BULLETIN OF MARINE SCIENCE, 55(2-3): 470-483, 1994

DISTRIBUTION, PERSISTENCE, AND GROWTH OF GROUPERS (PISCES: SERRANIDAE) ON ARTIFICIAL AND NATURAL PATCH REEFS IN THE VIRGIN ISLANDS

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ABSTRACT

We examined patterns of distribution, persistence, and growth of groupers (especially Nassau grouper, *Epinephelus striatus*), which recruited to or colonized 52 one cubic-meter concrete-block reefs and 10 natural patch reefs off St. Thomas, USVI. The artificial reefs comprised five shelter treatments: 24 large holes, 12 large holes, 24 small holes, 12 small holes, and holeless controls. Although small individuals (<15 cm TL) of the two most abundant species, *E. striatus* and *E. afer*, were distributed evenly among these treatments, larger individuals were usually more abundant on large-hole reefs. *E. striatus* and *E. afer* partitioned the artificial reefs by depth, ranging from 6 to 12 m, with *E. striatus* occurring deeper than *E. afer*. Tagged individuals demonstrated persistence on and homing to specific reefs. Overall, Nassau grouper was the most abundant of six species of *Epinephelus* observed on the artificial reefs. However, this was not the case on natural reefs or in commercial catches, which were dominated by *E. cruentatus*, *E. fulvus*, and *E. guttatus*. Growth rates of a distinct recruit cohort of Nassau grouper on the artificial reefs were comparable to those estimated in other recent field studies. Mean monthly growth rates ranged from 0.84 to 1.17 cm·month^{-1}, and mean growth from the first month of observation (mean size = 8.7 cm) through the eleventh month (19.5 cm) was 10.8 cm. Persistence of the cohort during the year was low, with an 85.4% decline from 158 to 23 individuals over 8 months, presumably due to predation. Due to apparent recruitment overfishing caused by decimation of the local spawning aggregation off St. Thomas, Nassau grouper catches have declined dramatically in recent years. Given the differential distribution of adult Nassau grouper between artificial and natural reefs, we conclude that artificial reefs of the appropriate design may enhance the local abundance of this commercially valuable species.

Groupers (Family Serranidae) are prized food fishes worldwide and have suffered severe overfishing, especially in the Caribbean (reviews by Sadovy, 1989, in press; Richards and Bohnsack, 1990; Russ, 1991). The Nassau grouper, *Epinephelus striatus,* is particularly prized and vulnerable. This species, like most large groupers, forms large spawning aggregations (Smith, 1972; Shapiro, 1987) which are often severely overexploited (Bannerot et al., 1987). In fact, the only large spawning aggregation of *E. striatus* around St. Thomas, U.S. Virgin Islands, was overfished to extirpation, and has not recovered in the decade following its demise (Olsen and LaPlace, 1979; Beets and Friedlander, 1992), apparently resulting in recruitment overfishing.

The impact of overfishing this top predator has not been rigorously examined. Competitive release of small groupers and other species may have occurred (Bohnsack, 1982; reviewed by Russ, 1991). Indeed, smaller groupers, such as *E. cruentatus, E. fulvus,* and *E. guttatus,* have replaced *E. striatus* in commercial landings, and *E. guttatus* has further replaced *E. striatus* at its previous spawning site south of St. Thomas (Beets and Friedlander, 1992).

The Nassau grouper attains large sizes (>900 mm TL) and spawns in site specific aggregations during full moon periods from December to March in the Caribbean (Colin, 1992, unpubl. ms). With the loss of the spawning aggregation south of St. Thomas, U.S. Virgin Islands (USVI) the nearest documented spawn-

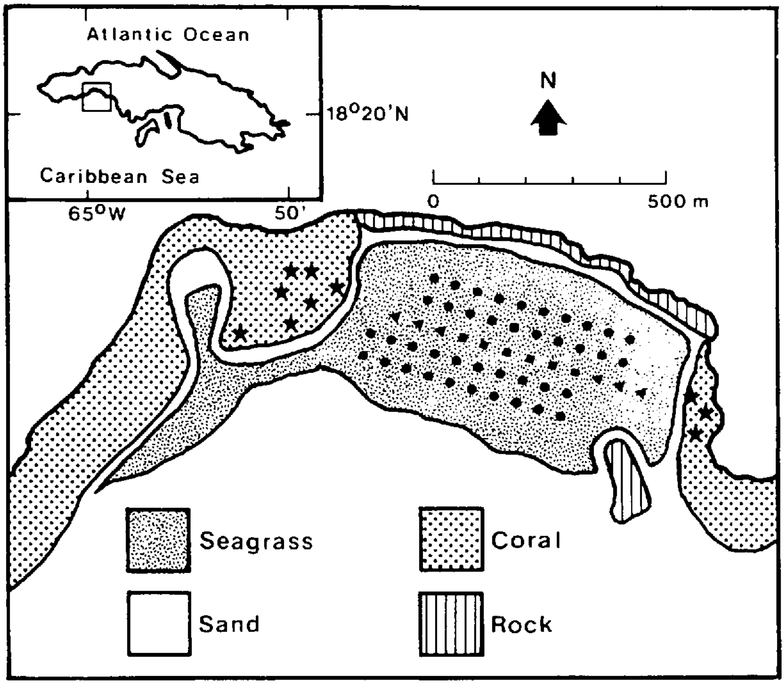


Figure 1. Map of the study area in Perseverance Bay, St. Thomas, U.S.V.I. Squares: locations of six artificial reefs in Set I constructed in 1984; triangles: locations of six reefs in Set II constructed in 1987; circles: locations of 40 reefs in Set III constructed in 1988; stars: locations of 10 monitored natural patch reefs.

ing aggregations are located along the edge of the northeastern insular shelf of the British Virgin Islands (BVI), about 30 km northeast of St. Thomas (Beets and Friedlander, 1992). The BVI share an insular platform with the USVI (excluding St. Croix) and Puerto Rico. In the BVI, large individuals of *E. striatus* are commonly landed. The known spawning aggregations on this portion of the insular shelf are viable and presently receive light fishing pressure. With the predominantly westerly currents in this region, larval drift from the BVI spawning aggregations is presumed to be important in maintaining grouper abundances in the U.S. islands. Thus, recruitment of Nassau grouper in the USVI may depend on viable spawning aggregations in BVI waters.

In this study, we focused on the local enhancement of groupers using artificial reefs, with specific interest in the Nassau grouper. A unique, local recruitment event which occurred during the period of our study allowed us to follow the growth and persistence of large numbers of juvenile *E. striatus* on these reefs. We speculate that this was an unusual event, having occurred only once on our artificial reefs during 6 years of observations. We provide evidence that the recruitment and colonization of artificial reefs by Nassau grouper were very selective, with low abundance on natural patch reefs relative to other groupers. We also report data on the distribution, persistence, and growth rate of groupers on these reefs.

Methods

Site Description and Study Design.—Three sets of artificial reefs were constructed in 1984, 1987 and 1988, respectively, in a large seagrass bed at Perseverance Bay on the south side of St. Thomas (Fig.

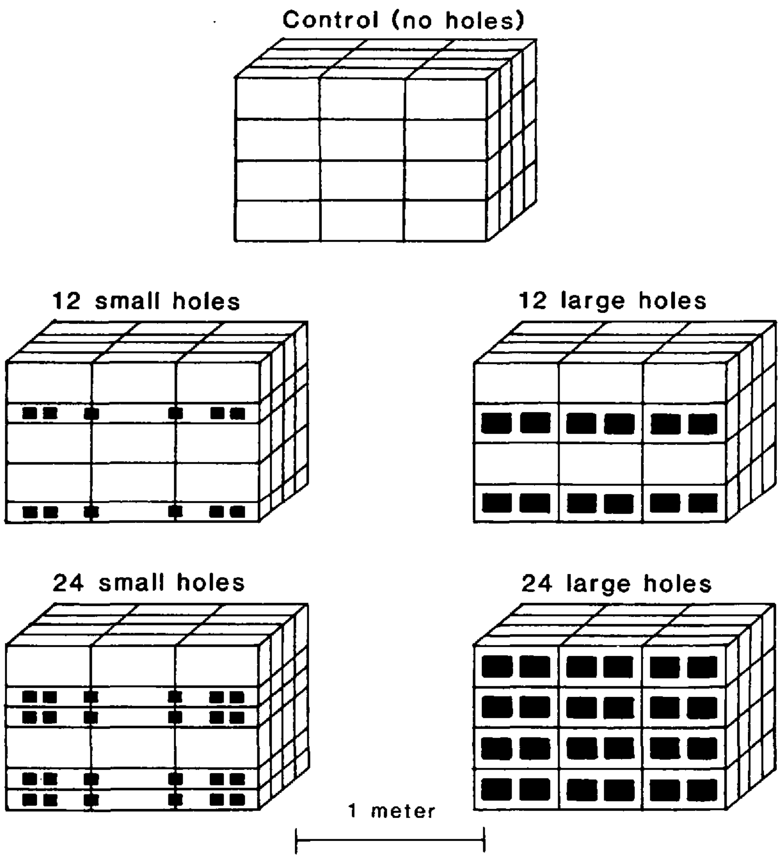


Figure 2. Designs of the five treatments of artificial reefs; the holes pass through each reef.

1). The benthos at this site was primarily mixed seagrass (*Thalassia testudinum* and *Syringodium filiforme*) and algae, with the density of seagrass declining with increasing depth.

All reefs were constructed of concrete blocks on plywood platforms overlying the seagrass/sand substrate, and were of the same size and dimensions (ca. 1 m^3), which is the size of small patch reefs in this area. The experimental design ultimately included five treatments of various hole sizes and numbers: (1) controls with no holes, (2) 12 small holes (4 × 6 cm), (3) 24 small holes, (4) 12 large holes (12 × 14 cm), and (5) 24 large holes (Fig. 2; for detailed descriptions of reef and experimental designs see Hixon and Beets, 1989, 1993).

We constructed the reefs in a complete randomized-block design, with 5 rows of 10–12 reefs each parallel to shore along the 6, 7, 8, 10, and 12-meter isobaths (Fig. 1). Each reef was 50 m from adjacent artificial reefs and a minimum of 100 m from nearby natural reefs or rocky shoreline. We built the first set of reefs (N = 6) in June, 1984 (Set I). Two replicates of each of three treatments were included: controls, 12 large holes, and 24 large holes. We constructed the second set of reefs (N = 6) in July, 1987 (Set II), which also included two replicates of each of three treatments: controls, 24 small holes, and 24 large holes. The final set of reefs (N = 40) were built during July, 1988 (Set III), and included eight replicates of each of all five treatments. In September 1989, all 52 reefs (and most of the natural patch reefs we studied) were destroyed by Hurricane Hugo.

Additionally, 10 natural patch reefs, approximately 1 m^3 in size, were selected for comparative monitoring within the study area (Fig. 1). As parts of continuous reef tracts, these reefs were much less isolated than the artificial reefs, and our census data indicated that occupants were more transient.

Periodically, all reefs were visually censused using complete counts described by Hixon and Beets (1989, 1993). Total lengths of individual fish were easily and accurately estimated as individuals passed or rested beside concrete blocks of previously measured dimensions. The total lengths of all fish on each reef were recorded to the nearest centimeter.

Table 1. Abundance of groupers on artificial and natural reefs in Perseverance Bay, St. Thomas, from 1984 to 1989. Data presented are the grand mean number of fish per reef per census (±standard error).

Reef treatment	*E. striatus*	*E. afer*	*E. cruentatus*	*E. fulvus*	*E. guttatus*
Artificial reef set I: N = 2 reefs/treatment: 1984 to 1989					
0 holes	1.12 (±0.52)	0.01 (±0.02)	0.03 (±0.03)	0.07 (±0.07)	0.03 (±0.03)
12 large	2.22 (±0.78)	0.11 (±0.08)	0.05 (±0.05)	0.03 (±0.03)	0
24 large	2.75 (±0.55)	0.32 (±0.28)	0.15 (±0.15)	0	0.17 (±0.17)
Artificial reef set II: N = 2 reefs/treatment: 1987 to 1989					
0 holes	2.32 (±1.32)	0.09 (±0.09)	0	0.04 (±0.04)	0.09 (±0.09)
24 small	3.14 (±0.04)	0.09 (±0)	0.27 (±0)	0.04 (±0.04)	0.04 (±0.04)
24 large	2.83 (±1.04)	0.09 (±0.09)	0.23 (±0.14)	0.04 (±0.04)	0.04 (±0.04)
Artificial reef set III: N = 8 reefs/treatment: 1988 to 1989					
0 holes	1.60 (±0.30)	0.71 (±0.41)	0	0.06 (±0.06)	0.02 (±0.02)
12 small	1.90 (±0.19)	0.42 (±0.18)	0.02 (±0.02)	0	0.06 (±0.06)
24 small	2.42 (±0.35)	0.04 (±0.04)	0.04 (±0.04)	0	0.02 (±0.02)
12 large	1.00 (±0.25)	5.02 (±1.11)	0.06 (±0.03)	0.08 (±0.04)	0.21 (±0.03)
24 large	2.31 (±0.18)	3.56 (±0.72)	0.06 (±0.03)	0.02 (±0.02)	0.02 (±0.02)
Natural reefs: N = 10 reefs: 1988 to 1989					
Natural	0.04 (±0.03)	0	0.24 (±0.02)	0.20 (±0.06)	0.08 (±0.03)

Tagging Observations.—To determine reef fidelity and homing ability, we tagged groupers with color-coded anchor tags inserted at the base of the dorsal fin. Fish were tagged during two different periods. During our preliminary observations in 1987, we tagged two *E. striatus* and released them on their original reef. In 1989, we tagged 17 grouper of three species and released them on their original reefs. To test for homing, we also tagged 31 grouper of two species and released them on reefs 140 m away from their original reefs.

Growth and Persistence Estimates.—The large number of *E. striatus* juveniles colonizing the 40 reefs of Set III allowed a sufficient sample to estimate juvenile growth and document persistence over the final 11 months of our study (six censuses). Juvenile growth rates were obtained by calculating the difference of the mean total length of all fish in the cohort between census periods.

All statistical analyses were run using the SYSTAT microcomputer statistical system (Wilkinson, 1988).

Results

Abundances on Artificial and Natural Reefs.—The species composition and abundances of groupers on the first two sets of artificial reefs were similar (Table 1; Fig. 3A, B). The most abundant species overall was *E. striatus,* followed by four smaller species: *E. afer* (mutton hamlet), *E. cruentatus* (graysby), *E. fulvus* (coney), and *E. guttatus* (red hind). The third set of artificial reefs supported the same five grouper species, plus the only individual of *E. morio* (red grouper) observed on any of our study reefs. This individual persisted for 6 months on one reef along the 12 m isobath, the deepest of our reefs.

On the third set of artificial reefs, *E. afer* was frequently more abundant than *E. striatus* (Table 1; Fig. 3C). During the last census, typical of all censuses, the largest number of *E. afer* was at the shallowest depth (6 m, Fig. 4), where seagrass density was greatest. Mean abundance of *E. striatus* was greatest at the middle depth (8 m) where the older reefs (Sets I and II) and largest number of large-hole reefs were located. Within depths, the greatest abundance of each species occurred on different reefs, with *E. afer* concentrated on reefs with few or no individuals of *E. striatus* and vice versa.

The abundances of small individuals (<15 cm) of the two most abundant spe-

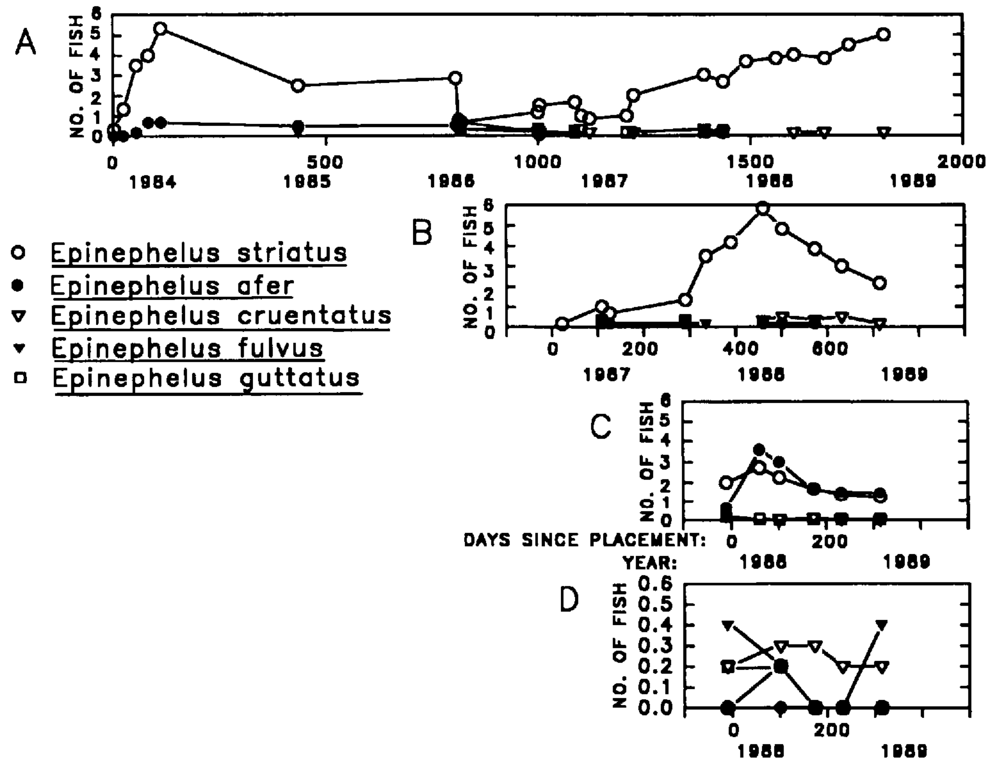


Figure 3. Mean abundances of five grouper species observed on three sets of artificial reefs: A: Set I (N = 6 reefs); B: Set II (N = 6 reefs); C: Set III (N = 40 reefs); and D: 10 natural patch reefs. For the artificial reefs, the number of days from reef construction are indicated along each abscissa, and all four graphs are aligned by date for comparison.

cies, *E. striatus* and *E. afer,* were not significantly different among artificial reef treatments (Table 2; Figs. 5A, 6A). However, larger individuals of both species tended to be more abundant on large-hole reefs (Figs. 5B, 6B), and there were some significant differences in abundance among treatments for these larger fish (Table 2).

In contrast to the artificial reefs, the absolute abundance of *E. striatus* on natural patch reefs was low, and the abundance of *E. striatus* was lower than that of other grouper species (Table 1; Fig. 3). Two grouper species, *E. cruentatus* and *E. fulvus,* were much more abundant on natural reefs than on artificial reefs as was *E. guttatus* in lower numbers. *E. afer,* a species which most commonly inhabits seagrass habitats, was absent on natural reefs monitored.

Persistence on Artificial Reefs.—Persistence of juvenile *E. striatus* on artificial reefs during their first year was low. During the October 1988 census, following an uncommon major pulse of recruitment, we observed 158 small juveniles. This number declined by 85.4% to 23 individuals by June 1989 (Table 3). The decline of smaller individuals (<15 cm TL) was presumably due to predation, since there was no observable redistribution to surrounding natural reefs. The simultaneous increase of individuals on the first set of reefs (Set I) during this period (Fig. 3A) was due to movement of larger individuals (>15 cm TL) from adjacent experimental reefs and/or immigration from outside the study area.

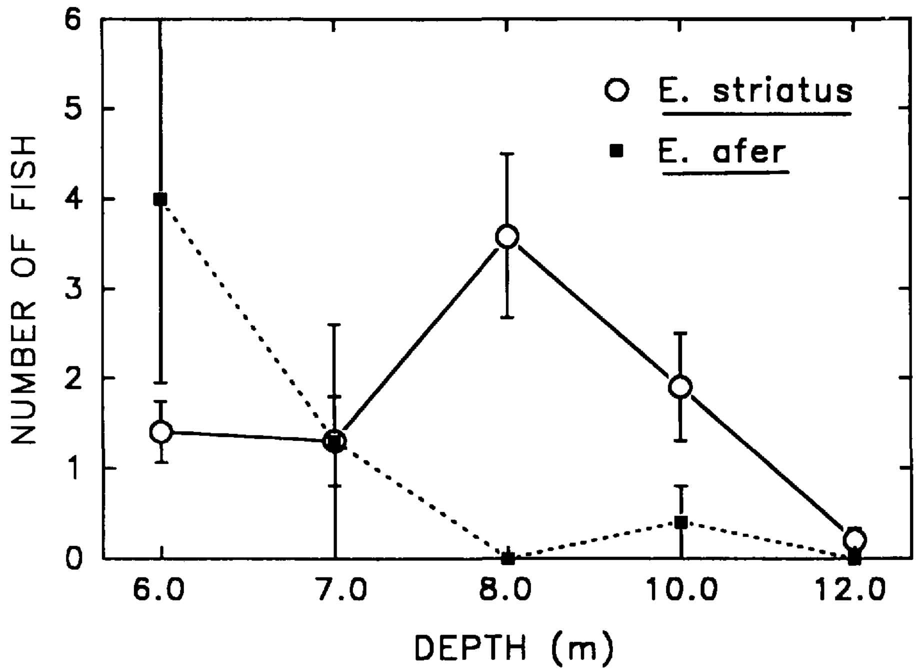


Figure 4. Abundances of *Epinephelus striatus* and *E. afer* on 52 artificial reefs occurring at five depths during the final census (6/12/89). Data presented are the mean number of fish per reef with standard error (N = 10 reefs per depth, except at 8 m depth, where N = 12).

Of two *E. striatus* tagged in 1987, one individual (31 cm SL) disappeared immediately, while the other fish (24 cm SL) persisted on its original reef for at least 85 days. During the homing study in 1989, 15 of the 17 grouper tagged and released on their original reefs persisted for over 2 weeks, until the end of the study (Table 4). These grouper demonstrated striking reef fidelity and homing. Only one of 50 tagged fish was observed on a reef other than where it was tagged. Of the 31 grouper which were displaced to reefs 140 m away from where they were captured, 29 homed to their original reef within 10 days (Table 4).

Juvenile Growth.—Large numbers of juvenile *E. striatus* were observed during the first census following placement of the final set of 40 artificial reefs (Table 3). Small juveniles (3–8 cm TL) were first observed in small burrows beneath the bases of the reefs. As juveniles grew, they moved to the holes in the reefs.

The growth rate of juveniles within this cohort appeared to be constant over the 11-month period of observation (Fig. 7). Mean growth rates of juveniles within the size range observed (3.0–27.0 cm TL) ranged from 0.8 to 1.2 cm·month^{-1} (Table 3). The overall mean growth of the juvenile cohort from the first month of observation (mean size = 8.7 cm TL) to month 11 (mean size = 19.5 cm TL) was 10.8 cm. Estimated annual growth for the cohort was 12.05 cm.

Discussion

Grouper Distributions on Artificial vs. Natural Reefs.—Nassau grouper numerically dominated other groupers on artificial reefs during our study. Larger individuals (20–40 cm TL) were most abundant on large-hole reefs, where individual

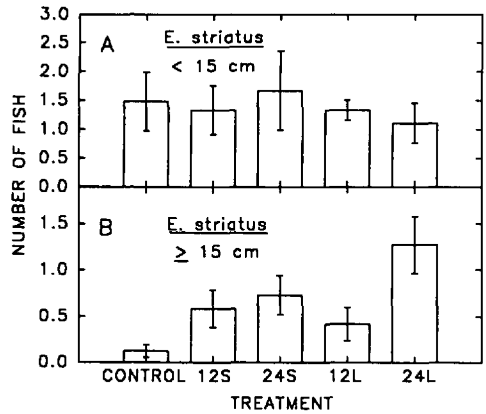
Table 2. Repeated-measures analysis of variance of the abundance (number of fish per reef) of two size classes of *Epinephelus striatus* and *E. afer* among 5 artificial reef treatments (Set III; N = 8 reefs each) during the last year of observations (6 censuses). Data were ln(x + 1) transformed for analysis. Bonferroni multiple comparisons: underlined means are not significantly different ($P > 0.05$).

		Small *E. striatus* (<15 cm)			
Source	SS	df	MS	*F*	*P*
Treatment	3.825	4	0.956	1.491	0.232
Error	17.961	28	0.641		
	Multiple comparisons (treatment/mean number of fish)				
12 large	24 large	12 small		0 holes	24 small
0.562	1.104	1.333		1.479	1.667
		Large *E. striatus* (≥15 cm)			
Source	SS	df	MS	*F*	*P*
Treatment	8.211	4	2.053	5.265	0.003
Error	10.918	28	0.390		
	Multiple comparisons (treatment/mean number of fish)				
0 holes	12 large	12 small		24 small	24 large
0.125	0.417	0.583		0.729	1.271
		Small *E. afer* (<15 cm)			
Source	SS	df	MS	*F*	*P*
Treatment	2.690	4	0.673	1.345	0.278
Error	14.005	28	0.500		
	Multiple comparisons (treatment/mean number of fish)				
24 small	24 large	12 small		12 large	0 holes
0.042	0.229	0.333		0.583	0.625
		Large *E. afer* (≥15 cm)			
Source	SS	df	MS	*F*	*P*
Treatment	33.569	4	8.392	3.196	0.028
Error	73.528	28	2.626		
	Multiple comparisons (treatment/mean number of fish)				
24 small	12 small	0 holes		24 large	12 large
0	0.063	0.083		3.333	4.438

fish tended to occupy individual holes. Tagging studies indicated that there was site fidelity and strong homing.

For unknown reasons, *Epinephelus striatus* appeared to prefer artificial reefs over natural reefs during our study. Mean abundance of *E. striatus* was much greater on artificial reefs than on natural patch reefs of similar size. We speculate that this pattern was due to preference because Nassau grouper were typically larger than and appeared to be aggressively dominant over other grouper species.

Relative abundances of grouper species on our artificial reefs were not similar to those on natural reefs in the study area or elsewhere in the U.S. Virgin Islands, nor to those in Virgin Islands commercial fisheries landings (Fig. 8). *E. cruentatus* and *E. fulvus* dominated the 10 natural patch reefs in our study area, and these two species plus *E. guttatus* dominated grouper abundances in visual census samples taken on natural reefs elsewhere in the U.S. Virgin Islands (Beets, 1993). *E. fulvus* and *E. guttatus* have dominated grouper abundances in commercial fisheries landings during recent years (U.S.V.I. Division of Fish and Wildlife, unpubl. fisheries files). *E. afer* tend to occupy seagrass areas exclusively, as was observed at the two shallowest rows of artificial reefs (6.0 and 7.5 m deep) where seagrass density was greatest. The small adult body sizes of *E. afer* and *E. cruentatus*



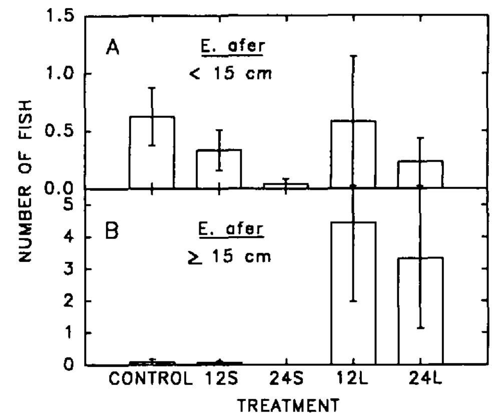


Figure 5 (left). Abundances of two size classes of *Epinephelus striatus* among five artificial-reef treatments in Set III. A: small fish (<15 cm TL); B: large fish (≥15 cm TL). Reef treatments are: CONTROL: no hole reefs; 12S: 12 small holes; 24S: 24 small holes; 12L: 12 large holes; 24L: 24 large holes. Data presented are the grand mean number of fish per reef (each reef averaged over all 6 censuses) with standard error (N = 8 reefs per treatment).

Figure 6 (right). Abundances of two size classes of *Epinephelus afer* among five artificial-reef treatments in Set III. A: small fish (<15 cm TL); B: large fish (≥15 cm TL). Reef treatments and data presented as in Figure 5.

usually allow escapement through the legal mesh size used in fish traps (38 mm), which is the primary gear type in the U.S. Virgin Islands.

A strong recruitment pulse of *E. striatus* in 1988 allowed this species to dominate the abundance of grouper on artificial reefs during the final year of our study. Such sporadic events may have a large influence on fish assemblage structure (Doherty and Williams, 1988; Doherty, 1991; Williams, 1991), although Shpigel and Fishelson (1991) noted few changes in fish communities following the removal of *Cephalopholis* groupers from Red Sea reefs.

The differential persistence of large groupers on artificial reefs of specific shelter characteristics relative to the uniform distribution of small individuals among reef treatments indicates the importance of habitat structure in determining local fish abundances (Roberts and Ormond, 1987; Hixon and Beets, 1989, 1993). Additionally, *E. striatus* and *E. afer* appear to have partitioned the artificial reefs in our study by depth, similar to habitat partitioning by *Cephalopholis* congeners in

Table 3. Growth of juvenile Nassau grouper observed on 52 artificial reefs from July 1988 to June 1989

	Census date										
	7/23/88		10/4/88		11/15/88		1/27/89		3/15/89		6/12/89
Number of fish	99		158		129		99		87		23
Mean size (cm TL)	8.7		11.4		12.9		15.2		17.0		19.5
Mean size difference between censuses (cm)		2.7		1.5		2.3		1.8		2.5	
Number of days between censuses		73		45		73		47		89	
Growth (cm·month $^{-1}$)		1.1		1.0		0.9		1.2		0.8	

Mean growth of cohort from 7/88 to 6/89 = 10.80 cm
Estimated annual growth of cohort = 12.05 cm

Table 4. Persistence and homing of tagged groupers on artificial reefs in 1989 (fish were tagged and returned to original reefs or translocated to reefs 140 m away)

Species	Released on original reef		
	Tagged (No.)	Persisting on original reef (No.)	Observed on adjacent reef (No.)
E. afer	14	14	0
E. guttatus	1	1	0
E. striatus	2	0	1
Total	17	15	1
	Translocated		
	Tagged (No.)	Homing to original reef (No.)	Observed on adjacent reef (No.)
E. afer	27	27	0
E. striatus	4	2	0
Total	31	29	0

the Red Sea (Shpigel and Fishelson, 1989). Whether this pattern was due to competitive interactions awaits experimental tests (Hixon, 1980; Larson, 1980).

Overall, the local distribution and abundance of groupers in our system appear to be influenced by multiple ecological processes, including recruitment, competition, and habitat structure (Hixon, 1991; Jones, 1991; Sale, 1991).

Growth of Nassau Grouper.—The smallest juveniles of Nassau grouper we observed (3–8 cm TL) were closely associated with the substrate, usually in small burrows under reefs. Other observers have described similar behavior of recently settled groupers (Colin et al., unpubl. ms.). Occasionally, we observed several juveniles on a single reef, but they were normally segregated in separate burrows. We observed predation by small juveniles on smaller juvenile grunts, which were frequently abundant (Hixon and Beets, 1993).

Very few studies have documented the early natural growth of groupers. Most growth estimates for groupers have been calculated from large individuals and yield poor approximations of juvenile growth. Surprisingly little growth information exists for *E. striatus* in particular (Manooch, 1987). The juvenile growth rates of *E. striatus* obtained in the present study are comparable to those documented for other grouper species (Table 5). The size range of juveniles in this

Table 5. Summary of data on early growth of Caribbean groupers

Species (Source)	Size range (cm)	Growth rate ($cm \cdot month^{-1}$)
Epinephelus cruentatus (Nagelkerken, 1979)	8.1–14.1	0.6
E. guttatus (Sadovy et al., 1992)	4.0–11.5	1.1
E. fulvus (Colin et al., unpubl. ms.)	5.0–13.5	0.8
E. striatus (Colin et al., unpubl. ms.)	3.0–14.5	0.8
E. striatus (present study)	8.7–19.5	1.0
Mycteroperca microlepis (McErlean, 1963)	8.1–14.1	2.0

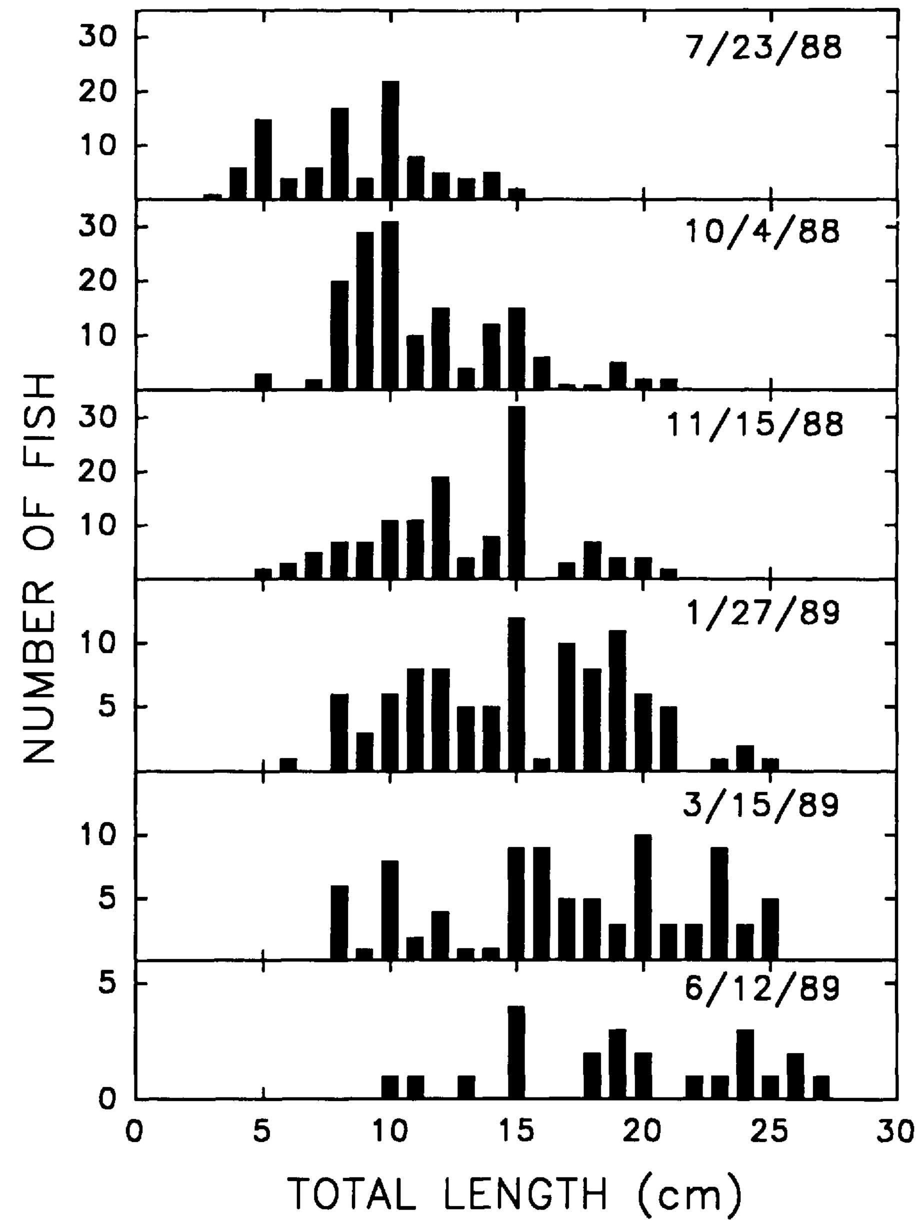


Figure 7. Length frequency data of juvenile *Epinephelus striatus* observed on 52 artificial reefs during six censuses from July 1988 to June 1989.

study was intermediate to that presented for small juveniles by Colin et al. (unpubl. ms) and Bush and Ebanks-Petrie (in press), and therefore, fills a gap in our knowledge of this species (Table 6).

Based on ageing data provided in previous investigations (Colin et al., unpubl. ms; Bush and Ebanks-Petrie, in press), the juvenile fish observed in our study were in age class 0+ to 1+. Colin et al. (unpubl. ms) determined from otolith

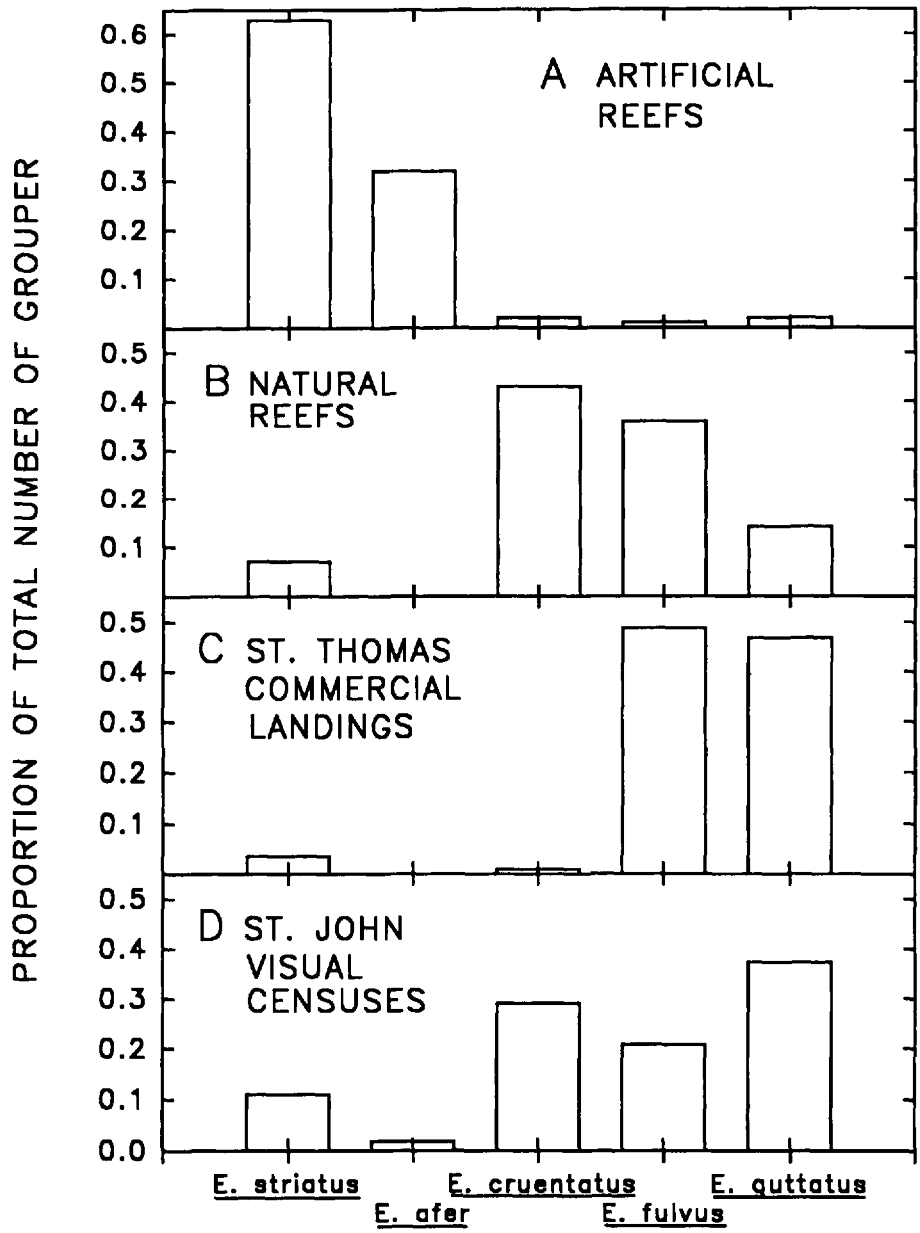


Figure 8. Comparison of overall relative abundances of five grouper species in four independent data sets from the U.S. Virgin Islands: A: 52 artificial reefs during present study (all censuses pooled); B: 10 natural patch reefs during present study (all censuses pooled); C: commercial landings data for St. Thomas and St. John (port samples of trap catches collected by U.S.V.I. Division of Fish and Wildlife, 1989–1991); D: visual point-census data from natural reefs around St. John (over 1,000 samples gathered from 1989 to 1991 [Beets, 1993]).

analysis that *E. striatus* larvae remain 35–50 days in the plankton and settle at 2.4–2.6 cm SL. These data suggest that the 3–8 cm TL juveniles first observed on artificial reefs in July 1988 were spawned 2–9 months earlier and had settled 1–8 months earlier. This estimate roughly corresponds to the known spawning

Table 6. Summary of data on size-specific growth rates of Nassau grouper (*Epinephelus striatus*)

Age*	Mean size	Growth rate
Colin et al. (unpubl. ms.)		9.6 $\text{cm}\cdot\text{year}^{-1}$
60 days	3.0 cm SL	0.7 $\text{cm}\cdot\text{month}^{-1}$
90 days	3.7 cm SL	0.7 $\text{cm}\cdot\text{month}^{-1}$
120 days	4.4 cm SL	1.0 $\text{cm}\cdot\text{month}^{-1}$
150 days	5.4 cm SL	
Present study		12.05 cm·year
—	8.7 cm TL	1.1 $\text{cm}\cdot\text{month}^{-1}$
—	11.4 cm TL	1.0 $\text{cm}\cdot\text{month}^{-1}$
—	12.9 cm TL	0.9 $\text{cm}\cdot\text{month}^{-1}$
—	15.2 cm TL	1.2 $\text{cm}\cdot\text{month}^{-1}$
—	17.0 cm TL	0.8 $\text{cm}\cdot\text{month}^{-1}$
—	19.5 cm TL	
Bush and Ebanks-Petrie (in press)		
3 yr	43.0 cm TL	3.5 $\text{cm}\cdot\text{year}^{-1}$
4 yr	46.5 cm TL	7.5 $\text{cm}\cdot\text{year}^{-1}$
5 yr	54.0 cm TL	6.5 $\text{cm}\cdot\text{year}^{-1}$
6 yr	60.5 cm TL	

* Age determined from otolith analysis.

period in December–February (Smith, 1972; Burnett-Herkes, 1975; Olsen and LaPlace, 1979; Colin et al., 1987; Colin, 1992, unpubl. ms).

In conclusion, we believe that artificial reefs may be a valuable means of enhancing grouper stocks at least in the U.S. Virgin Islands. There appears to be differential settlement/colonization by different species between artificial and natural reefs. Artificial reefs of the correct design may enhance the local abundance of selected grouper species, in this case Nassau grouper. However, because groupers are easily overexploited, wise management decisions, such as protection of spawning aggregations (Bohnsack, 1989) and establishment of marine reserves (Plan Development Team, 1990), will also be necessary to insure long-term stock enhancement of these long-lived, slow-growing species.

Acknowledgments

We thank P. Taylor for early collaboration and B. Bauscher, D. Booth, R. Davis, A. Friedlander, U. Hixon, J. Lucas, L. Muehlstein, J. Munro, L. Patterson, R. Peck, S. Prosterman, D. Prulhiere, M. Sabino, and T. Turner for field assistance. The University of the Virgin Islands (courtesy of W. MacLean, L. Ragster, and L. Heikkila) provided generous logistic support. Y. Sadovy provided valuable comments. We thank A. Wilkes and two anonymous referees for thorough reviews. Funded by the University of Puerto Rico Sea Grant Program through grants PD-33 R/LR-06, PD-42 R/ER-40, and R/ER-40-12, and by a grant from the Oceanic Research Foundation.

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DATE ACCEPTED: May 10, 1993.

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