

Assessing the Potential for Fish Migration From Marine Reserves to Adjacent Fished Areas in the Soufriere Marine Management Area, St. Lucia

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ABSTRACT

The movement of reef fish was investigated by tagging and visual recapture methods in two protected areas and two adjacent fishing areas in the recently established Soufriere Marine Management Area, St. Lucia. A total of 2,301 fish from 10 families were tagged, and visual recaptures were conducted weekly by SCUBA surveys for nine weeks following tagging. The maximum visual recapture proportion was 44%, and decreased with time following tagging. The mean dispersal distance from the release point over the nine week survey period differed significantly between families, being highest for Carangids (~260 m) and Labrids (~110 m), and lowest for Holocentrids (~15 m) and Serranids (~10 m). For most families, mean dispersal distance was <50 m, and did not differ significantly with time following tagging or between study sites. There was no significant effect of protection from fishing (i.e., Marine Reserve) on the movement of fish. Moreover, most individuals in all families showed strong homing behavior and site attachment, quickly returning to their capture point when released some 100 m to 800 m away. These results demonstrate that the potential export of fish biomass from protected areas to adjacent fishing areas through emigration of catchable fish is negligible under the conditions in the management area during the first year following zoning. Current theory predicts that the extent of movement and probability of fish re-locating their home sites will increase markedly at the higher fish densities that characterize mature protected areas. Under these conditions export of catchable fish to adjacent fished areas will increase. This remains to be demonstrated as the Soufriere Marine Management Area matures.

KEY WORDS: Fish tagging, marine protected areas, reef fish movement, St. Lucia

INTRODUCTION

Coral reef-associated fisheries are socio-economically important in many developing countries (Munro and Williams, 1985), but over-harvesting of reef fish is increasingly prevalent (e.g. Koslow *et al.*, 1988; 1989; Roberts and Polunin, 1991). The development of appropriate management strategies for these fisheries is critical, but is complicated by their multispecies nature and by the use of several gear types in harvesting (Bohnsack, 1990; Russ, 1991).

Marine protected areas (MPAs) are management tools with the potential to overcome some of the management constraints associated with coral reef fisheries. Within an MPA a portion of the reef environment is designated non-extractive (Marine Fishery Reserves), and is excluded from the direct effects of fishing. This is predicted to increase fish abundance both within the reserve and in adjacent unprotected areas through net emigration from the reserve, and through higher recruitment to the unprotected areas of larvae produced in the reserve (Rowley, 1994; Bohnsack, 1994). MPAs are conceptually simple, holistic approaches to resource management that are more successfully implemented and enforced than gear or effort restrictions (Roberts and Polunin, 1993). They are particularly practical management tools for developing countries, and are being established world-wide as an alternative to species-population models of fisheries management (Roberts and Polunin, 1991; Polunin *et al.*, 1996).

Despite the prevalence of marine reserves, there are relatively few biological studies that have successfully quantified reserve effects on adjacent fisheries (Rowley, 1994). Several studies have now documented higher fish biomass within reserve areas (e.g. Alcalá, 1988; Polunin and Roberts, 1993; Rakitin and Kramer, 1996), but there is little evidence for increased yield in adjacent fished areas following reserve establishment, and the specifics of the biological mechanisms by which MPAs are hypothesized to affect fisheries are not well understood.

One mechanism proposed for the positive effect of marine reserves on fish abundance in adjacent areas is density-dependent movement of catchable fish from reserve areas to adjacent areas as fish abundance in the reserve areas increases. Alcalá and Russ (1990) reported reduced commercial catch rates in adjacent fishing areas following the collapse of a marine reserve in the Philippines, and suggested that the higher rates before collapse had been the consequence of emigration from the reserve. Definitive evidence of emigration from coral reef

reserves is scarce, although there are estimates of the net export of some temperate species from marine protected areas (e.g. Attwood and Bennett, 1994). Despite this, the emigration effect is often used to convince fishermen that their lack of access to reserve areas will be compensated for by higher catch rates in adjacent areas (Hatcher, 1995; McManus, 1996). Additional data to support this claim are clearly required. More specifically, detailed information is required on the types and scales of reef fish movement, on the extent to which such movements are taxon-specific, and on how patterns of movement differ with changes in fish habitat and fish abundance induced by protection from fishing mortality and anthropogenic damage.

Here we report the preliminary results of mark-recapture experiments conducted within the context of a broader study of the effect of a recently established marine management area on the fish and fisheries of Soufriere, St. Lucia (Hatcher *et al.*, 1995). The objectives are to provide initial measures of reef fish dispersion in both reserve and non-reserve habitats, to compare these across commercially important fish taxa, and to apply these results to assessing the potential of marine reserves to enhance the availability of catchable fish in adjacent areas through emigration (i.e. "spillover", *sensu* Rowley, 1994).

MATERIALS AND METHODS

The Soufriere Marine Management Area

The town of Soufriere and its picturesque surroundings in the southwest of St. Lucia are experiencing significant growth in tourism. The increased demands placed upon the resources of the fringing reefs have led to conflicts among user groups, including coastal fishers (Renard, 1995, Nichols and George, *in press*). In recognition of the need for integrated management, local NGOs, government agencies and representatives of user groups drafted a multiple use zoning plan for the Soufriere Marine Management Area (SMMA) (Anonymous, 1994).

The zoning regulations for the SMMA were implemented on August 1, 1995. The area incorporates approximately 11km of coastline, about 50% of which is bordered by narrow fringing, wall and patch reefs (Goodridge, *et al.*, *In Press*). Twenty three management zones within the SMMA include three zoning levels that delegate priority use to fishers, yachts, or recreational groups and another that allows all activities by all three user groups. In addition, there are five marine reserve areas (totalling 38% of the total zoned area and 49% of the total reef area), where no form of harvesting, resource extraction or destructive activity is permitted. Fishing is permitted in all other areas, provided that the priority user group is unaffected.

Study Sites

Two marine reserves (RESa & RESb) and two adjacent non-reserve (fishing

priority) areas (NRa & NRb) were chosen as paired tag/release sites in each of two regions of the SMMA: a. Petite Piton, b. Grand Caille (Figure 1). Site selection was based primarily on the presence of a reserve in habitat that had contiguous reef spanning a common RES-NR boundary, but also on the necessity of independent, paired replicates for use in an orthogonal experimental design (Hatcher *et al.*, 1995). This selection ensured that natural barriers (e.g., extensive sand sheets) would not potentially constrain the movement of reef fish between sites. The centre point ('point 0') of each tag/release site was established 200 m from the common boundary of the protected and fishing area, with transects extending 200 m in both directions along the fringing reef parallel to shore from the site's "point 0". The transects were established at 5 m and 15 m depth, and were marked with styrofoam reference buoys every 10 m to orient SCUBA surveys (see Visual Recaptures).

Fish Abundance

Visual fish counts (method of Williams, 1982) were conducted using 5m wide strip transects of 10 - 50 m length, to estimate densities of selected species at each site. The diver slowly swam the mid-line of the transect, counting either demersal or swimming species within 2.5 m on either side of the diver. The counts were done in conjunction with visual censuses for tags (see Visual Recaptures) using the styrofoam reference buoys to indicate transect length.

Fish capture and tagging

Reef fish were captured using traditional Antillean-style "Z-traps", from an area within a 30m radius of "point 0" of each site. All fish from one trap at a time were held in a shaded, 200 l plastic bin of sea water on the boat, transported to the release point and released immediately tagging. The time any fish was out of water never exceeded 60 seconds, and the total time to tag and release a trap full of fish never exceeded 30 minutes. Thus, the proportions of fish taxa tagged reflected their abundance in the catch. Trapping and tagging were conducted at the different sites sequentially, with the transfer of activities to the next site occurring when a minimum of 200 fish had been tagged (2 to 3 days work).

A total of 2,301 reef fish from 10 families were tagged over two temporally independent tagging experiments initiated in October, 1995 and March, 1996. The species composition of the combined catch is shown in Table 1. All fish were tagged using Floy® anchor tags (FD-68B), injected into the dorsal musculature and anchored between the dorsal spines. Tag colour and tag location (Right-side:RS or left-side:LS) were chosen such that the site and date of tag/release could be identified for each fish. Tagged fish were always released at "point 0" of the study site, which was marked with a surface buoy.

During the second experiment, each trap location was marked with coded

flagging tape to indicate the exact point of initial fish capture. The tag information for each fish was then recorded in the context of its trap code, to allow comparisons between the initial capture position and all future observations of any individual.

Tendencies to return to the capture position (homing behavior) were also tested in the second experiment by releasing fish at distances 100 m - 800 m away from their initial capture point and recording the location(s) of their subsequent visual recapture(s).

Visual recaptures

Underwater surveys for tagged fish began the day after the first tagging session, and were conducted at least weekly at all sites for up to 9 weeks. The surveys started at one end of the transect (depending on current direction) and proceeded along the 200m preceding and following "point 0". During the survey, each tagged fish observed was noted on an underwater slate. The information recorded included species, tag colour, tag location (RS or LS), and tag number if possible. The direction and distance of tagged fish from point 0 was estimated to the nearest metre using the transect reference buoys.

Analysis of movement

The fish location data were analyzed for each family four ways:

- i) As the mean distance of the tagged fish from point 0 (Measure 1), to provide an overall measure of the dispersal of the fish after release from a fixed point, regardless of the capture position of the fish.
- ii) As the mean distance of the tagged fish outside the 30 m zone around point 0, within which all fish were captured (Measure 2). This was calculated to obtain a measure of dispersal away from a capture/release area that would not be confounded by homing behavior.
- iii) As the mean distance of the tagged fish from its initial capture point (Measure 3), to measure the extent of subsequent dispersal from that point (or inversely the degree of site attachment of the tagged fish). This measure could only be calculated for fish that were recognizable as individuals (through the tag number code), and was confined primarily to Holocentrids, due to the mobility and/or wariness of most other species. The data for measure 1 was pooled from experiments 1 and 2, while data for measures 2 and 3 were only from experiment 2.
- iv) The homing behavior of fish was investigated and quantified as the percentage of fish observed to return to their initial capture points when released at distances 100 m to 800 m away from the capture point (the greatest distance set by the maximum length of two adjoining sample transects).

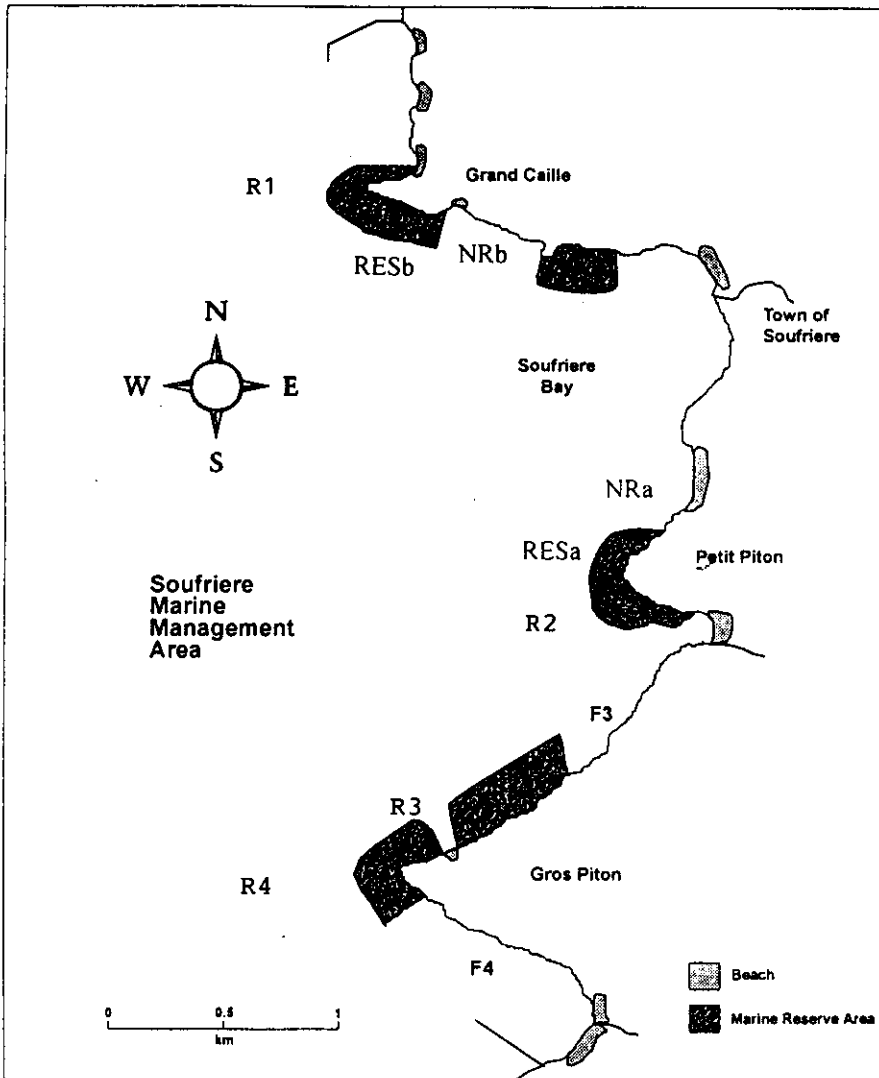


Figure 1. Chart of the Soufriere Marine Management Area, showing marine Reserves (stippled) and adjacent Fishing zones. Paired Experimental sites within reserves (RES) and not within reserves (NR) are plotted (a & b).

RESULTS

Fish Abundance

The visual census data do not provide evidence that reef fish densities are higher in reserves than in non-reserve areas. The mean densities of reef fish recorded in visual surveys at the four study sites are shown for all fish combined, for fish families, and for individual species in Table 1. For all species combined, mean densities of reef fish did not differ significantly between zones or among 2333; $p > 0.05$). When between-site variation tested at the family level, however, densities differed significantly between sites for Acanthuridae, Holocentridae, Scaridae, and Serranidae (Kruskal-Wallis test: $p < 0.05$ in all cases; Table 1).

Fish tagging and Visual Recapture

Reef fish belonging to the families: Holocentridae, Acanthuridae, Scaridae, Haemulidae, Labridae and Balistidae dominated the trap catches, and therefore comprise the bulk of the species tagged (Table 2).

A total of 3,560 visual recaptures of tagged fish were recorded (note that an individual tagged fish can be visually recaptured in several surveys during an experiment). The percentage of fish visually recaptured decreased with time after tagging at all study sites, both when all fish were combined and when the common families were considered separately (Figure 2). Changes in the percentage of fish visually recaptured following tagging could reflect tag loss, fish mortality, and/or the movement of fish outside of the survey zones.

Fish Dispersal

Differences among families — The mean distances that tagged fish were observed from their release point (Dispersal Measure 1) are shown for the more common fish families at the study sites in Table 3, and frequency distributions of observed distances from release points are shown in Figure 3. The mean distances from release points differed significantly between families (Kruskal-Wallis test: $O^2 = 338.5$; $p < 0.0001$), values being highest for Carangids and Labrids, and lowest for Holocentrids (Table 3).

The mean distances that tagged fish were observed outside of the 30 m zone around the release point, i.e. the 30 m zone within which all fish were initially captured (Dispersal Measure 2), are shown in Table 4. This dispersal measure again differed significantly among families (Wilcoxon test: $O^2 = 28.38$; $p = 0.0004$), but in somewhat different pattern as that obtained from Dispersal Measure 1 (compare Tables 3 and 4). The Labrids again showed high dispersal and Holocentrids were again low, but the Balistids and Scarids showed greater movement than the Mullids and Haemulids by this method.

Table 1. The mean densities of reef fish (as number/50 m²) at the four study sites within the SMMA (Figure 1) and at all sites combined, as determined from replicate visual censuses (n). The standard error of the means are given in brackets.

SPECIES	NRA (34)	RESA (12)	NRB (27)	RESB (34)	ALL SITES (97)
<i>Clepticus parrae</i> (Creole wrasse)	81.20 (30.4)	20.80 (7.08)	82.40 (17.16)	66.80 (13.5)	73.17 (11.4)
<i>Myripristis jacobus</i> (Blackbar Soldierfish)	23.10 (2.35)	24.30 (3.66)	11.90 (1.32)	8.09 (1.93)	16.77 (1.33)
<i>Acanthurus bahianus</i> (Ocean Surgeon)	1.35 (0.23)	1.99 (0.49)	0.96 (0.24)	3.72 (0.64)	1.90 (0.22)
<i>Mulloidichthys martinicus</i> (Yellowtail Goat)	4.99 (1.17)	0	0.58 (0.17)	0.68 (0.14)	1.89 (0.56)
<i>Holocentrus rufus</i> (Longspine Squirrelfish)	1.56 (0.30)	1.00 (0.22)	2.60 (0.41)	1.63 (0.31)	1.77 (0.18)
<i>Sparisoma aurofrenatum</i> (Parrot - Redband)	1.22 (0.27)	1.80 (0.73)	1.36 (0.19)	1.38 (0.19)	1.35 (0.13)
<i>Ocyurus chrysurus</i> (Yellowtail Snapper)	2.04 (0.50)	1.60 (0.51)	0.84 (0.18)	0.75 (0.21)	1.22 (0.18)
<i>Spari soma viridae</i> (Parrot - Stoplight)	0.96 (0.25)	0.80 (0.37)	1.16 (0.22)	1.62 (0.26)	1.22 (0.13)

Table 1 (continued).

SPECIES	Nra (34)	RESa (12)	Nrb (27)	RESb (34)	ALL SITES (97)
<i>Scarus taeniopterus</i> (Parrot - Princess)	0.43 (0.14)	1.80 (0.66)	0.72 (0.14)	1.21 (0.22)	0.86 (0.11)
<i>Caranx ruber</i> (Bar Jack)	0.87 (0.38)	1.6 (0.68)	0.24 (0.14)	0.58 (0.26)	0.62 (0.16)
<i>Scarus vetula</i> (Parrot - Queen)	0.43 (0.14)	0	0.72 (0.16)	0.83 (0.21)	0.62 (0.10)
<i>Lutjanus mahogoni</i> (Mahogany Snapper)	0.74 (0.23)	1.60 (0.81)	0.720.22	0.25 (0.10)	0.64 (0.12)
<i>Acanthurus coeruleus</i> (Blue Tang)	0.18 (0.05)	0.33 (0.06)	0.80 (0.16)	0.58 (0.19)	0.47 (0.07)
<i>Scomberomorus regalis</i> (Cero Mackerel)	0.44 (0.15)	0.60 (0.25)	0.28 (0.10)	0.33 (0.12)	0.36 (0.07)
<i>Holocentrus marianus</i> (Longjaw Squirrelfish)	0.18 (0.09)	0.50 (0.13)	0	0.73 (0.18)	0.30 (0.06)
<i>Epinephelus cruentatus</i> (Graysby)	0.35 (0.10)	0.33 (0.09)	0.21 (0.08)	0.27 (0.13)	0.29 (0.05)
<i>Epinephelus fulvus</i> (Coney)	0.22 (0.06)	0.25 (0.06)	0.17 (0.07)	0.05 (0.05)	0.17 (0.03)

Table 1 (continued).

FAMILY	Nra (34)	RESa (12)	Nrb (27)	RESb (34)	ALL SITES (97)
Holocentridae	24.90 (2.38)	25.83 (3.99)	14.46 (1.29)	10.45 (2.29)	18.85 (1.37)
Scaridae	3.04 (0.49)	4.40 (0.49)	3.96 (0.51)	5.03 (0.39)	4.05 (0.27)
Acanthuridae	1.52 (0.25)	2.33 (0.48)	1.83 (0.36)	4.30 (0.65)	2.38 (0.24)
Lutjanidae	0.74 (0.23)	1.60 (0.81)	0.72 (0.22)	0.25 (0.10)	0.64 (0.12)
Serranidae	0.58 (0.11)	0.58 (0.15)	0.38 (0.09)	0.32 (0.15)	0.46 (0.06)
ALL FISH POOLED	116.57 (31.8)	74.92 (8.57)	100 (19.1)	89.05 (14.8)	100.21 (12.5)

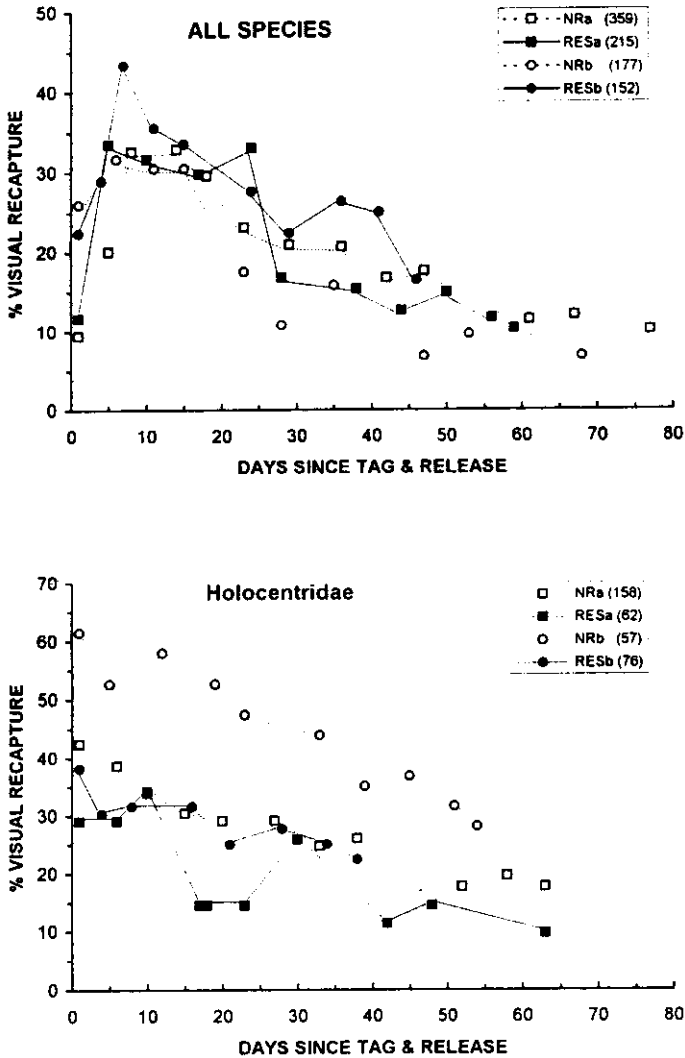


Figure 2. Percentage of tagged fish that were visually recaptured during the second experiment, plotted against the number of days since tag and release at the four study sites in the Soufriere Marine Management Area, St. Lucia (shown in Figure1). a. All species combined and b. Squirrel fishes

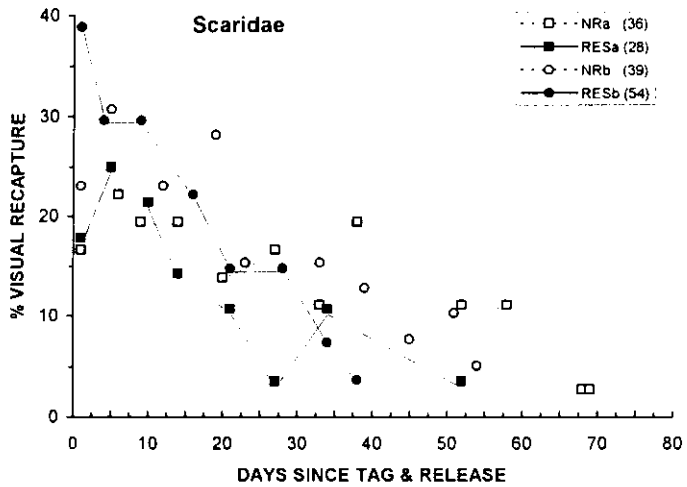
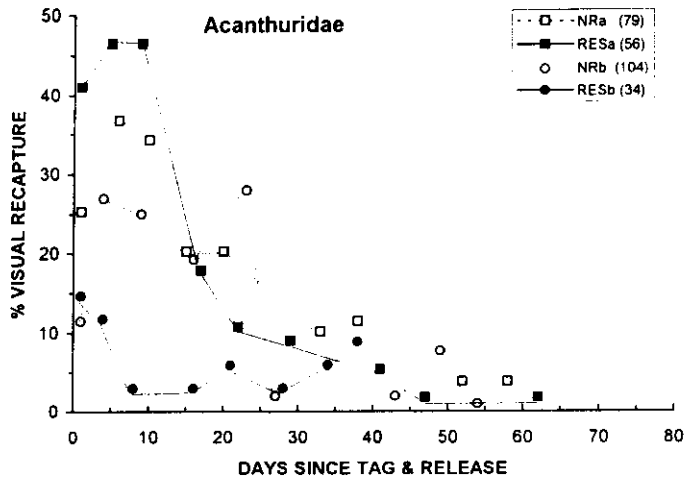


Figure 2 (cont.). Percentage of tagged fish that were visually recaptured during the second experiment, plotted against the number of days since tag and release at the four study sites in the Soufriere Marine Management Area, St. Lucia (shown in Figure1). c. Surgeon fishes and d. Parrot fishes.

Table 2. The number of fish tagged and released in each family tagged and released at each study site and at all sites combined within the SMMA (Figure 1). The number of samples is the total number of days on which both 400m transects at each site were searched for visual recaptures.

Family	Number	NRa	RESa	NRb	RESb	TOTAL
Holocentridae	3	346	373	218	157	1,094
Acanthuridae	3	97	134	112	49	392
Scaridae	4	51	95	67	133	346
Labridae	1	75	31	5	9	120
Ballistidae	4	30	32	18	16	96
Haemulidae	4	6	36	1	53	96
Serranidae	4	9	26	10	10	55
Mullidae	2	12	14	0	24	50
Lutjanidae	5	5	7	3	8	23
Carangidae	2	3	6	8	5	22
Other	7	5	0	1	1	7
Total	39	641	754	443	465	2,301
No. of Samples	expt. 1	23	20	17	16	76
No. of Samples	expt. 2	17	14	11	11	53

Table 3. Mean distances (m) that tagged fish were observed from their release point (point 0), presented separately for the 4 study sites within the SMMA (see Figure 1) and for all sites combined. The standard error is given in brackets. n = the total number of visual recaptures of tagged fish. n/d = "no data".

Family	SITES						n
	NRa	RESa	NRb	RESb	All Pooled		
Carangidae	n/d	488	187.7 (58.)	n/d	258.0 (63.)	8	
Labridae	112.2 (18.)	122.1 (39.7)	89.3 (80.)	93.5 (87.)	113.3 (16.)	118	
Lutjanidae	52.3 (32.)	52.2 (7.5)	n/d	59.4 (10.)	54.7 (11.)	35	
Mullidae	71.3 (17.)	35.3 (7.0)	n/d	39.8 (5.9)	53.1 (8.0)	88	
Haemulidae	24.6 (3.5)	35.3 (3.4)	n/d	54.9 (4.7)	47.7 (3.7)	161	
Acanthuridae	22.1 (3.3)	26.0 (2.7)	67.3 (7.7)	26.6 (6.3)	35.7 (2.7)	545	
Balistidae	39.3 (13.)	40.7 (5.9)	14.6 (3.1)	29.2 (5.1)	35.1 (5.2)	119	
Scaridae	47.9 (9.5)	23.6 (2.7)	16.1 (1.4)	31.6 (4.1)	30.7 (2.7)	423	
Serranidae	8.7 (1.7)	19.9 (3.2)	7.0 (5.6)	20.5 (6.0)	15.1 (1.9)	70	
Holocentridae	13.0 (0.3)	16.3 (0.9)	15.5 (0.5)	11.7 (.62)	14.1 (0.3)	1,985	

Table 4. Mean distances (m) that tagged fish were observed from the nearest border of the 30 m capture zone, presented separately for the four study sites in the SMMA (Figure 1) and for sites combined. The standard error is given in brackets. n = the total number of visual recaptures of tagged fish. n/d = "no data".

FAMILY	SITES					ALL POOLED	n
	NRa	RESa	NRb	RESb			
Labridae	229.67 (36.39)	n/d	n/d	n/d	n/d	220.15 (36.92)	20
Balistidae	293.33 (52.39)	70.00 (10.00)	n/d	31.00 (29.00)	n/d	149.00 (46.81)	8
Scaridae	195.73 (51.73)	17.50 (12.50)	61.67 (16.20)	95.00 (42.97)	n/d	115.39 (22.86)	33
Acanthuridae	130.63 (58.76)	34.71 (11.32)	130.10 (16.04)	125.00 (35.00)	n/d	109.80 (13.05)	74
Mullidae	96.92 (25.48)	n/d	n/d	50.80 (15.12)	n/d	102.65 (23.08)	23
Haemulidae	n/d	30.00 (10.00)	n/d	33.33 (4.13)	n/d	48.19 (13.36)	32
Holocentridae	n/d	1	n/d	20.00 (5.00)	n/d	13.67 (6.96)	3
Serranidae	n/d	5	n/d	n/d	n/d	5	2

The mean distances that tagged fish were observed from their initial capture positions (Dispersal Measure 3) again differed significantly among families (Wilcoxon test: $O^2=129.5$; $p < 0.0001$), being higher for Scarids (18.90 m \pm 7.09) and Acanthurids (10.78 m \pm 1.46) than for Holocentrids (2.65 m \pm 0.12).

Differences among sites — The mean distances that tagged fish were observed from their release point (Dispersal Measure 1) differed significantly between sites for Acanthurids (Wilcoxon test: $O^2 = 66.2$; $p < 0.0001$; due primarily to high value at site NRb), Scarids ($O^2 = 38.3$; $p = 0.009$; due primarily to high value at site NRA), and Holocentrids ($O^2 = 19.7$; $p < 0.0002$; (higher at sites RESa and NRb; Table 3). These among-site differences did not relate to either the reserve/non-reserve status of the site (Table 3) or the density of the fish family at that site (compare Tables 3 and 1). Between-site differences in Dispersal Measure 1 were not significant for the other dominant fish families (they could not be analyzed for others because of low recaptures at some sites).

The mean distances that tagged fish were observed outside of the 30 m zone around the release point (Dispersal Method 2) differed significantly between sites only for Acanthurids (Table 4; Wilcoxon test: $O^2 = 10.6$; $p < 0.02$), the difference again driven by the high value at NRb.

The mean distances that tagged fish were observed from their initial capture positions (Dispersal Measure 3) differed significantly between sites only for Holocentrids ($O^2 = 25.3$; $p < 0.0001$), but the magnitudes of these differences were small (NRA = 2.38 m, RESa = 2.68 m, NRb = 3.49 m, RESb = 2.30 m).

Differences with time following tagging — The distances that tagged fish were observed from their release point (Dispersal Measure 1) did not increase with days following tagging for any fish families (Linear regression analysis: $p > 0.05$ in all cases). Similarly, the distances that fish were observed from their capture points (Dispersal Measure 3) did not increase with days following tagging for any fish families (linear regression analyses; $p > 0.05$ in all cases). The distances that fish were observed outside of the 30 m zone around their release point (Dispersal Measure 2) increased with days following tagging only for Labrids, but the independent variable explained barely 20% of the variation ($r^2 = 0.214$, $p < 0.04$; Figure 4). These results do not demonstrate that fish belonging to any of the families studied move further from their capture and release locations during the first two to three months following release.

Homing Behavior

The percentage of individual fish returning to their capture locations following release at sites 100 m - 800 m away from their capture locations is shown in Figure 5. Most fish families showed strong homing behavior, with Holocentrids having the highest percentage of return to capture location, followed by Scarids, Balistids, Serranids and Acanthurids. Most returns to the capture location had occurred in less than 24 hours following release.

DISCUSSION

Most of the coral reef fish followed in this study spent the 7 to 11 weeks of observation within a few tens of metres of the locations where they were caught. Only the highly mobile Carangids and Labrids regularly moved further than 100 m (*Caranx ruber* were observed as far as 500 m, and *Clepticus parrae* as far as 600m away from the release site), while individual Acanthurids, Haemulids, Scarids and Balistids were only occasionally observed beyond the 100m mark. Tag returns for the artisanal reef fishery in the Soufriere region do not expand these distances, despite the widespread use of traps, seines, gill nets, hand lines and spear guns in the SMMA (Goodridge *et al.*, In Press). Furthermore, those fish released as far as 800 m from their capture site returned to it, demonstrating that some of these fish can move large distances in short periods, but suggesting strong site tenacity and homing behavior for most families.

The results of our study are in agreement with both theoretical and empirical studies of reef fish movement, but are constrained by the spatial-temporal scales of measurement. Most reef fish species are considered to be sedentary at the reef-scale, occupying home ranges of limited extent as permanent residents of a single reef throughout their post-settlement life (Reese, 1973; Sale, 1991). Return migrations over distances of hundreds of metres up to a few kilometres occur in some species for purposes of feeding (Ogden and Buckman, 1973), sheltering (Hobson, 1972) and reproduction (Johannes, 1978). We have limited ability to discern such migrations in our data because the temporal scale of sampling was too coarse. Diurnal migrations beyond the extent of the survey area could be expected to increase both the mean and the variance of the measured displacements, unless the timing of migration and sampling were well-correlated. Families with species known to migrate diurnally (e.g. Scaridae, Haemulidae) did not exhibit particularly high dispersion over the reefs of the SMMA (Tables 3 and 4, Figure 3). But the relatively rapid depletion of the tagged populations of Scarids (Figure 2d) and particularly Acanthurids (Figure 2c) compared to all tagged fish (Figure 2a) or more sedentary Holocentrids (Figure 2b), suggest that longer-term migration of members of these families out of the survey area may be significant (given reasonable assumptions of confounding due to differential tag loss and natural mortality).

Appledoorn *et al.* (In Press) document migrations of Haemulids over tens of metres in resting schools on reefs, over hundreds of metres to nocturnal feeding grounds in adjacent seagrass beds, and over kilometres to offshore reefs as a function of ontogeny. We did not see evidence of such movements, in part because censuses were only conducted during daylight hours, and also because there are no seagrass beds or offshore reefs adjacent to the narrow fringing reefs of Soufriere (which plunge steeply to depths in excess of 100 m within 1 km of

shore).

Order-of-magnitude differences in the short-term ambit of reef fish exist among families, among species within families, and among individuals within species populations (Bohnsack, 1990). For example, accurate tracking of goat fish and jacks by Holland, *et al.* (1993, and K. Holland, *pers.comm.*, 1995) demonstrated well-defined diurnal migrations of tens of metres for the Mullids and hundreds of metres for the Carangids (results in agreement with ours: Tables 3), but in the latter group a few individuals moved tens of kilometres.

The Labrids are a diverse family, with individual species' behaviours resulting in territories of a few tens of metres to home ranges of over a kilometre (Thresher, 1984). One of the most mobile species we tagged in the SMMA was the Creole Wrasse (*Clepticus parrae*: Tables 3 and 4, Figure 4), which forms schools that range along the reef crest. In contrast, the Holocentrids and Serranids appear to be consistently site-attached, showing small ranges and strong homing behavior (Tables 3 and 4, Figures 3 and 5).

An important implication of our results for the use of marine fishery reserves as replenishment areas for adjacent fished areas in the SMMA is that many of the fish which are important to the artisanal fishery do not move beyond the boundaries of the designated reserves. The reefs of the SMMA are so narrow at the scales of the marine reserves (hundreds of metres) that they can be considered one-dimensional (along-shore) for the purposes of modelling fish dispersion (c.f. Attwood and Bennett, 1994). The only boundaries which can be fished are the narrow, across-reef boundaries. Only those catchable species which regularly move the hundreds of metre distances characterizing reserve lengths are likely to contribute significantly to fishers catches unless there is a large change in the species diversity or home range size as a result of protection. It is noteworthy that in the one demonstrated case of significant spillover from a reserve (Russ and Alcalá, 1989) a single species of Caesionid was responsible for most of the increased catch outside the reserves. That fish has an analogous life history and movement pattern to the Creole Wrasse, which is a major component of the reef fish catch in the SMMA.

Our results demonstrate no significant effect of protection from fishing mortality on the movement of reef fish during the first year following zoning of the SMMA. No effect was predicted, given the time scales of years that are required for MPAs to accumulate the large increases in abundance and biomass that are thought to support the export of catchable fish (Roberts and Polunin, 1993; Rowley, 1994). As the marine reserves of the SMMA mature and the cooperation of the fishers in observing reserve boundaries improves with time, it will be valuable to repeat these experiments to document any spillover to the fishery (Hatcher *et al.*, 1995).

While there were significant differences among sites in the movement of

fish belonging to a few families, these resulted mainly from variation in sample size. The four sites can be considered as good replicates of the fringing reef habitats of the SMMA in terms of reef fish movement. We conclude that this study, while not a true "before" measurement of reef fish movement in the SMMA, provides the essential benchmark measure of initial conditions, against which future assessment of reserve effects can be contrasted as the SMMA matures (Hatcher *et al.*, 1995).

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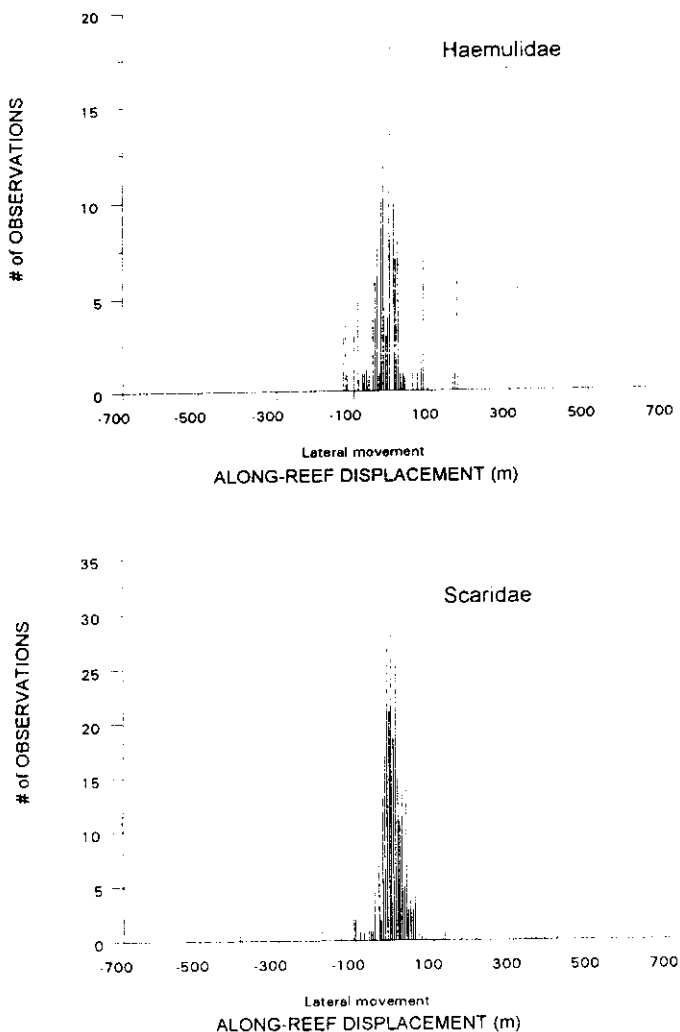


Figure 3. Frequency distributions of along-reef displacement from their release point at which tagged fish were observed (Dispersion Measure 1, see text), during the entire period of observations. Data from all sites combined are presented for the eight most abundant families of reef fish captured in the Soufriere Marine Management Area, St. Lucia. a. Grunts, b. Parrot fishes, c. Squirrel fishes, d. Wrasses, e. Surgeon fishes, f. Groupers, g. Goat fishes, h. Trigger fishes.

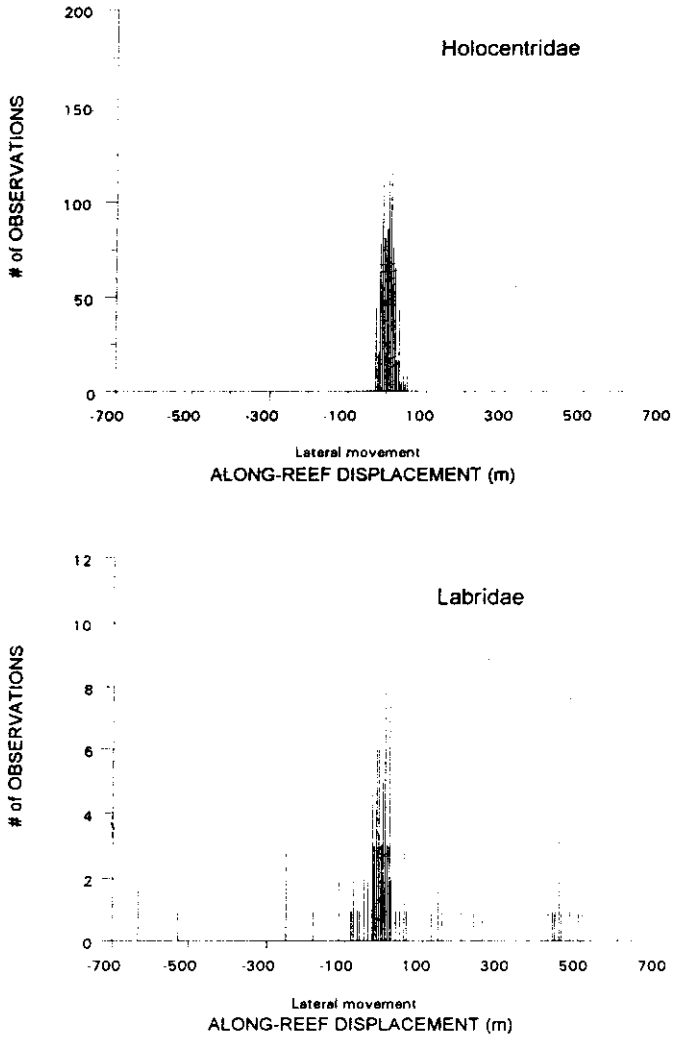


Figure 3 (continued).

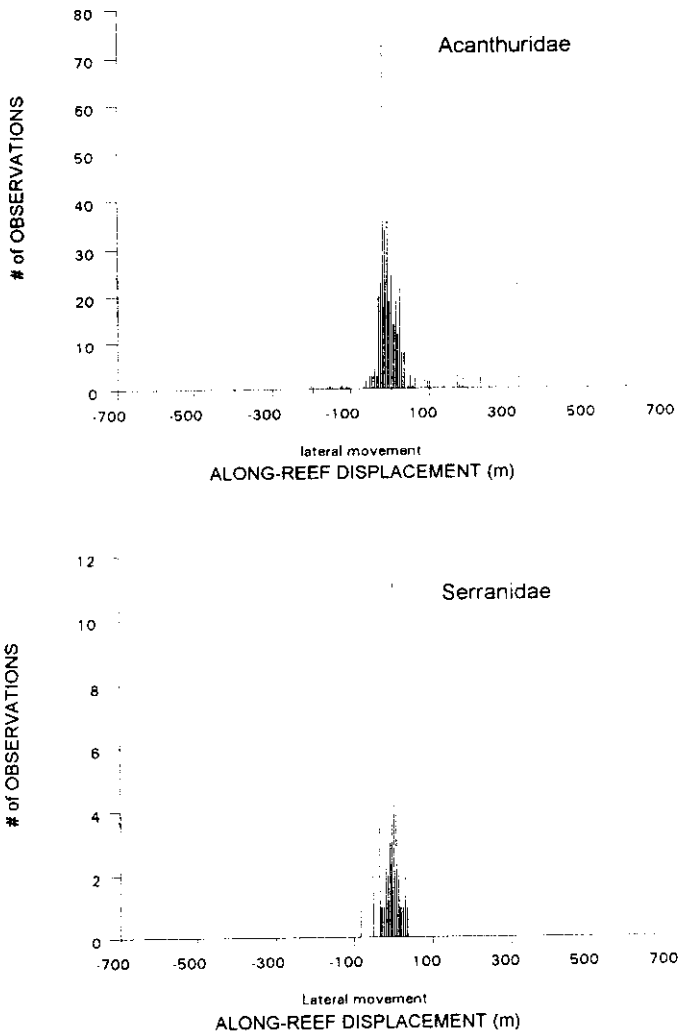


Figure 3 (continued).

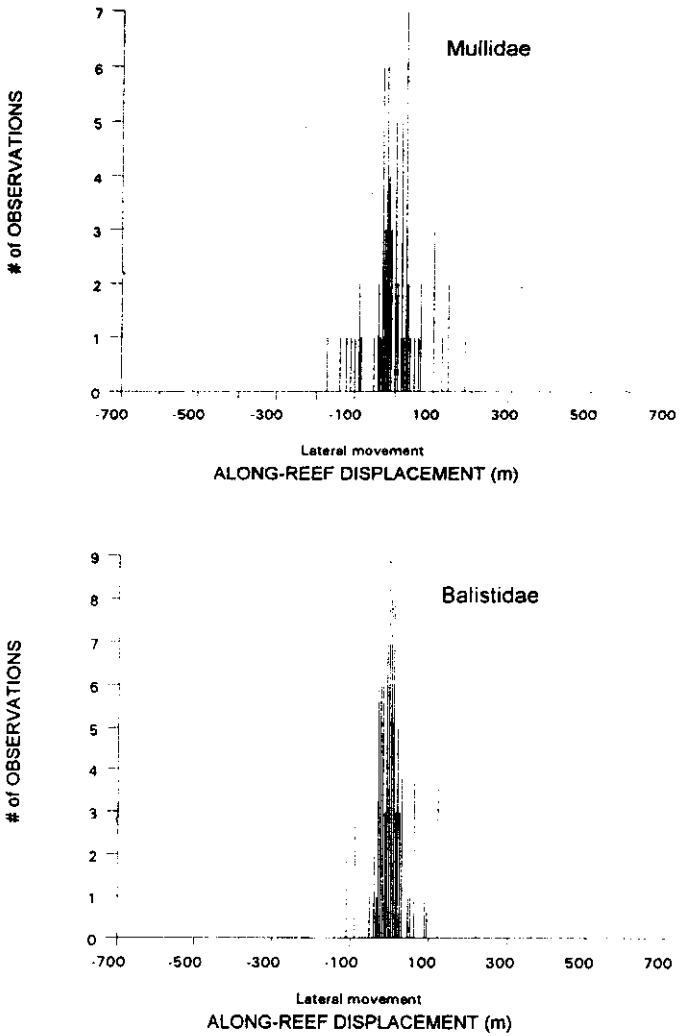


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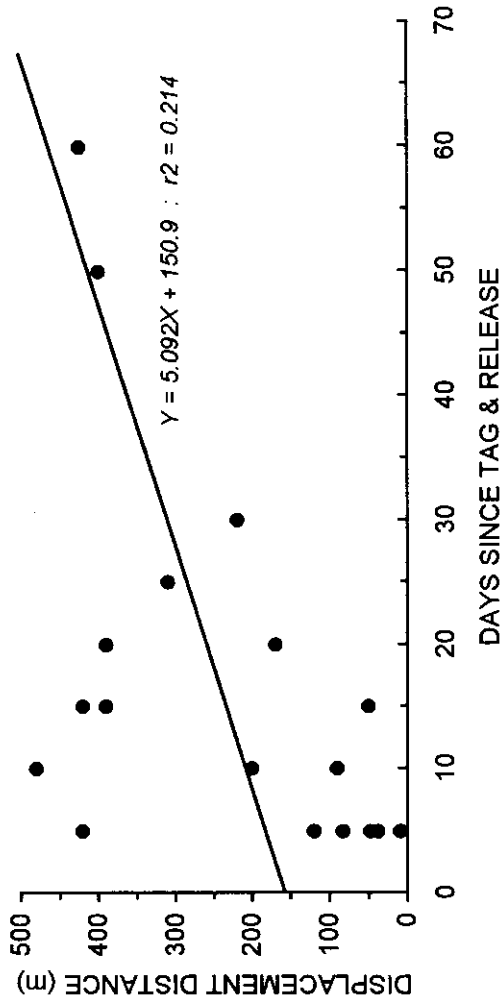


Figure 4. Distance from the boundary of the 30m x 30m release zone within which tagged Labrids (*Clepticus parrae*) were observed (Dispersion measure 2, see text), plotted against the number of days since tag and release in experimental sites in Soufriere, St. Lucia. Least-squares linear regression line is fitted.

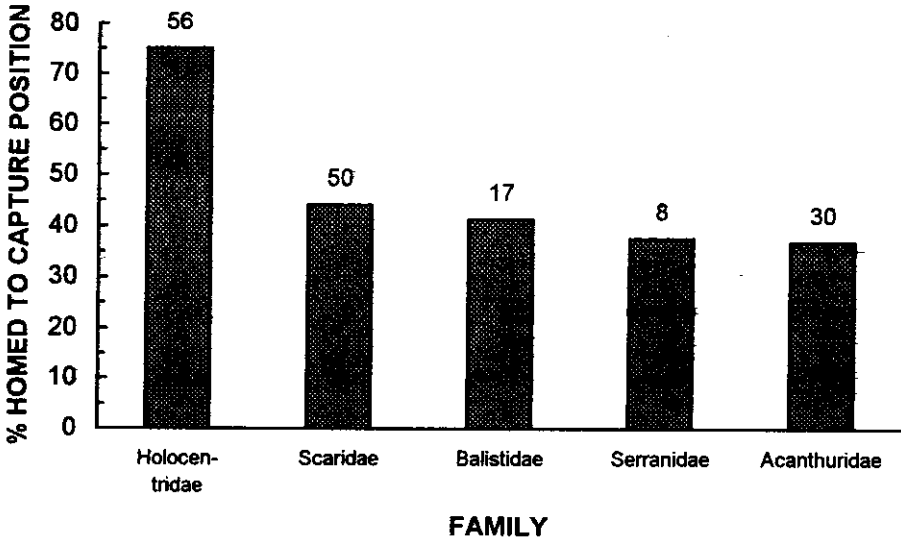


Figure 5. Percentage of tagged fish observed at their site of capture within 24 hours following release at locations ranging from 100m to 800m away within the Soufriere Marine Management Area, St. Lucia. The total number of fish tagged, released and recaptured is shown for each of five families: a. Squirrel fishes, b. Parrot fishes, c. Trigger fishes, d. Groupers, e. Surgeon fishes.

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