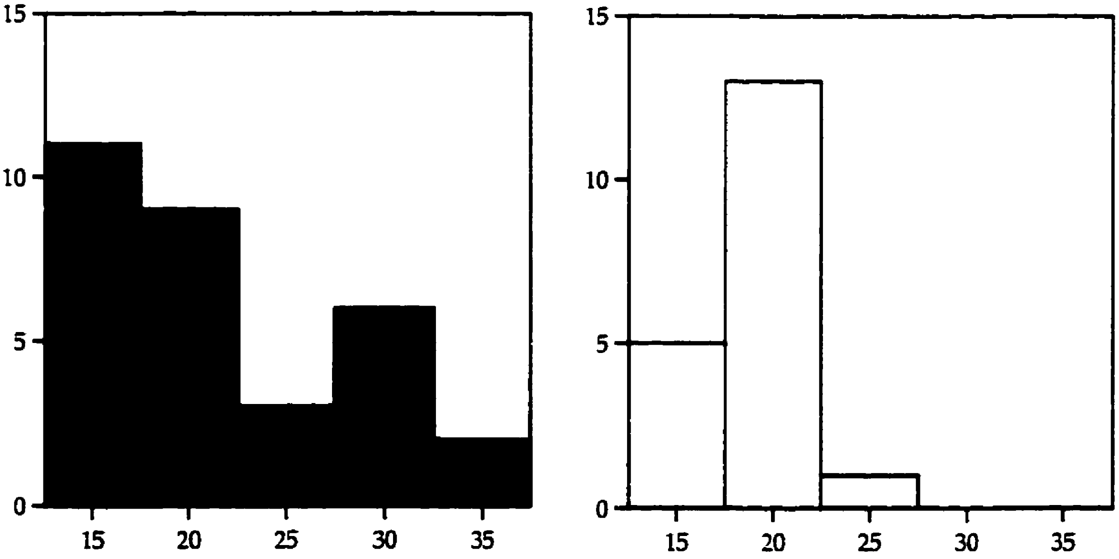
Caranx ruber



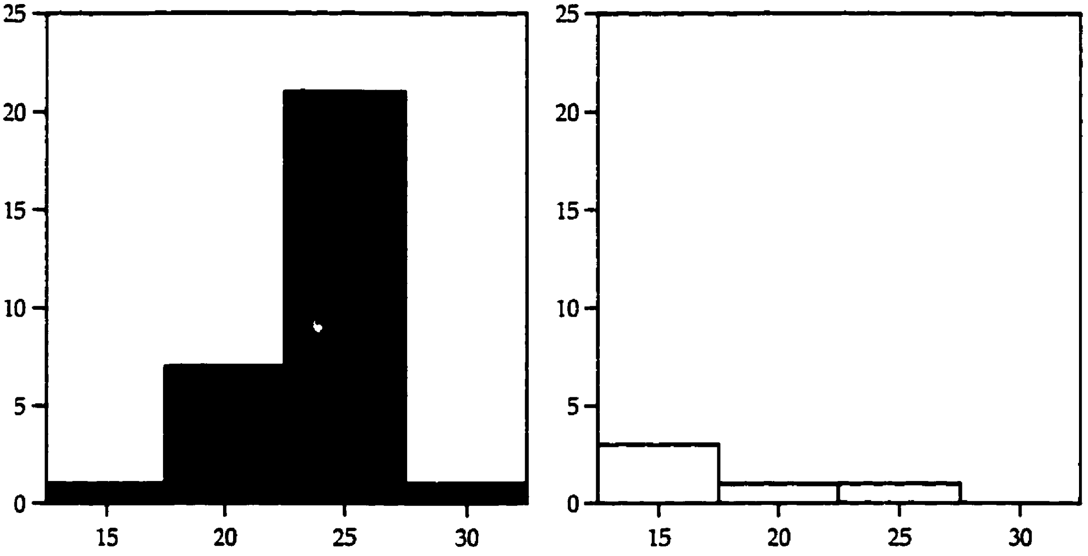
Epinephelus cruentatus



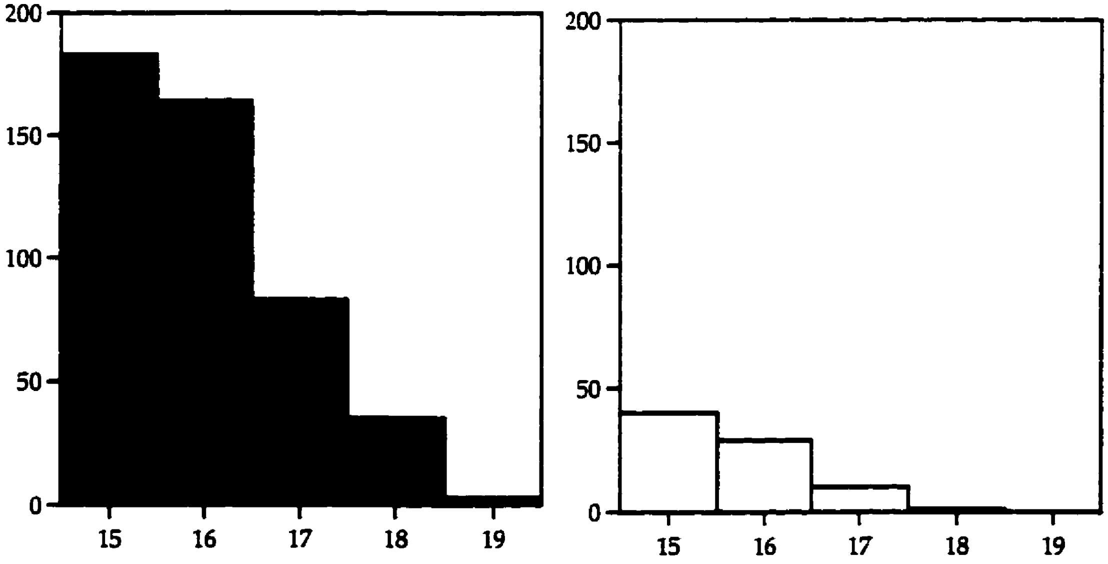
E. fulvus



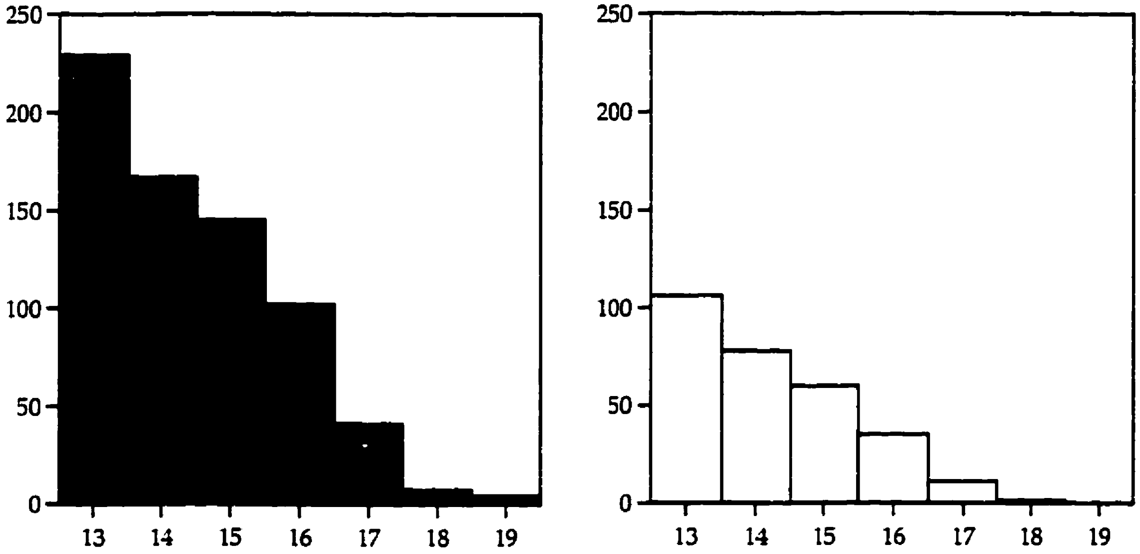
Haemulon carbonarium



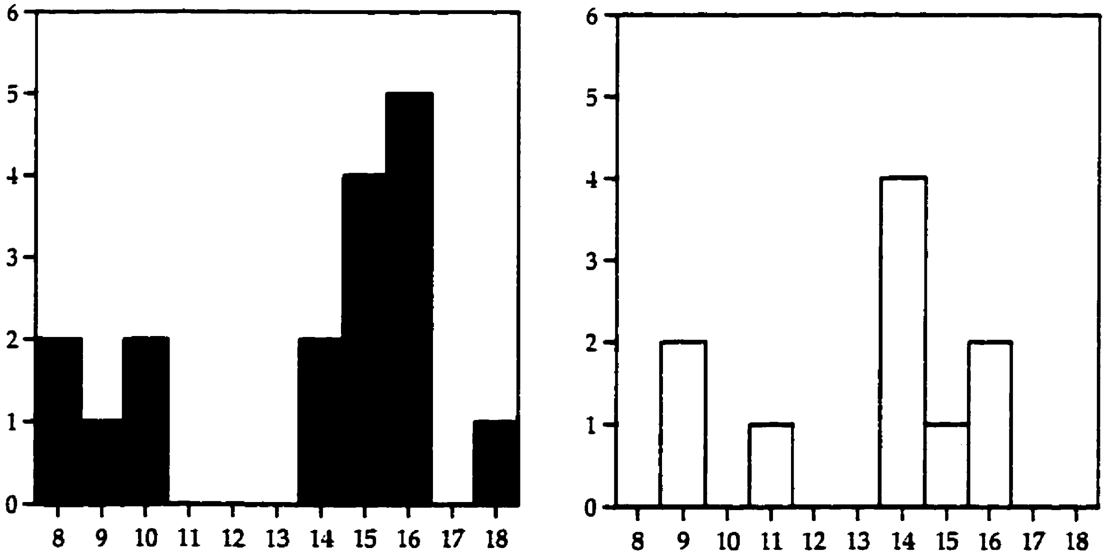
H. chrysargyreum



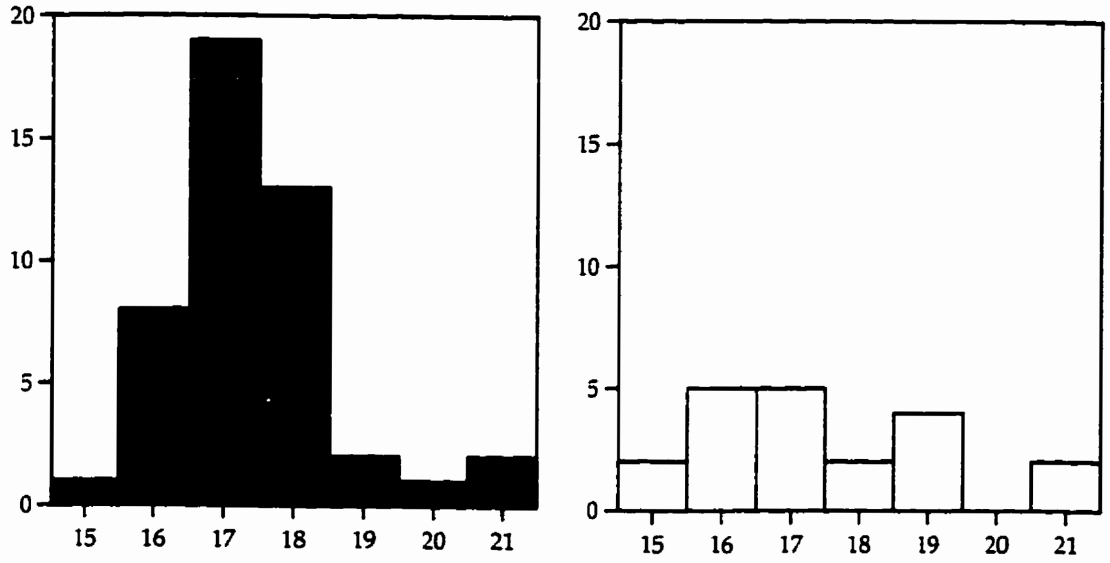
Haemulon flavolineatum



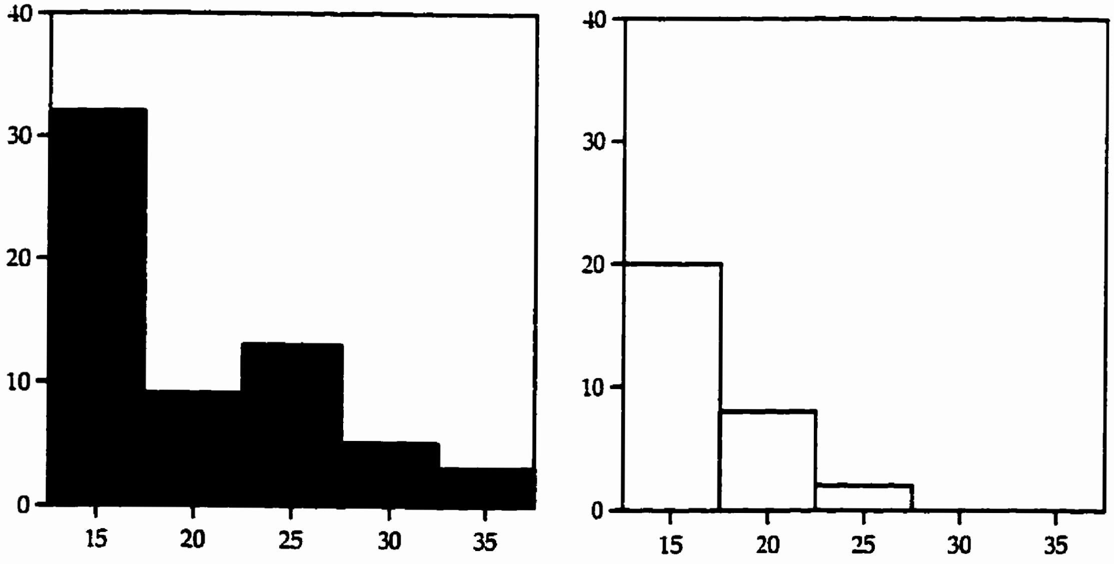
Holocanthus tricolor



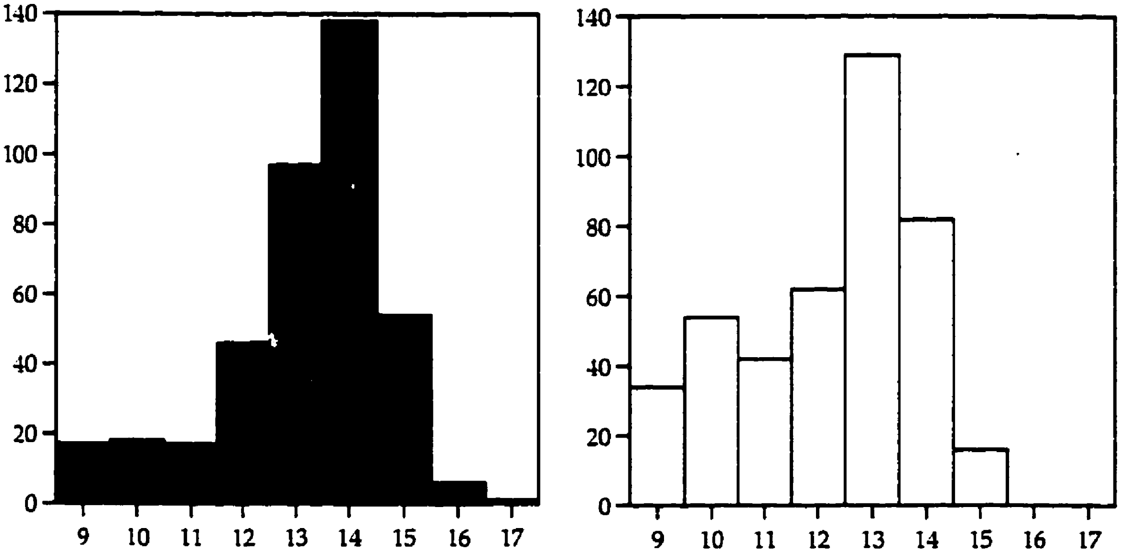
Holocentrus rufus



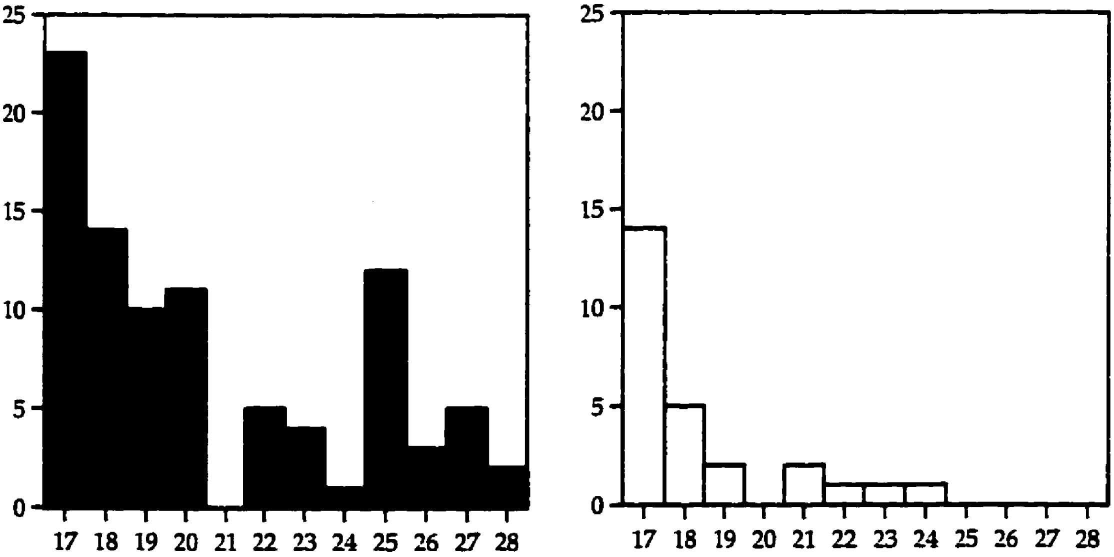
Lutjanus mahogani

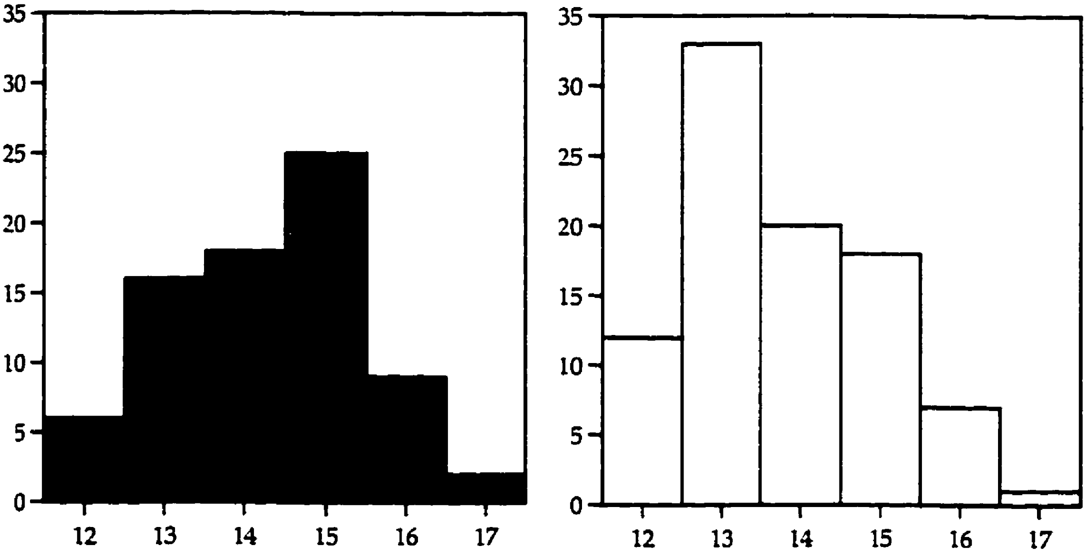


Microspathodon chrysurus

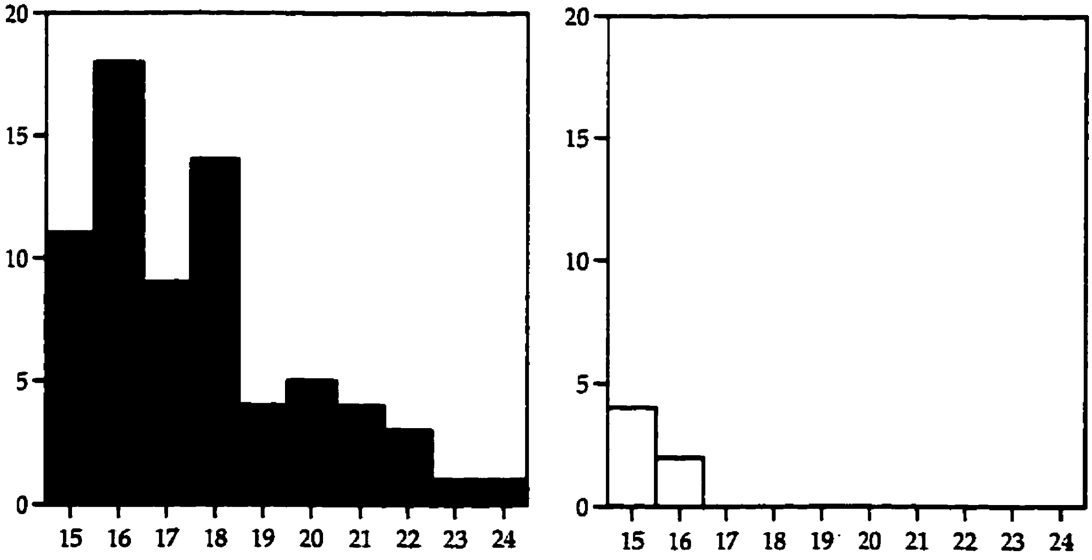


Mulloidichthys martinicus



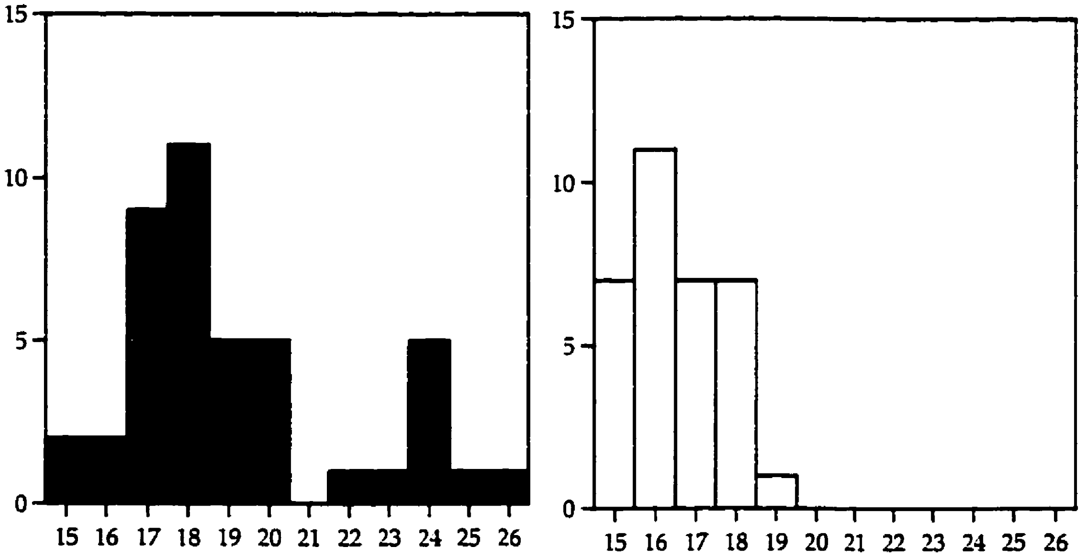


Myripristis jacobus

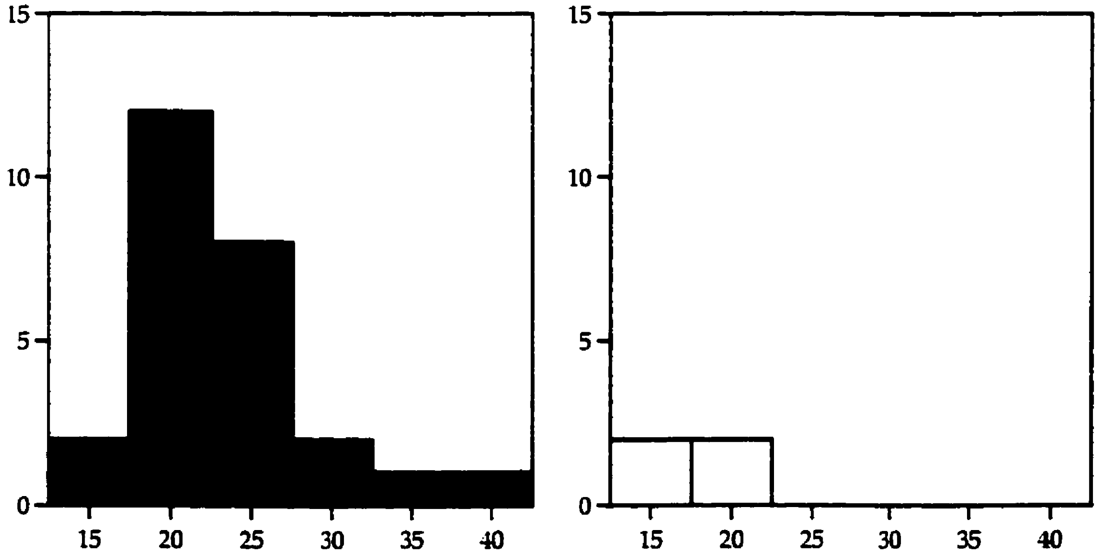


Scarus iserti

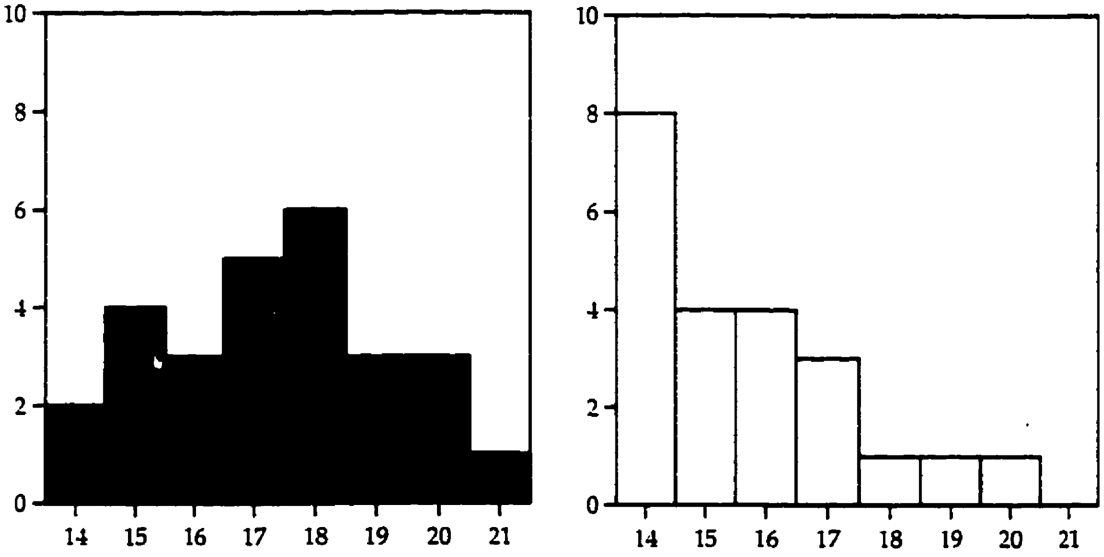
Scarus taeniopterus



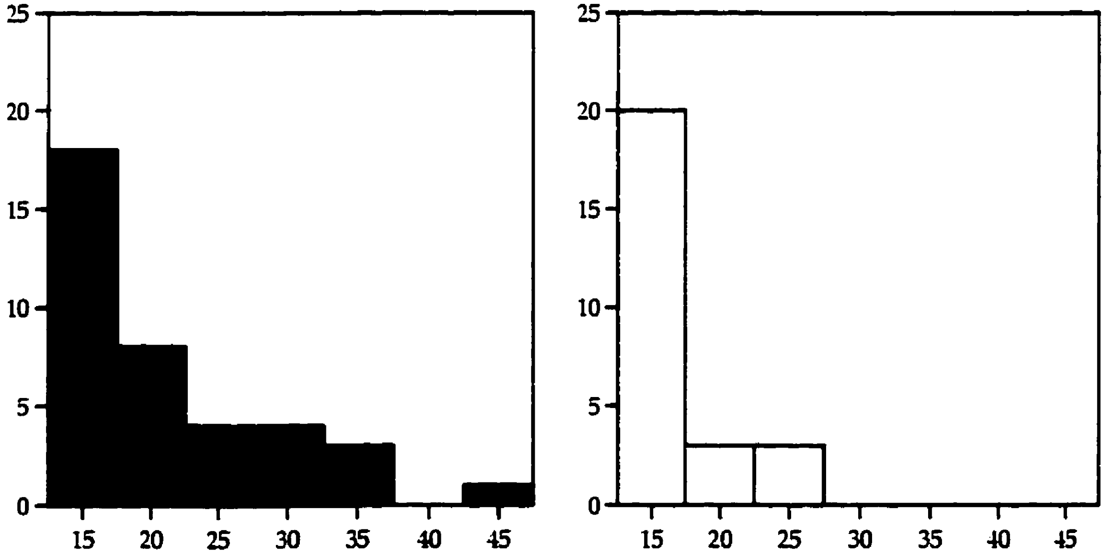
S. vetula



Sparisoma aurofrenatum



S. viride



Appendix 3. Habitat characteristics of the 20 study sites.
Sites are listed in order from South to North (see Figure 3 for site locations).

Site	Mean depth (m)	Rugosity index	Algal cover	Live coral cover	Percent sand	Percent rubble	Percent reef
SB5	3.6	1.17	69%	9%	13%	34%	54%
SB4	6.4	1.31	48%	27%	11%	25%	65%
SB6	7.8	1.07	12%	48%	67%	20%	13%
SB8	5.0	1.12	17%	30%	72%	0%	28%
SB1	3.8	1.40	40%	39%	19%	5%	76%
NB1	3.5	1.35	51%	11%	34%	7%	59%
NB2	4.7	1.32	33%	41%	39%	2%	59%
NB9	5.7	1.17	35%	20%	57%	1%	42%
NB8	5.8	1.12	41%	12%	64%	3%	33%
NB7	4.0	1.28	43%	19%	29%	3%	68%
BMR	**5.0**	**1.23**	**39%**	**26%**	**41%**	**7%**[1]	**50%**
HE1	3.3	1.26	43%	25%	15%	10%	76%
HE2	4.9	1.26	59%	15%	15%	14%	72%
HE3	4.5	1.24	50%	28%	19%	8%	73%
HE4	4.9	1.24	39%	31%	14%	13%	72%
HE5	5.1	1.10	21%	29%	62%	4%	34%
BA1	4.6	1.13	35%	13%	47%	10%	43%
BA2	4.9	1.18	43%	19%	32%	13%	56%
BA3	5.1	1.17	37%	13%	42%	8%	50%
BA5	4.5	1.13	38%	5%	47%	10%	43%
BA4	5.6	1.09	20%	26%	63%	10%	27%
NR	**4.7**	**1.18**	**39%**	**20%**	**36%**	**12%**[1]	**55%**

[1] Geometric mean ($\log_{10}$-transformed rubble)

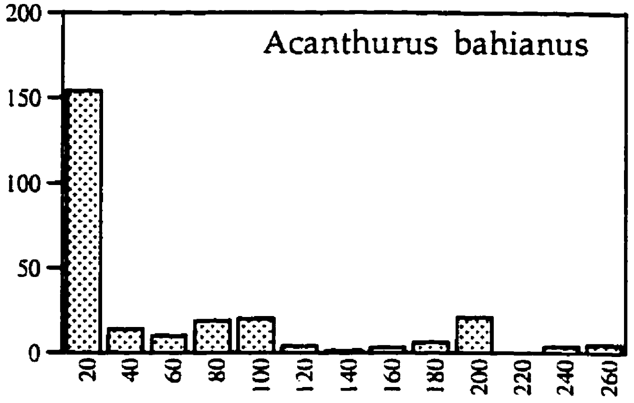
Appendix 5. Habitat characteristics of the 20 study sites.
Sites are listed in order from South to North (see Figure 3 for site locations).

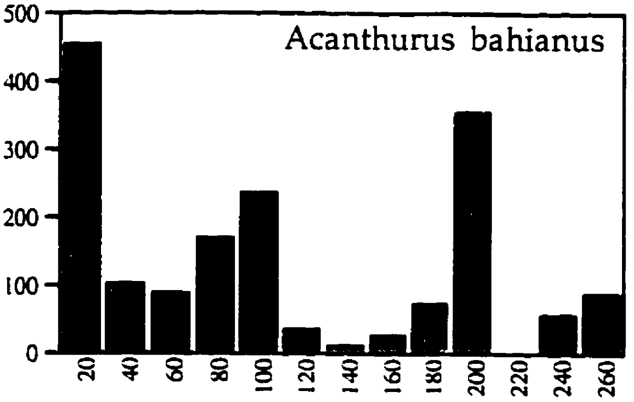
Site	Mean depth (m)	Rugosity index	Algal cover	Live coral cover	Percent sand	Percent rubble	Percent reef
SB5	3.6	1.17	69%	9%	13%	34%	54%
SB4	6.4	1.31	48%	27%	11%	25%	65%
SB6	7.8	1.07	12%	48%	67%	20%	13%
SB8	5.0	1.12	17%	30%	72%	0%	28%
SB1	3.8	1.40	40%	39%	19%	5%	76%
NB1	3.5	1.35	51%	11%	34%	7%	59%
NB2	4.7	1.32	33%	41%	39%	2%	59%
NB9	5.7	1.17	35%	20%	57%	1%	42%
NB8	5.8	1.12	41%	12%	64%	3%	33%
NB7	4.0	1.28	43%	19%	29%	3%	68%
BMR	**5.0**	**1.23**	**39%**	**26%**	**41%**	**7%**[1]	**50%**
HE1	3.3	1.26	43%	25%	15%	10%	76%
HE2	4.9	1.26	59%	15%	15%	14%	72%
HE3	4.5	1.24	50%	28%	19%	8%	73%
HE4	4.9	1.24	39%	31%	14%	13%	72%
HE5	5.1	1.10	21%	29%	62%	4%	34%
BA1	4.6	1.13	35%	13%	47%	10%	43%
BA2	4.9	1.18	43%	19%	32%	13%	56%
BA3	5.1	1.17	37%	13%	42%	8%	50%
BA5	4.5	1.13	38%	5%	47%	10%	43%
BA4	5.6	1.09	20%	26%	63%	10%	27%
NR	**4.7**	**1.18**	**39%**	**20%**	**36%**	**12%**[1]	**55%**

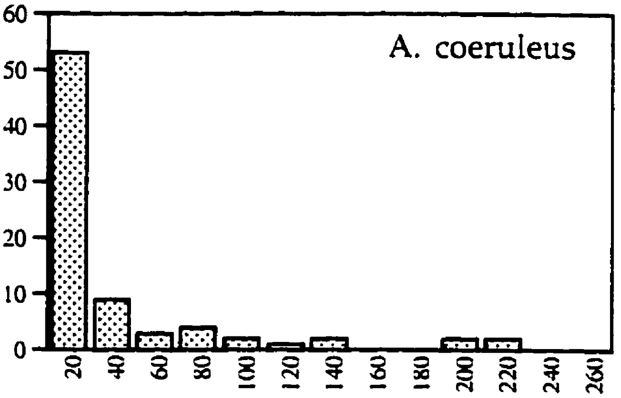
1. Geometric mean (log$_{10}$-transformed rubble)

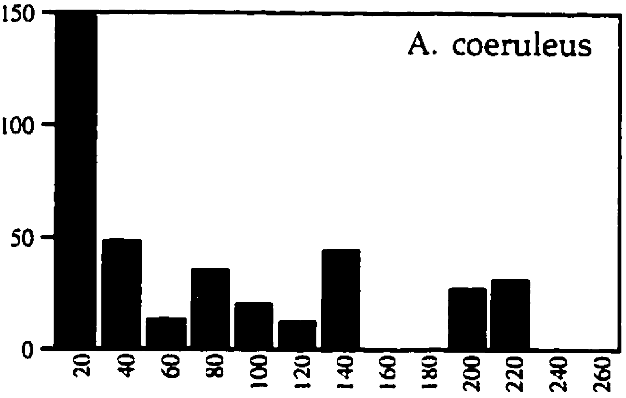
Appendix 6. Frequency distribution of the maximum inter-trap distances (m) for the 13 species with at least 10 recaptured individuals and 5 recaptures of at least one individual. Left panel: uncorrected frequency distributions. Right panel: weighted frequency distributions (see **Methods – III. Fish movements – Correction for bias due to the distribution of recapture effort**). Panels are in alphabetical order by family and species.

ACANTHURIDAE

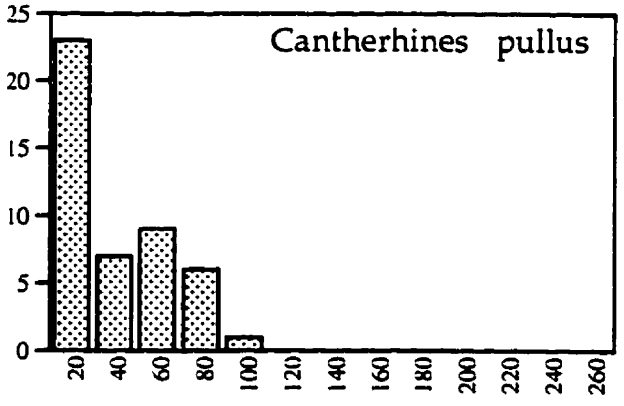


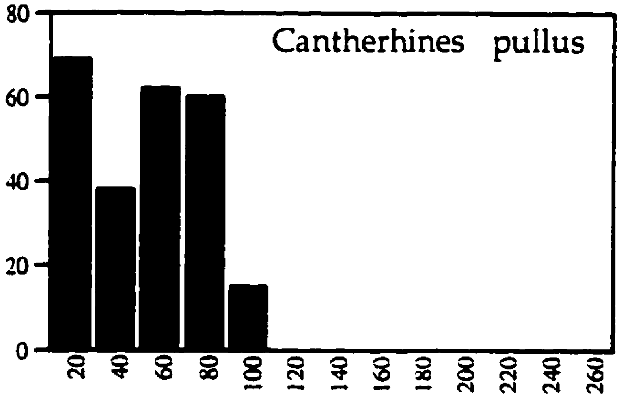




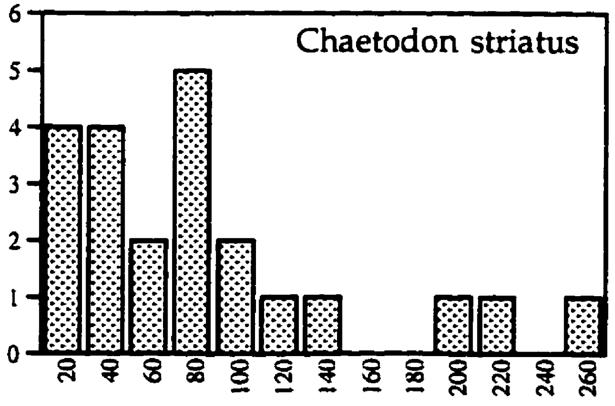


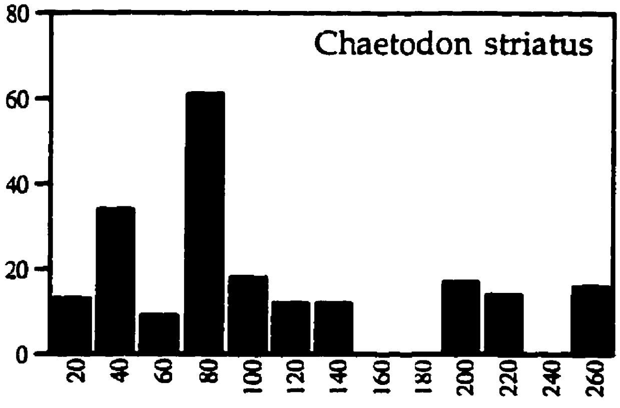
BALISTIDAE



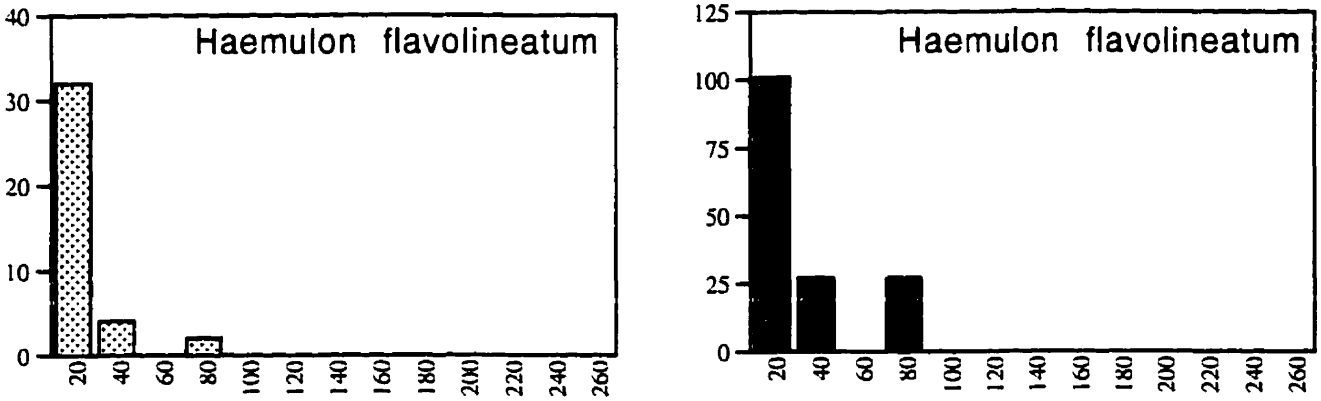


CHAETODONTIDAE





HAEMULIDAE



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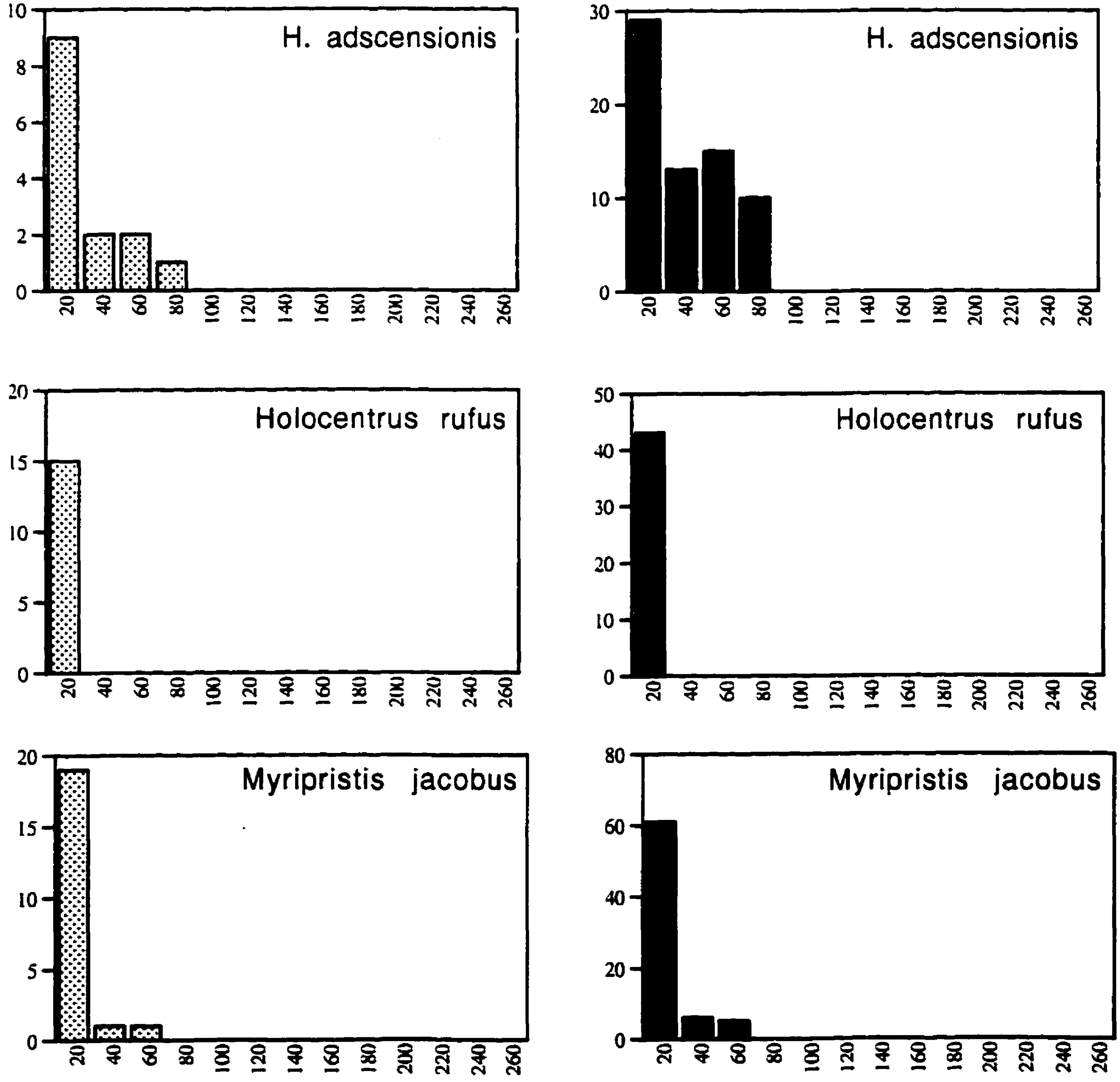

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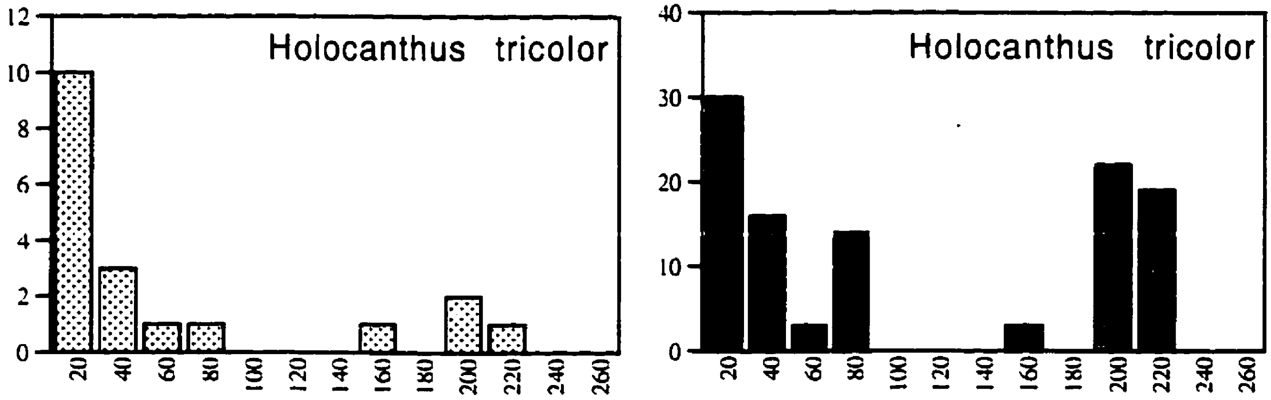

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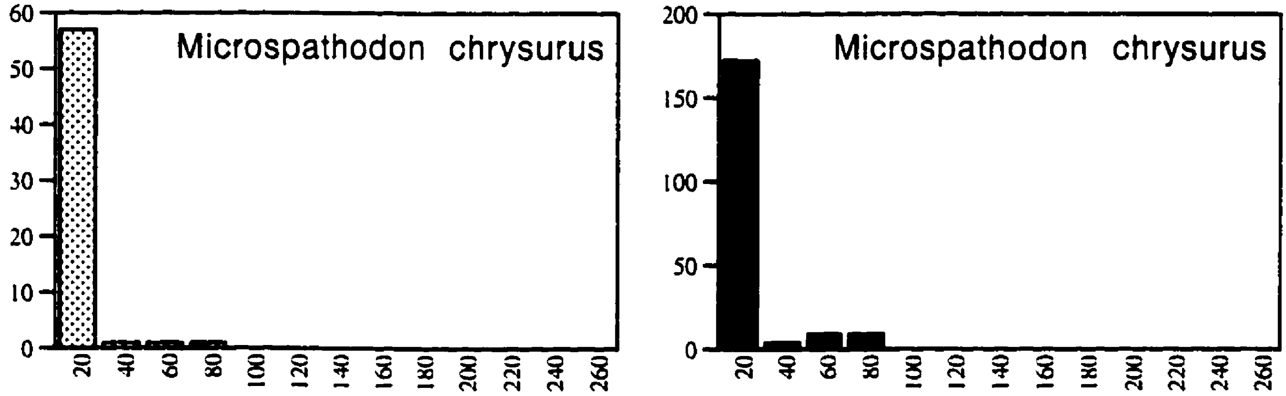
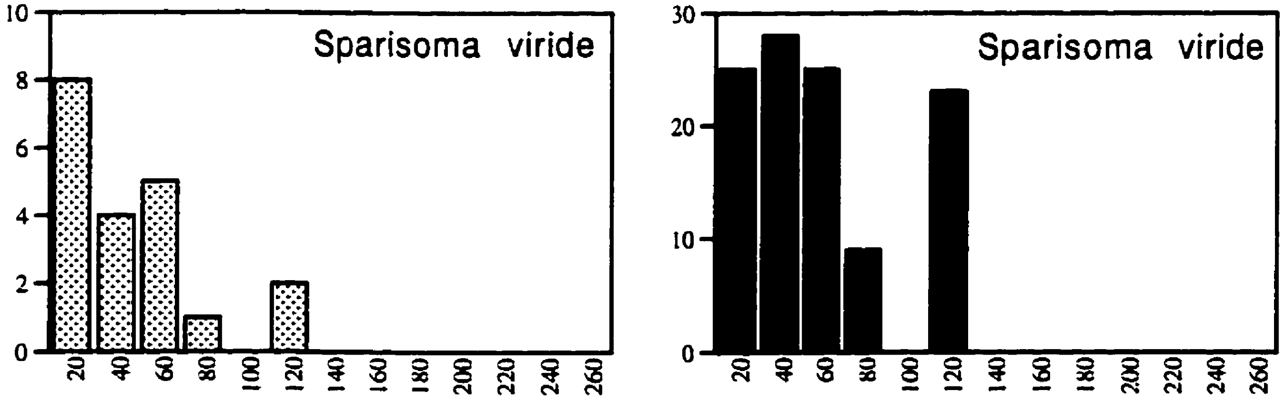
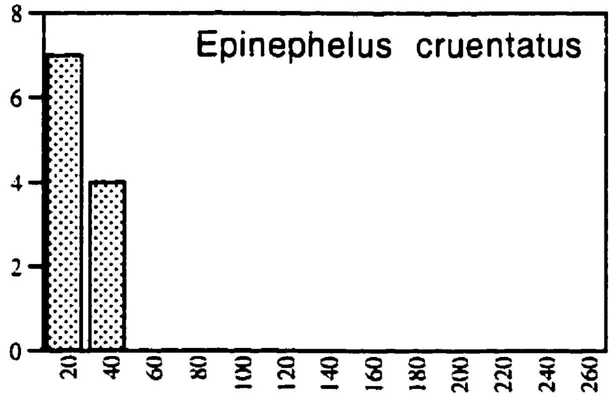


SCARIDAE



SERRANIDAE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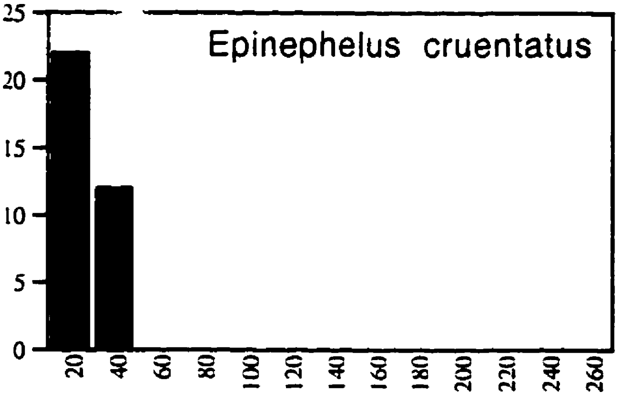
6
4
2
0
20 40 60 80 100 120 140 160 180 200 220 240 260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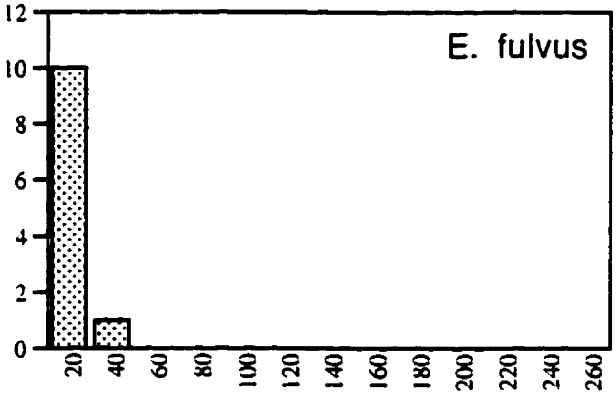
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6
4
2
0
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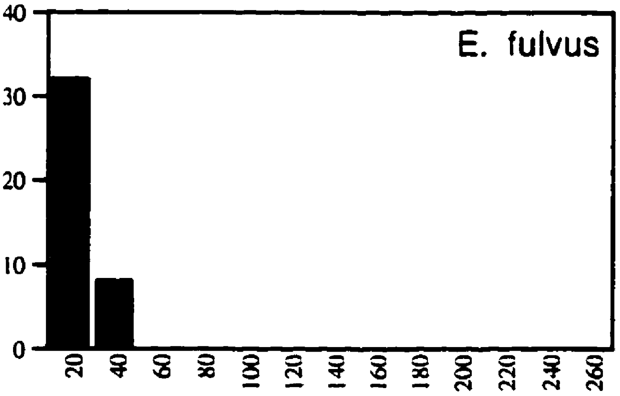
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