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CORAL REEF PAPER

DENSITY, SPECIES AND SIZE DISTRIBUTION OF GROUPERS (SERRANIDAE) IN THREE HABITATS AT ELBOW REEF, FLORIDA KEYS

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ABSTRACT

We examined the density, size and species distribution of groupers in three habitats on an inshore-to-offshore transect across Elbow Reef, Florida Keys: high-relief spur-and-groove (4–9 m depth), relict spur-and-groove (10–20 m), and deep fore reef slope (21–30 m). Physical relief was greatest in the high-relief spur-and-groove (up to 3 m), lowest in the relict spur-and-groove habitat (<0.5–1 m), and intermediate in the deep fore reef slope habitat (1–1.5 m). Benthic coverage in the three habitats was dominated by algae (>30%). There were significant differences in the density, size, and species distribution of groupers among the three habitats. Graysby, *Epinephelus cruentatus,* was numerically dominant, constituting 82–91% of individuals observed. Black grouper, *Mycteroperca bonaci,* and Nassau grouper, *E. striatus,* were more abundant in high to moderate relief habitats, whereas red hind, *E. guttatus,* was more abundant in the low-relief habitat. The size distribution was shifted towards smaller sizes in lowest relief habitat and towards larger sizes in areas with greater (>0.5 m) vertical relief. We suggest that fishing pressure in the Florida Keys has resulted in an offshore grouper assemblage dominated by graysby, a small grouper species (<40 cm total length) which is not targeted by fishermen, and that habitat selection and biological interactions have significantly influenced the ecological structure of the grouper assemblage of this coral reef.

Fishing selectively removes larger individuals from a population and can dramatically affect the abundance, size/age structure, and reproduction of fishes (PDT, 1990). Over time, this results in a shifting baseline expectation of what the population should be in a "natural" state; new generations of people accept the status of fish stocks when they begin fishing as the baseline status of the resource (Pauly, 1995). A shift in expectations occurs over many years and a loss of understanding of the population characteristics of the true natural status of the stocks. Currently, there is no accepted definition of a natural grouper assemblage.

Many studies have related the distribution of fishes to physical or biological features of coral reefs (reviewed in Jones, 1991). Among groupers (Family Serranidae) many species exhibit different distributions by habitat type. For example, there were significant differences in the abundance and size of groupers among different types of habitats in Madagascar (Vivien, 1973, in Williams, 1991), Republic of Maldives (Sluka and Reichenbach, in press), the Red Sea (Shpigel and Fishelson, 1989), the Bahamas (Alevizon et al., 1985), and the Florida Keys (Sluka and Sullivan, 1996). Since groupers are an important fishery resource throughout the world, the distribution of these fishes among habitats is of particular interest. This study presents data collected at one bank reef area encompassing three habitat types on an inshore-to-offshore transect in the upper Florida Keys. The objectives of the study were to (1) describe the physical relief and benthic coverage of habitats and (2) compare the density, species composition, and size distribution of groupers among the three habitat types.

MATERIALS AND METHODS

STUDY AREA. The study area was located at Elbow Reef, a bank reef in the upper Florida Keys. Grouper fishing in the Florida Keys has been intense and management regulations have been implemented with increasing severity. Spear-fishing has been prohibited at Elbow Reef (and all of Key Largo National Marine Sanctuary) since 1960. Fish trapping was prohibited in Florida waters in 1980, in federal waters to a depth of 30.5 m (100 ft) in 1983, and in all Atlantic federal waters in 1992. Currently only hook-and-line fishing is allowed at Elbow Reef and in the immediately surrounding areas. A size limit of 51 cm (20 in) and a bag limit has been imposed for many grouper species. Harvest of jewfish (*Epinephelus itajara*) and Nassau grouper (*E. striatus*) was prohibited in 1990 and 1991, respectively.

Elbow Reef can be divided into three habitat types based on depth, relief, and benthic composition: (1) high-relief spur-and-groove, (2) relict spur-and-groove, and (3) deep fore reef slope. The first two habitat types were sampled in April and September 1993, and January, April, September, and December 1994, but the third type was sampled only in December 1994. High-relief spur-and-groove reefs are constructional in origin and were built primarily by *Acropora palmata* during the early Holocene (approximately 6000 y.b.p.) (Shinn, 1963, 1980). The high-relief spurs at Elbow Reef are oriented roughly northwest to southeast, 2–3 m wide, and separated by sand grooves 2–3 m wide. The sand grooves are 7–9 m in depth, while the shallowest portions of the spurs are 4–5 m in depth. The spurs are currently not dominated by *A. palmata*, but rather by coralline algae, *Millepora complanata, Montastrea annularis, Palythoa caribaeorum*, and *Gorgonia ventalina* (Jaap, 1984; Jaap et al., 1988). Seaward of the high-relief spur-and-groove habitat is the relict spur-and-groove habitat, which extends from 10–20 m depth on the fore reef slope of the Florida Keys. The relict spur-and-groove habitat consists of more closely spaced (<1.5 m), low-amplitude (<1 m vertical relief) spurs and has been called "deeper (>10 m) live-bottom habitat" (Bohnsack et al., 1987), "slope platform" (Jaap, 1984), and "deep spur-and-groove zone" (Wheaton and Jaap, 1988). The break in slope marks the beginning of a relatively steep drop-off, where depth increases from 20 to 30 m over a relatively short distance (50–65 m). Along this deep fore reef slope, relict spurs and grooves are evident and are similar in orientation to the relict spur-and-groove habitat, but have slightly greater relief. Below 30 m, the deep fore reef slope gives way to a sand plain.

Habitat surveys. Transects and random quadrat surveys were used to quantify physical relief and bottom coverage. In each habitat, depth, relief, and substratum coverage were measured along two transects 25-m in length oriented inshore to offshore and placed along the tops of spurs. Depth was measured every meter along transects, while maximum vertical relief was determined by the depth difference between tops of spurs and depth of sand grooves. In each 1-m section of transect, a chain with a link-size of 1 cm was orientated along the contour of the spur and compared to a linear distance to give an index of substrate complexity (Luckhurst and Luckhurst, 1978).

Bottom coverage of sediment, algae, sponges, and corals was determined using the Braun-Blanquet method (Van den Hoek et al., 1975), which uses quadrats to visually estimate percent coverage. In each habitat, 1-m² quadrats along the two 25-m transects were visually scored using the coverage classes: absent (0%), less than 1, 1–5, 5–25, 25–50, 50–75, and greater than 75%.

Grouper surveys. Grouper occurrence and length were determined by SCUBA divers. A 20-m transect line, placed parallel to the depth gradient in each habitat, was searched in high-relief and relict spur-and-groove habitats to a width of 6 m on each side of the transect line. The transect width was reduced to 2.5 m in the deep fore reef slope due to constraints of limited bottom time at depth (30 m). The entire transect area was searched, including crevices, holes, and underhangs (GBRMPA, 1979).

Prior to diving, observers were trained on land to estimate the total length (TL) of fish within a particular size category (Bell et al., 1985). While this process did not account for refraction experienced underwater, it allowed the observer to determine whether they consistently under- or over-estimated size. Observers, using a ruler underwater to assist in estimating length, recorded fish in five size categories: <5, 6–15, 16–25, 26–35, and >35 cm TL.

Statistical analyses. Grouper density data were non-normal as determined by the Kolmogorov-Smirnov test (Zar, 1984). Kruskal-Wallis ANOVA was used to test for differences in density among the three habitat types. Non-parametric multiple comparison tests for unequal sample size and tied ranks were used to determine which habitat types had significantly different densities (Zar, 1984). Chi-square tests were used to test for differences in the size and species distributions among habitats. Some species were combined into an "other" category for analysis because of low expected frequencies in the X^2 test (Everitt, 1992). All null hypotheses were tested at a significance level of $\alpha = 0.05$.

Results

Habitat characteristics. Physical relief was greatest in the high-relief spur-and-groove habitat (up to 3-m vertical relief), with a mean depth change of 28 cm m^{-1} and a measured substrate complexity of 151 cm m^{-1}. In contrast, the relict spur-and-groove habitat had very low relief (<1 m), with a mean depth

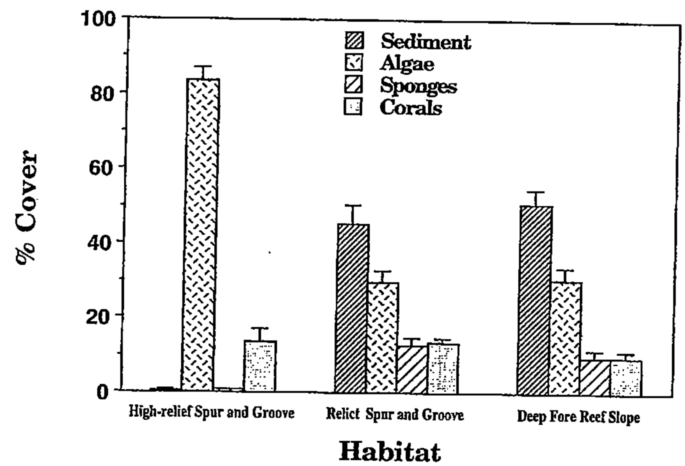

Figure 1. Mean (± 1 SE) percent cover of bottom components in the high-relief spur-and-groove (4–9 m depth), relict spur-and-groove (10–21 m), and deep fore reef slope (>22 m) habitats at Elbow Reef, Florida Keys.

change of 11 cm m-1 and a substrate complexity of 113 cm m^{-1}. Physical relief in the deep fore reef slope habitat was intermediate with maximum vertical relief 1.5 m and mean depth change of 13 cm m^{-1}. Substrate complexity was not measured on the deep fore reef slope.

Sediment coverage was low in the high-relief spur-and-groove habitat (<1%), moderate in the relict spur-and-groove habitat (45%), and greatest in the deep fore reef slope (51%) (Fig. 1). Algae were the dominant lifeform type in all three habitats (>30%). Algal cover was greatest in the high-relief spur-and-groove habitat (80%), but considerably lower (<35%) in the relict spur-and-groove and deep fore reef slope habitats. In the high-relief spur-and-groove habitat, most of the algal cover consisted of coralline algae, *Halimeda* spp., and *Dictyota* spp., while algal composition in the deeper reef habitats was primarily *Dictyota* spp. and *Lobophora variegata.* In contrast to algae, sponges and corals had lower coverage (<15%). Sponge cover was greatest in the relict spur-and-groove and deep fore reef slope habitat, while coral cover was similar (9–13%) among the three habitats. Coral composition in the high-relief habitat consisted of *M. complanata, A. palmata,* and *Agaricia agaricites.* In contrast, coral composition in relict spur-and-groove and deep fore reef slope were similar and dominated by *M. annularis* and *Siderastrea siderea.*

GROUPER ASSEMBLAGES. The density of several grouper species was significantly different among the three habitat types (Table 1). All species were rare, except for graysby *Epinephelus cruentatus,* ranging from 1 yellowfin grouper *Mycteroperca venenosa* to 12 Nassau grouper *E. striatus* and 12 black grouper *M. bonaci* observed in the 164 surveys. Graysby was the dominant species, comprising 88% of the total individuals (n = 350) observed at Elbow Reef (range of 82–91% by habitat type). Black and Nassau grouper were more abundant in the high- and moderate-relief habitats (Fig. 2). Red hinds were only observed in the low-relief habitat. The species distributions were significantly different from each other ($\chi^2 = 36.69$, df = 8, $P < 0.001$).

The size distributions of groupers among the three habitat types were significantly different ($\chi^2 = 48.54$, df = 6, $P < 0.001$), with more larger individuals (>35 cm) in high- to moderate-relief habitats than the low-relief habitat. Seven-

Table 1. Mean (1 SE) grouper density (no. 100 m^{-2}) in three habitat types at Elbow Reef, Florida Keys. The number of individuals observed of each species is given by n. Sites where no grouper of a particular species were observed are indicated by —. Significance indicates the results of Kruskal-Wallis ANOVA testing for differences in mean grouper density among habitats. Non-parametric multiple comparison tests were used to determine which habitats were significantly different by species. H = high-relief spur-and-groove, R = relict spur-and-groove, and D = deep fore reef slope. Sample size indicates the number of transects surveyed in each habitat type.

		Habitat type				
	n	High-relief spur	Relict spur	Deep fore reef slope	Significance	Multiple comparisons
Sample size		56	58	50		
Epinephelus adscensionis	3	—	—	0.06 (0.04)	$P > 0.05$	—
E. cruentatus	308	0.28 (0.05)	1.10 (0.12)	1.36 (0.15)	$P < 0.001$	H < R = D
E. fulvus	4	—	0.03 (0.02)	—	$P > 0.05$	—
E. guttatus	10	—	0.05 (0.02)	—	$P < 0.001$	H = D < R
E. striatus	12	0.04 (0.02)	0.01 (0.01)	0.04 (0.03)	$P > 0.05$	—
Mycteroperca bonaci	12	0.03 (0.01)	—	0.12 (0.05)	$P < 0.05$	H = R, D = H, R < D
M. venenosa	1	0.01 (0.01)	—	—	$P > 0.05$	—
All species combined	350	0.35 (0.05)	1.20 (0.12)	1.58 (0.16)	$P < 0.001$	H < R = D

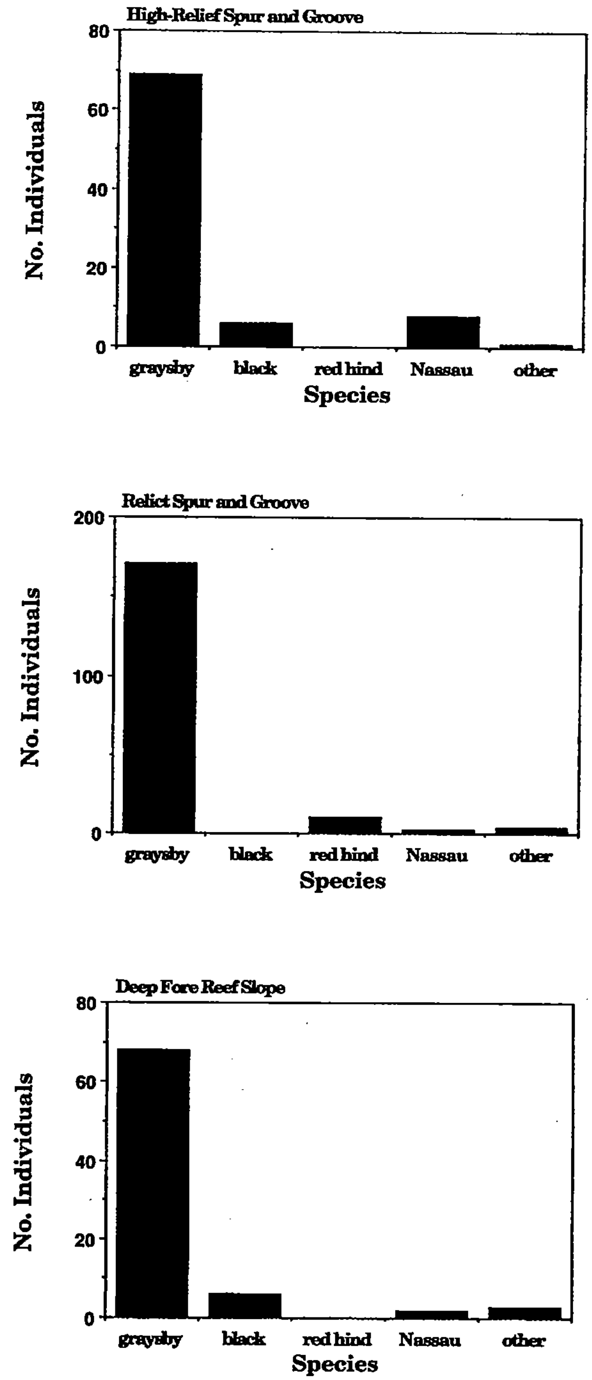

Figure 2. Grouper species distribution in high-relief spur-and-groove, n = 84 (top), relict spur-and-groove, n = 187 (middle), and deep fore reef slope, n = 79 (bottom) habitats at Elbow Reef, Florida Keys. Species combined into other category were rock hind, coney, and yellowfin grouper.

teen percent of all individuals observed in the high-relief spur-and-groove habitat were greater than 35 cm, at the relict spur-and-groove 1%, and at the deep fore reef slope 13% (Fig. 3). The lowest relief habitat was dominated by smaller individuals (57% less than 15 cm).

Discussion

It appears that fishing pressure is affecting the overall abundance of grouper species in the upper Florida Keys, while habitat and possibly biological interactions are affecting small-scale distribution patterns among habitat types. Graysby are the most abundant species of grouper on offshore coral reefs of the Florida Keys, while inshore patch reefs were dominated by red (*Epinephelus morio*) and black (*M. bonaci*) grouper (Sluka, 1995). It has been shown that areas which are heavily fished result in grouper assemblages dominated by species which do not attain large sizes (Bohnsack, 1982; Watson and Ormond, 1994). The graysby is a small species which does not usually attain sizes over 40 cm TL (Nagelkerken, 1979), while species such as red and black grouper attain maximum sizes of 94 and 135 cm TL, respectively (Manooch and Mason, 1987; Stiles and Burton, 1994). Among offshore coral reef habitats, the distribution of graysby differed by the type of habitat; smaller graysby were more abundant in the lower relief habitats, whereas larger graysby were more abundant in the higher relief habitats. This is consistent with the findings of Sluka (1995) who showed that for a particular coral reef, larger graysby were observed more often to use microhabitats of higher relief than smaller graysbys. The other species of grouper were much rarer at the study site and in general in the Florida Keys. The small number of individuals observed prohibits definitive statements about habitat use at this site by these rarer species, but it appears that larger grouper species such as Nassau grouper (*Epinephelus striatus*), black grouper, and yellowfin grouper (*M. venenosa*) are found more often in higher relief habitats; the abundances of these species are likely most affected by fishing pressure.

Coral reef fishes in general, and groupers specifically, are highly susceptible to fishing pressure (Russ, 1991). Population parameters such as density and size distribution are particularly sensitive to fishing pressure (Russ and Alcala, 1989). Evidence suggests that grouper abundance throughout the Caribbean has declined dramatically due to intense fishing (Claro et al., 1990; Beets and Friedlander, 1992; Sadovy and Figuerola, 1992; Sadovy, 1994). In the Florida Keys, the harvest of groupers has declined dramatically over the past 10 yrs (Bohnsack et al., 1994). The harvest of two species of grouper, the jewfish (*Epinephelus itajara*) and Nassau grouper, has been prohibited in the U.S. South Atlantic. The decrease in abundance of larger species of grouper can influence the structure of coral reef fish assemblages (Goeden, 1982). The low numbers of targeted grouper species at Elbow Reef is indicative of the intense fishing pressure in the Florida Keys. Densities of these target species (Nassau grouper, black grouper, and yellowfin grouper) ranged from 0.01–0.12 100 m^{-2} at Elbow Reef. In the rest of the Florida Keys, densities were similar, ranging from 0.01–0.13 100 m^{-2} (Sluka, 1995; unpubl. data). However, in an area of the Dominican Republic which was intensively fished historically (Parque Nacional del Este), these species were not observed in transects surveyed similarly to this study (Pugibet et al., in press). In the less intensively fished Exuma Cays, Bahamas, densities of these species were much higher, ranging from 0.10–0.90 100 m^{-2}. Thompson and Munro (1978) and Bohnsack (1982) have shown that heavily fished areas have grouper assemblages dominated by smaller species, a second-order effect. A second-order effect may be

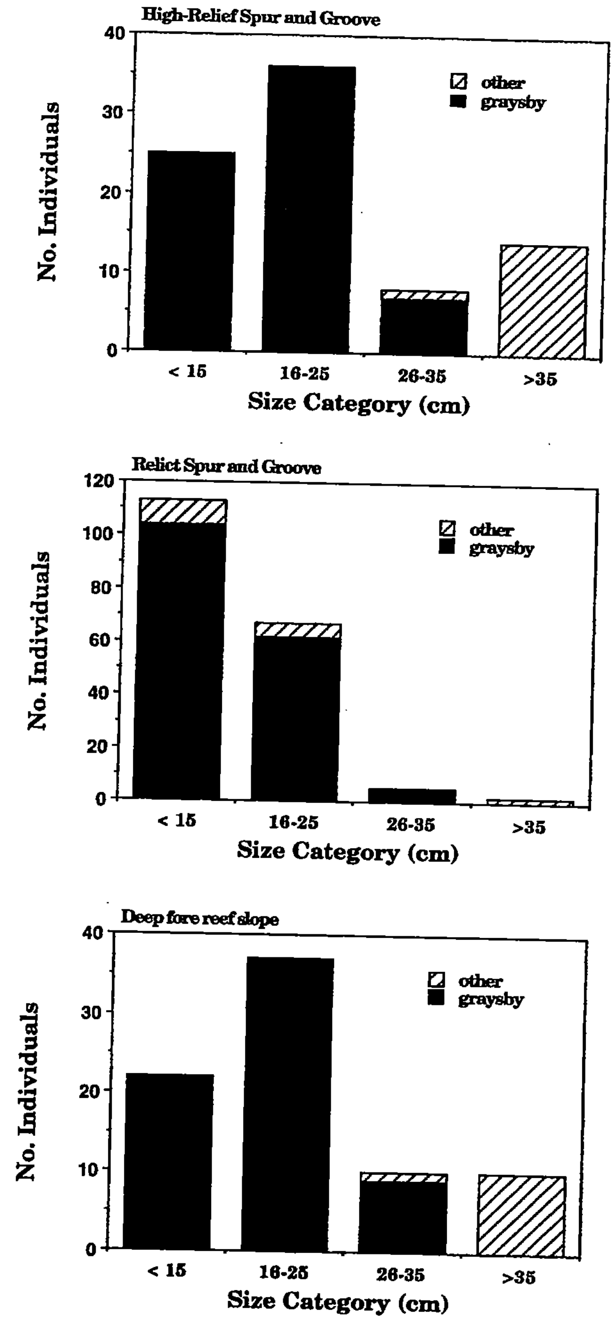

Figure 3. Size distributions of all grouper species combined for high-relief spur-and-groove, n = 84 (top), relict spur-and-groove, n = 187 (middle), and deep fore reef slope, n = 79 (bottom) habitats at Elbow Reef, Florida Keys. Species combined into the other category were rockhind, coney, red hind, Nassau grouper, black grouper, and yellowfin grouper.

defined as an indirect influence of fishing on species at lower trophic levels than species targeted by fishermen. The removal of larger individuals of other species at Elbow Reef may have allowed graysby to increase in density because of reduced competition and/or predation.

Graysby preferentially occupy portions of a habitat type with specific features such as high vertical relief (Nagelkerken, 1979; Sluka, 1995). However, the density of graysby in the highest relief habitat at Elbow Reef was significantly lower than the other habitats. Graysby preferentially occupied areas of high relief in Curação and density was significantly correlated to the percent coverage by *M. annularis* and *Agaricia* spp. (Nagelkerken, 1979). These corals exhibit growth forms that provide much shelter. Graysby may have a preference for these two types of corals, which could explain the lower density in the high-relief habitat at Elbow Reef; the shallower high-relief habitat was historically formed by *A. palmata* and there was very little coverage by *M. annularis* or *Agaricia* (< 1% cover). The graysby's association with *M. annularis* and *Agaricia* is more likely related to structure, so that another explanation besides species-specific preferences for certain corals must be given to account for the observation that more graysby were found in low-relief habitat than high-relief habitat.

Sluka and Sullivan (1996) suggested that the aforementioned finding was due to one or some combination of the following three processes: (1) sampling bias, (2) biological interaction, presumably with larger groupers, and/or (3) differences in habitat use. Small graysby (5–15 cm) were most abundant in the low-relief habitats. Visual surveys could be biased in their lack of ability to detect smaller, cryptic fish. An increase in structure or crevices may limit observations of smaller groupers. We believe that sampling bias is not the case due to results from Sluka (1995) who showed that within a given habitat type, larger graysby were found in higher relief micro-habitats than smaller graysby. Thus, among site differences in habitat use concur with within-site observations. Studies on the bias involved in sampling groupers visually are mixed; Nagelkerken (1979) showed a bias of visual censuses towards underrepresenting smaller individuals in high relief habitats, while Kulbicki (1990) showed no significant differences in estimates of grouper abundance between rotenone stations and visual sampling. Larger species of groupers behaviorally dominate smaller species (Shpigel and Fishelson, 1989). In order to reduce competition for resources, the smaller individuals may utilize lower-relief habitats and then ontogenetically shift habitat use with size. Ontogenetic shifts in habitat with age/size have been postulated for grouper for many years, however, clear evidence to support this theory has only recently emerged (Ross and Moser, 1995). In most cases, it is assumed that grouper settle inshore and then move offshore with age/size. However, graysby likely settle in these deep, low-relief habitats and may move both shallower and deeper among offshore coral reef habitat types as they increase in age/size (Sluka and Sullivan, 1996).

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