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Spatial dynamics of the Nassau grouper *Epinephelus striatus* in a Caribbean atoll

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ABSTRACT: Worldwide, chronic overfishing has depleted populations of large predatory reef fishes and caused unexpected, top-down changes in coral reef ecosystems. Groupers are especially susceptible to overexploitation, because they aggregate to reproduce at specific locations and times. An understanding of the spatial dynamics of these fishes is critical for fisheries management and conservation. However, movements and migration dynamics of endangered reef fishes are poorly known. We show, using acoustic telemetry, that Nassau groupers *Epinephelus striatus* exhibit highly synchronised migration to spawning sites, despite their otherwise solitary habits. Reproductive adults leave their individual territories in shallow waters near the winter full moons, and migrate to the same spawning site up to 4 times yr^{-1}. At the spawning site, a remarkable population-wide depth change occurs within an hour as individuals dive to a maximum depth of 255 m. Our results greatly expand the previously known migration frequency and depth range of this species, and reveal an unexpected yet predictable complexity of adult fish migration between habitats. Effective conservation of this threatened species requires that deeper reefs and the timing of migration events be incorporated into fisheries management plans.

KEY WORDS: Nassau grouper · Site fidelity · Swimming speed · Migration · Acoustic telemetry · Grouper conservation

INTRODUCTION

The Nassau grouper *Epinephelus striatus* is an endangered predator that inhabits coral reefs and spawns in shallow waters of the western Atlantic Ocean and Caribbean Sea (Heemstra & Randall 1993, Domeier & Colin 1997). The species is extremely susceptible to overexploitation, because individuals aggregate to spawn at specific times and locations (Colin 1992, Sadovy & Eklund 1999, Sala et al. 2001). In the past, each spawning site harbored 30 000 to 100 000 groupers, but abundances and the numbers of spawning aggregations have greatly declined, due to overfishing, and spawning aggregations have decreased in size and/or disappeared in many countries (Carter et al. 1994, Claro & Lindeman 2003, Sadovy & Domeier 2005). As a consequence of overexploitation, the Nassau grouper is now listed as 'endangered' by the World Conservation Union (IUCN; www.redlist.org).

There were at least 10 Nassau grouper spawning aggregations in Belize prior to 1990 (Heyman 2001, Paz & Grimshaw 2001), each harboring up to 30 000 groupers (Carter et al. 1994, Sala et al. 2001). Presently, only 3 of these aggregations contain 1000 to 5000 individuals (Belize National Grouper Census 2005, Belize Department of Fisheries, Belize City, Belize). In November 2002, the government of Belize enacted a law to close fishing on all historical and current grouper spawning sites, in an effort to stop the

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decline, with the hope that the protected spawning aggregations will repopulate overfished areas.

Little information is available with which to evaluate the potential for repopulating diminished grouper stocks, either by recruitment or migration of adults. The fate of Nassau grouper larvae is currently unknown and there are few published studies on grouper migration. Observations of 2 adults suggest that Nassau groupers have the potential to move up to 250 km from spawning areas on contiguous reefs (Carter et al. 1994, Bolden 2000), but localized spatial dynamics of spawning adults are poorly understood. In addition, long-range movements of a small portion of the population are common for many fishes, yet the importance of infrequent adult migrations is not known.

Our goal was to estimate spawning site fidelity and describe the spawning migration dynamics of the Nassau grouper for one of the last remaining spawning aggregations in Belize. We conducted scuba surveys for a 6 yr period and tagged and tracked Nassau groupers for 3 yr at Glover's Reef, Belize, using acoustic telemetry and tag-recapture techniques to study grouper distributions and movements.

MATERIALS AND METHODS

Study site. Glover's Reef (16° 44′ N, 87° 48′ W) is the southernmost of 3 atolls off the coast of Belize (Fig. 1). The atoll is located about 45 km east of the mainland and 30 km east of the Mesoamerican Barrier Reef. Glover's Reef is an elongated rectangular atoll about 32 km long and 12 km wide (384 km^2). The reef on the eastern side of the atoll is better developed than on the western side. A spur and groove system of coral ridges lies perpendicularly to the fore-reef on the windward north and east sides of the atoll. There are 3 main channels in the atoll: one in the northeastern corner of the atoll, a second in the south, and a third between Northeast Caye and Long Caye. On the seaward side of the reef, the fore-reef slopes gradually to the drop-off. The fore-reef is about 300 m to 1.5 km wide, and the edge of the drop-off occurs at variable depths between 15 and 70 m. The drop-off becomes progressively deeper from the south to the north, falling steeply (almost vertically) to a depth of about 1000 m on the eastern (windward) side and 500 m on the western (leeward) side of the atoll. In some areas there is a series of ledges or terraces occurring at various depths below the drop-off.

The Nassau grouper spawning site is located in a spur and groove system of corals approximately 1 km off the reef crest on the northeastern portion of the atoll (Sala et al. 2001). There are 8 main coral ridges and 9 sand channels within the spawning site at depths between 25 and 35 m. Below the coral ridges, a gently sloping bottom, covered by corals with a few sandy patches, stretches down to the shelf edge at a depth of 45 m. The slope becomes steeper at the shelf edge, and at a depth of 70 m the reef wall becomes completely vertical. Grouper abundance is greatest where most spawning occurs in an area of about 2 ha at the core of the spawning site. The spawning aggregation (Fig. 2), which harbored 15 000 Nassau groupers in 1975, is now reduced to less than 3000 groupers (Sala et al. 2001).

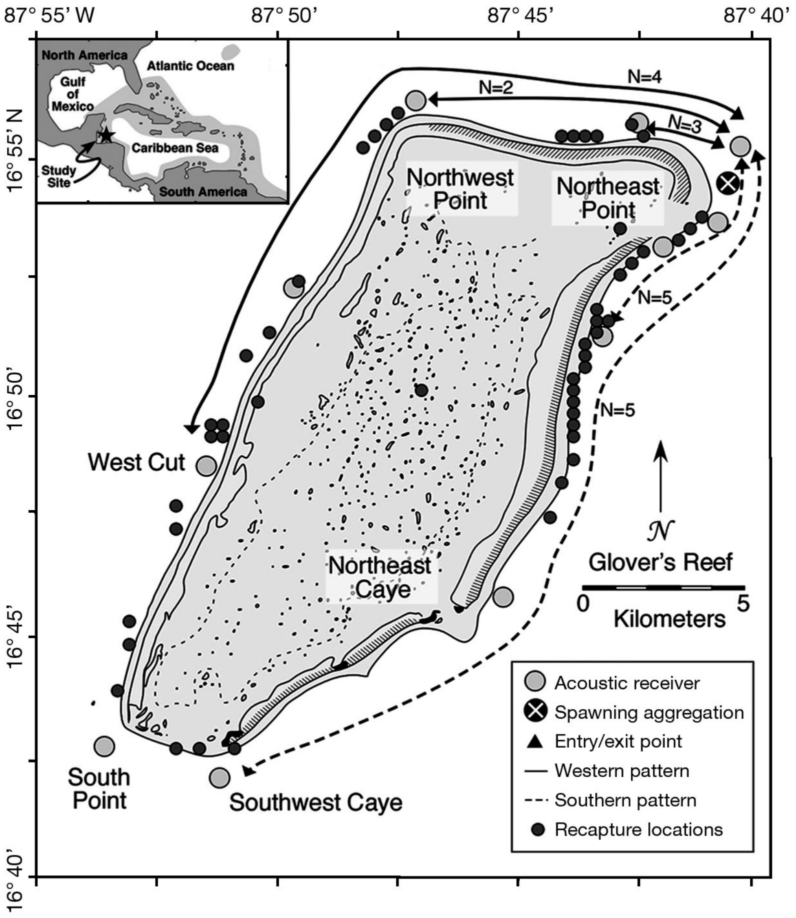

Fig. 1. *Epinephelus striatus.* Map of Glover's Reef atoll, Belize, showing the location of the Nassau grouper spawning site and the array of underwater acoustic receivers used in this study. Locations at which tagged groupers were recaptured by fishermen are also shown. Lines represent patterns of movements of groupers to and from the spawning site. Arrowheads indicate the location at which fish entered and exited the receiver array. N: number of tagged groupers exhibiting a specific movement pattern

Fig. 2. *Epinephelus striatus*. Nassau groupers with pre-spawning markings at the Glover's Reef spawning site. Photo by Enric Ballesteros

Fish tagging. To determine the distribution of Nassau groupers on the atoll and their migratory movements before and after spawning, we used a tag-recapture approach, using a combination of externally placed dart tags (Floy Tags) and surgically implanted acoustic tags (Vemco). External tags allowed us to tag a large number of groupers at the spawning aggregation and to use catches from local fishers to determine distributions on the atoll during the non-reproductive season. Acoustic tags enabled us to track movements of groupers around the atoll and to determine spawning site fidelity.

We inserted dart tags into the fish using modified spear guns (75 cm long and powered by elastic bands) while scuba diving. Each tag consisted of a colored plastic tag (8 cm long, 2 mm diameter) covered by anti-fouling transparent tubing attached to a plastic dart. Darts were typically inserted in the dorsal musculature of fishes using a metal applicator attached to the end of a spear. We screwed the applicator to the end of an 85 cm long spear shaft and inserted a stopper (3 cm diameter) 2 cm below the tip of the applicator to prevent the spear from penetrating the fish more than needed to implant the dart tag. Tagging was successful and we were able to target the muscle below the dorsal fin, because Nassau groupers were curious and allowed us to approach within ≤2 m.

In 2001, 4 divers each completed 10 dives (total dive time of 24.1 h) to tag 284 groupers. In 2002, 4 divers each completed 10 dives (total dive time of 24.4 h) to tag 385 groupers. All groupers were tagged in the morning to prevent disruption of the spawning that occurs in the evening. Of the 669 Nassau groupers we tagged, we accidentally killed 7. Behavior of all other tagged fish did not appear to be unusual after the tagging, and we observed tagged groupers spawning on the day of tagging. Tags contained a message offering a reward (US $10 per tag) with the address and phone number of the Manager of the Wildlife Conservation Society's Glovers' Reef Marine Research Station in Middle Caye. To encourage tag returns, signs were posted at the primary local fishing villages, and leaders of the fishing community were told about the tagging study. When fishers returned the tags, they were asked to relate the time, location, method of capture, and depth at which the fish was caught. All fishers noted that captured fish appeared healthy and the areas around the tag insertion point contained no apparent lesions.

We surgically implanted acoustic transmitters in 15 and 30 Nassau groupers in 2001 and 2002, respectively, to evaluate spawning site fidelity and movements from and to the spawning site. Groupers were captured on the spawning grounds with hook and line with the help of local fishers. We did not identify sex of the 15 groupers tagged in 2001. In 2002, we tagged 15 females and 15 males; sex was determined externally (Sadovy & Eklund 1999), often by the extrusion of eggs or sperm on the tagging platform. Mean length of all fish caught was 72.8 cm. Mean length of females caught was 74.9 ± 2.1 cm (SE) and mean length of males was 71.9 ± 1.8 cm (SE). After capture, fish were placed in a tub containing an anesthetic (10% solution methyl-ethyl-sulfate) for an average of 5 min, until they were unresponsive to touch. We then surgically implanted sonic transmitters into the peritoneal cavity following standard methods used in both tropical and temperate waters (Zeller 1997, 1998a, Starr et al. 2004). After surgery, fish were placed in a tub of seawater to recover from the anesthetic and were released, on average, 20 min after capture. In January 2001, we implanted Vemco V16-5H tags into 15 fish. The V16-5H tags transmitted identification codes at random intervals between 75 and 90 s. Battery life was projected to be 17 mo. In January 2002, we used 2 different types of Vemco transmitters. In 20 groupers, we implanted V16p-4H coded tags that transmitted depth (pressure) information at random intervals between

50 and 148 s; in 10 fish, we inserted V16p-5H depth transmitters with random delays of 240 to 289 s. Battery life for each of these tags was expected to be >26 mo, but was <24 mo. All fish survived the tagging process. We also placed external dart tags on all groupers carrying acoustic tags. The reward for returned acoustic tags was US $15.

Fish tracking. Using scuba, we conducted daily underwater visual censuses at depths of 25 to 40 m each January from 2000 to 2005, when fish aggregated to spawn (Sala et al. 2001). Underwater visibility varied between 35 and 50 m. We counted groupers at the spawning site in 2 ways. First, each morning we counted groupers as we swam along all coral ridges in the spur and groove system, as well as at the shelf edge below the spur and groove habitats. Second, because groupers aggregate in dense schools to spawn in the afternoon (Colin 1992, Sala et al. 2001), we were able to estimate the number of groupers in the 1 to 3 schools we saw each day.

To quantify the distribution and abundance of Nassau groupers on Glover's Reef when the fish were not aggregated, we conducted visual censuses using standard underwater belt transect techniques (Brock 1982, McCormick & Choat 1987) at 15 sites evenly distributed around the atoll between the spawning periods of December 1999 and January 2000. We swam replicate belt transects (15 × 500 m or 15 × 1000 m transects, depending on the weather conditions and currents) at depths of 10 to 20 m and recorded the number of adult Nassau groupers observed. We sampled 6 sites on the western (leeward) side of the atoll, 6 sites on the eastern (windward) side, and 3 around the spawning site. In addition, we conducted underwater surveys throughout the atoll each May and October from 2001 to 2004.

The data obtained from these censuses were compared with the data on spatial distribution of tag recaptures reported by fishers. The tags returned by local fishers also enabled us to estimate fishing mortality. We used the fishing mortality rate to estimate the number of tagged groupers that were alive each month. Our estimates of site fidelity were based on the proportion of fish carrying acoustic tags that returned to the spawning site, relative to the tagged groupers estimated to be alive.

We placed 12 Vemco VR2 acoustic receivers around Glover's Reef to track the movements of groupers tagged with acoustic transmitters (Fig. 1). Receivers were moored in January 2001 at the edge of the reef drop-off in water depths of 20 to 33 m at narrow points on the shelf 100 to 300 m away from the reef crest, except at the spawning site where the receiver was moored at approximately 1 km from the reef crest. Moorings included an underwater float (located at about 10 m depth), line, and an anchor made of 4 concrete blocks with chain. The location of each receiver was recorded using a hand-held Global Positioning System (GPS) device. We conducted range tests and determined that the receiving range of the receivers was a radius of 750 m, thus receivers were positioned to record signals from tagged groupers moving between the reef wall and the reef crest or along the reef wall down to a depth of several hundred meters. Every January, May, and October from 2001 to 2005, we relocated the receivers, downloaded the data onto a laptop computer, replaced the batteries of the receivers, and replaced the receivers on their moorings the day after they were collected. Moorings stayed at the same place for the entire tracking study.

We used a remotely operated vehicle (ROV) in the afternoons of January 17 and 18, 2004 (10 and 11 d after the full moon), to search for groupers at or below the reef drop-off. On those days we deployed the ROV on the edge of the fore-reef, drove it down the vertical drop-off to a depth of 100 m, and recorded video images for 2 h from late afternoon until sunset using a digital video camera installed in the ROV. We could not conduct more ROV dives at later times because of strong northerly winds.

RESULTS

Broad-scale scuba surveys conducted between the spawning events of December 1999 and January 2000 indicated that the eastern side of the atoll had a significantly greater density of Nassau groupers (4.50 ± 0.4 [mean ± SE] groupers ha^{-1}) than the western side (0.83 ± 0.3 groupers ha^{-1}) (*t*-test; $t = 5.72$, df = 10, $p = 0.0002$). The density of Nassau groupers at the spawning site after the spawning season of December 1999 was 1.33 ± 0.4 ha^{-1}, 2 orders of magnitude lower than that during spawning, when up to 3100 groupers aggregated in less than 2 ha (Sala et al. 2001). Divers repeatedly witnessed spawning occurring in the late afternoon hours at the spawning site.

Local fishers returned 70 dart tags (10.5% of tagged fish) from groupers caught between January 2001 and January 2005, although they provided precise information on location and depth of re-capture for only 50 groupers. Twenty-five groupers were caught on the eastern side of the atoll, 12 on the western side, 10 on the northern side, and 3 inside the lagoon (Fig. 1). Groupers were caught at an average depth of 12.6 m (range = 5 to 23 m), using spear (83% of the re-captures) and hook and line (17% of the re-captures). No tagged fish were caught outside Glover's Reef.

Fishers returned tags from 31 of the 284 groupers tagged with dart tags in 2001. This catch rate equals an instantaneous annual rate of fishing mortality (F) of 0.12.

Within 1 yr from tagging in 2001, fishers caught 5 of the 15 fish tagged with acoustic transmitters, resulting in an estimated F of 0.40. Estimates of F from the second year of dart and sonic tagging were 0.06 and 0.14, respectively. Overall, of the groupers recaptured, 12 had been implanted with acoustic tags, representing 27 % of the fish carrying acoustic tags. The combined estimate of F from sonic tagging was 0.22.

The acoustic receivers placed around Glover's Reef recorded 610 534 transmissions throughout the study. The total number of signals recorded from each coded transmitter ranged from 1841 to 167 294, and averaged 28 069 signals per tag. The total number of signals recorded from each depth tag ranged from 22 to 64 338, and averaged 6317 signals per tag. Receivers located at the spawning site recorded transmissions from all tagged fish.

All tagged groupers expected to be alive, except for those fish caught by fishers within 12 mo of tagging, returned to the spawning site at least once every year from December to March. The number of tagged fish returning in a given month varied each year, depending upon whether the full moon was early or late in the month. The mean percentages of all tagged fish returning to the spawning site in December, January, February, and March were 43, 68, 60, and 23 %, respectively. Each winter, males carrying acoustic tags returned more often to the spawning aggregation site than females. Although about 50 % of tagged groupers of each sex returned in 2 mo each year, 39 % of males returned in 3 or 4 mo each year, whereas only 16 % of females returned in 3 or 4 mo (Table 1). Conversely, 32 % of females visited the spawning site only once, whereas 11.5 % of males visited only once.

The average date of arrival to the spawning site in all years was 0.9 d after the full moon and the average departure date was 10.7 d after the full moon (Fig. 3). The departure dates were remarkably similar among all months; however, the timing of grouper arrival to the spawning site differed among months and was strongly dependent upon the timing of the full moon. When the full moon was early in the month in December and January (2001), groupers arrived to the spawning site an average of 2.8 and 1.6 d, before the full moon, respectively. When the full moon was late in January (2001 and 2002), groupers arrived an average of 4.1 d after the full moon. This was similar to grouper arrivals in February and March, which were always after the full moon (averaging 2.5 and 1.9 d, respectively). The average time spent at the spawning site during the winter full moons was 11.6 d. Three tagged fish each year stayed 10 mo or more at the spawning site. The average date of arrival and departure was not significantly different between males and females (ANOVA, df = 2,17, *F* = 1.51, p >0.05).

Table 1. *Epinephelus striatus*. Number of months from December through March (2002 and 2003) that male and female groupers tagged with sonic transmitters returned to the Glover's Reef spawning aggregation site. The number of individual males or females represents the number of times per year that tagged groupers returned to the spawning site in a 2 yr period

No. months	No. male	% males	No. female	% females
1	3	11.5	8	32.0
2	13	50.0	13	52.0
3	8	30.8	3	12.0
4	2	7.7	1	4.0
Total	26	100.0	25	100.0

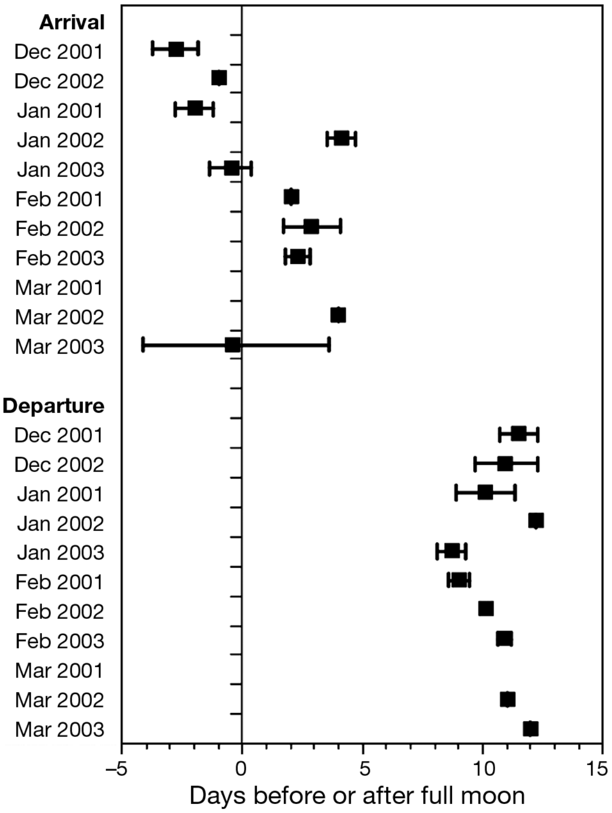

Fig. 3. *Epinephelus striatus*. Mean (±SE) number of days before and after the full moon that tagged groupers arrived at, and departed from, the spawning site

The times at which tag transmissions were recorded at each moored receiver enabled us to identify patterns of migratory movement by plotting the direct-line movements of tagged groupers between receiver locations. We collected sufficient data from 23 tagged fish to distinguish 3 different movement patterns. Of these 23 tags, 9 (39 %) showed a westward pattern of movement, 10 (44 %) showed a southward pattern, and 4 (17 %) remained at the spawning site (Fig. 1). All of the tagged fish that exhibited westward and southward movement patterns left and approached the spawning site from the same direction, respectively. Of the 19 groupers that exhibited westward or southward movements associated with spawning aggregations, 12 (63%) were recorded for the first and last time at the same receiver location. The other 7 groupers were recorded by receivers distributed along the direction they came from, but were not recorded at the original entry/exit point of the atoll. Periodically throughout the year, signals from tagged fish were recorded on the same receivers, indicating that groupers also showed strong fidelity to non-reproductive areas. All the Nassau groupers we saw in scuba surveys in May and October were solitary.

We collected sufficient data from 20 tagged groupers to estimate swimming speed to and from the spawning site. For each fish, we estimated mean swimming speed between adjacent receivers by dividing the distance between receivers by the time elapsed between the last and first times a tag transmission was recorded at the respective receivers. We then averaged the mean swimming speeds for each fish to obtain an average swimming speed for all groupers. We used only fish for which we had >5 swimming segments that extended >5 km (24 fish). Nassau groupers migrating to and from the spawning site averaged 1.90 ± 0.05 (SE) km h^{-1}. The speed of movement to the spawning site (for 127 swimming segments) was identical to the speed of travel away from the spawning site (139 swimming segments). Of note is the observation that several tagged groupers were recorded at receivers 30 km away from the spawning site and at the spawning site less than 24 h later. Male groupers swam significantly (*Z*-test, $p < 0.05$) faster than female groupers. Mean swimming speed was 2.0 ± 0.2 and 1.8 ± 0.2 (SE) km h^{-1} for males and females, respectively. This is equivalent to a speed of 0.8 body lengths s^{-1} for males and 0.6 body lengths s^{-1} for females. We also evaluated the time of day of grouper movements to the spawning site by using all swimming segments that were >5 km, and found that 16 tagged fish moved only during the day (defined as 1 h before sunrise through to sunset) and 8 fish moved both during the day and at night. Grouper swim speeds during the day averaged 1.96 ± 0.03 (SE) km h^{-1} and were significantly faster (*Z*-test, $p < 0.001$) than mean grouper swim speeds at night (1.4 ± 0.1 km h^{-1}).

Tagged groupers exhibited marked changes in depth at specific times throughout the year (Fig. 4). From May through December, groupers resided in narrow depth ranges (15 to 34 m range; mean ± SE, 22.3 ± 0.1 m) that have typically been reported for this species. In January, tagged groupers inhabited similar depth ranges while at the shallow spawning site. However, 7 or 8 d after the January full moon between 10:00 and 11:00 h, all tagged groupers migrated to deeper waters within 1 h of each other, (Fig. 5). This event was recorded on both February 4, 2002, and January 26, 2003. Before 10:00 h, depths of tagged groupers averaged 20.4 m ± 0.7 (SE). After 11:00 h, depths of tagged groupers averaged 71.9 m ± 0.1 (SE), with a maximum depth of 255 m (Figs. 4 & 5). For almost 3 mo after the groupers descended from the spawning site, no signals from tagged fish shallower than 50 m were recorded at any receiver around Glover's Reef (n = 30 fish in 2002,

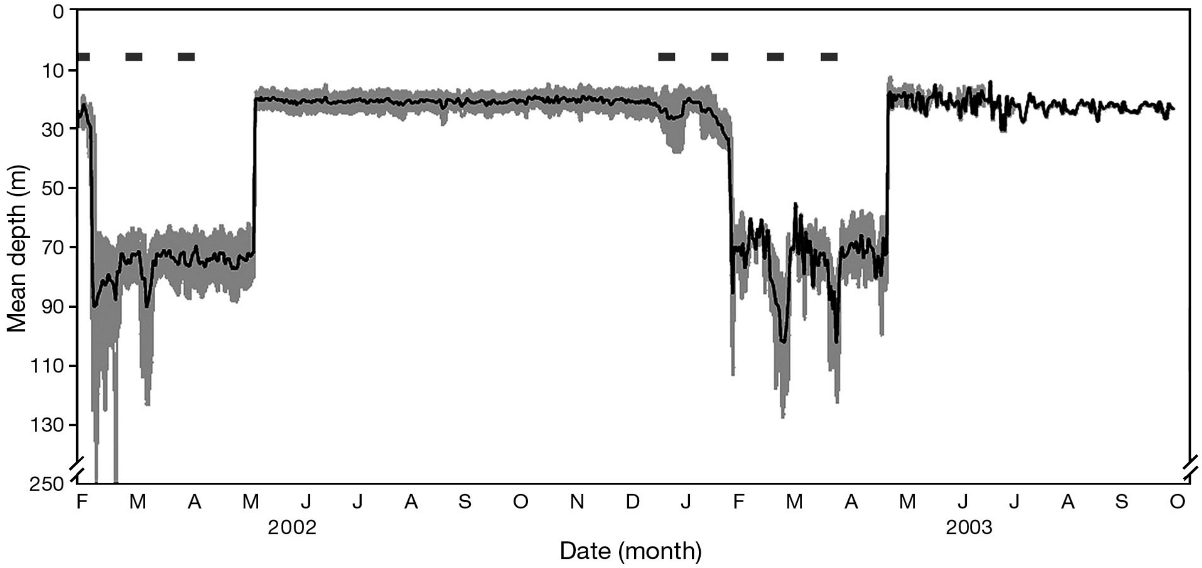

Fig. 4. *Epinephelus striatus*. Depth profiles of tagged Nassau groupers at Glover's Reef. The line represents average depth, and shading depicts range of minimum to maximum recorded depths. Each letter on the *x*-axis represents the first day of the month. Dashed lines at the top indicate the times when groupers were aggregating at the spawning site

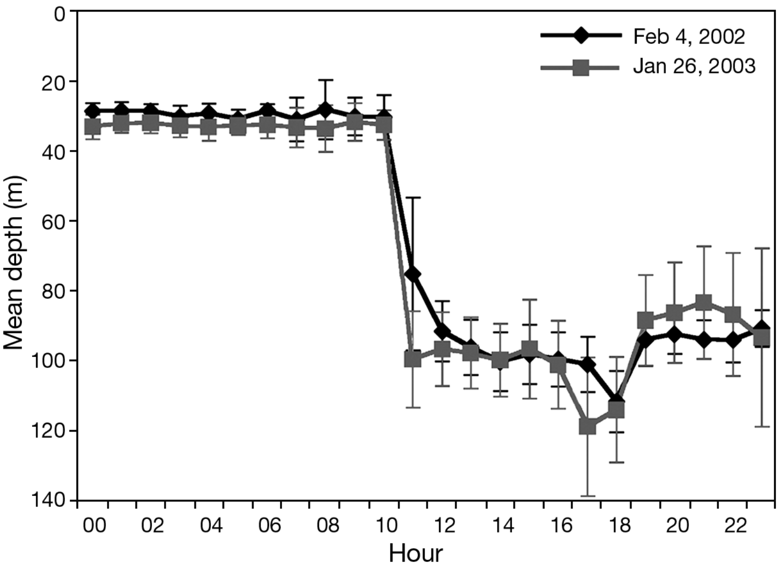

Fig. 5. *Epinephelus striatus*. Mean depth by hour (±95% CI) of tagged groupers on February 4, 2002 (average n = 12) and January 26, 2003 (average n = 8.4); tagged groupers left the spawning site on these days

17 fish in 2003). Interestingly, even the signals from tagged fish that returned to the spawning site near the full moons in February or March were from fish greater than 50 m depth. Again, on May 5, 2002, and April 26, 2003, 9 and 10 d after the April full moon in each year, respectively, tagged groupers ascended synchronously within an hour of each other from mean depths of 72 m to depths of about 20 m, and stayed there for the remainder of the year.

The ROV confirmed the presence of groupers on the deep reef below 60 m. Although the rough weather conditions did not allow us to extensively explore the reef edge and the deep reef wall, we observed a small school of about 50 Nassau groupers at 65 m on January 17, 2004. In addition, we observed schools (>25 individuals) of black groupers *Mycteroperca bonaci* at 70 m depth. We also observed, for the first time, the spawning of yellowfin groupers *M. venenosa* as they formed schools 5 to 10 m above the reef edge at 40 to 45 m, with groups of 6 to 8 individuals conducting fast ascents of about 5 m that resulted in spawning. We observed 3 gamete releases near sunset, between 17:41 and 17:45 h on January 18, 2004.

DISCUSSION

Swimming speeds and vertical movements

Previous studies reported groups of up to 50 groupers moving to spawning aggregations (Colin 1992). In Glover's Reef, the routes to the spawning site were remarkably consistent and predictable during migration. The swimming speeds were especially remarkable because they were rapid and consistent on both the migration to and the return from the spawning site.

The primarily daytime migration of Nassau groupers to the spawning site is similar to that reported by Zeller (1998b) for coral trout *Plectropomus leopardus*. Zeller (1998b) also reported consistent movements of coral trout in relation to spawning aggregation sites and phases of the moon. In his acoustic-tracking study, the maximum distance a coral trout moved to a spawning aggregation was 17 km. Several times, a single fish moved 17 km to and from the spawning site in one day. The average speed of movement was 0.66 km h^{-1}, about 0.33 times as fast as speeds we estimated for male Nassau groupers, and 0.36 times as fast as females. Conversely, swimming speeds for snapper *Pagrus auratus* were reported by Parsons et al. (2003) to be less than 0.5 m s^{-1}, slightly less than the speed of Nassau groupers en route to the spawning site. The maximum speeds reported for the snapper, however, were from short movements on the scale of tens of meters, not tens of kilometers.

Other fishes such as salmon (Salmonidae) (Dittman & Quinn 1996, McCormick et al. 1998), cod (Gadidae) (Rose et al. 1995), and herring (Clupeidae) (Ward et al. 2003) have predictable and synchronised migration routes, but population-wide spatial dynamics have not been reported for a large, sedentary reef fish. The swimming speeds we estimated for groupers are similar to the 1.9 to 2.4 km h^{-1} estimated for 6 species of Pacific salmon (Ogura 1994). Our estimates of grouper swimming speeds were slightly higher than 1.5 km h^{-1} estimated for migrating Chum salmon *Oncorhynchus keta* in the ocean (Tanaka et al. 2005), but slightly lower than 2.4 km h^{-1} reported for the same species in rivers (Quinn 1988). Grouper swimming speeds were also much lower than the instantaneous burst speeds of salmon (Hinch et al. 2002), and half as fast as the speeds of yellowfin tuna *Thunnus albacares* (Marsac & Cayre 1998). Conversely, mean grouper swimming speeds during migration were more than 2 to 7 times greater than migration swimming speeds (0.08 to 0.28 m s^{-1}) of cod *Gadus morhua* (Rose et al. 1995).

Nassau groupers were thought to live almost exclusively in shallow water (Bannerot et al. 1987, Sadovy & Eklund 1999). We learned that groupers occupy much deeper habitats than previously thought, and stay there for months at a time. There also seems to be a clear social component to the movement behavior of Nassau groupers, because tagged fish descended and ascended synchronously to and from deeper habitats. We suggest several hypotheses for this behavior. The first is that Nassau groupers returning to the spawning site in February and March are spawning, as indicated by the occurrence of ripe gonads in February in Belize (Carter et al. 1994). If Nassau groupers do spawn in deeper water, this would imply a much more diversified larval dispersal strategy than previously described, with 2 spawning periods in shallow waters in December and January, and 2 deep spawning periods in February and March. Several authors have suggested that reef fishes spawn at sites exposed to strong currents to ensure the maximum dispersal of larvae and reduce benthic predation (Johannes 1978, Thresher 1984); however, others believe that the location of spawning sites does not enhance dispersal (e.g. Colin et al. 1987), and that larval mobility combined with the regional oceanographic regime are more important in determining the fate of larvae (Paris et al. 2005). Because eggs of Nassau grouper float and reach the surface within 3 to 5 h of spawning, and newly hatched embryos are also positively buoyant within 2 to 3 d after hatching (Colin 1992), wind-driven currents may possibly be the single most important factor in determining larval transport during the first days after spawning. Shenker et al. (1993) suggested that wind-driven currents were important for settlement of young Nassau groupers. Dominant winds during and after the spawning events of December and January throughout the study period were typically northeastly, which might retain larvae in the vicinity of the atoll. We do not know what the early movements of eggs and larvae would be at the deep reef, as there may be currents at depth that carry plankton in directions different from wind-driven surface currents.

Our second hypothesis proposes that groupers occupy deep habitats after spawning to feed and recover. Carter et al. (1994) described the predominant diet of Nassau groupers in Belize to be fish (58%), benthic crustaceans (16%), and nektonic molluscs and cephalopods (6%). Most of the species that they reported in the diets, however, occur in shallower water. We are unaware of any particular food source that would explain why groupers would be foraging in deeper water. A more likely explanation is that the groupers are using the colder water to recover physiologically from the energy loss associated with spawning. If this were true, then there are interesting questions associated with the energetic trade-offs between slowing metabolism in colder water versus actively feeding to achieve post-spawning recovery. Also, if this were true, we do not know why groupers would return at depth to the spawning site in February and March.

Our third hypothesis proposes that groupers use deeper waters as a refuge from predators. The energy expended in spawning might make groupers seek shelter from predators, but the question arises as to why they would aggregate and move synchronously if that were the case? Also, we know that several species of sharks inhabit the 100 to 200 m depth range at Glover's Reef (E. Pikitch, PEW Institute of Marine Science, pers. comm.).

Mortality and site fidelity

The tag returns of fish carrying acoustic tags indicated that a high rate of fishing mortality occurs at Glover's Reef. We estimated values of fishing mortality from the first year of acoustic tagging that were near the $F = 0.37$ estimated by J. A. Baisre & J. Paez (reported in Sadovy & Eklund 1999). In subsequent years, the spawning site was protected by the Belize Department of Fisheries, and fishing mortality rates declined. We believe that the lower estimate of fishing mortality from fish tagged in 2002 is due to both reduced fishing and less reporting of captured tagged fish, as the Belize government was making a strong public effort to reduce fishing mortality of groupers in 2002. Tag returns from fish carrying acoustic tags yielded a higher estimate of fishing mortality than did the dart tags. This may be due to under-reporting of dart tags caught, because we paid more for the return of acoustic tags. The lower rate of fishing mortality provided by dart tags in both years of tagging was probably also due to tag loss, which has been shown to be high in coral reef fishes (Whitelaw & Sainsbury 1986).

All tag returns from fishers showed that Nassau groupers inhabiting Glover's Reef do not leave the atoll, suggesting that they are unlikely to swim long distances over deep water and that they require contiguous reef tracts to migrate. This is supported by the fact that large-scale movements of Nassau grouper (up to 250 km) have been reported only at large barrier reef systems or chains of islands connected by shallow water (Carter et al. 1994, Bolden 2000).

We are not surprised by the strong fidelity of Nassau groupers to a spawning site. Anecdotal information has indicated this fidelity, and Washckewithz & Wirtz (1990) provided evidence that one individual *Epinephelus costae* returned to the same spawning site near Madeira Island for at least 8 consecutive years. Strong spawning site fidelity has also been reported for other serranids by Zeller (1998b) (*Plectropomus leopardus*), Johannes et al. (1999) (*P. areolatus*, *E. polyphekadion*, and *E. fuscoguttatus*), Heyman et al. (2005) (*Lutjanus* *cyanopterus*), Nemeth (2005) (*E. guttatus*), and Pet et al. (2005) (*P. areolatus* and *E. fuscoguttatus*).

Zeller (1998b) reported high fidelity of coral trout to a spawning site, but indicated that not all reproduction occurred at one spawning site. He showed that only 31% of the mature fish tagged participated in a spawning aggregation. This is very different from our observations, but our results may be influenced by the fact that we caught and tagged fish that were already at the spawning grounds. Zeller (1998b) also reported that male coral trout made more trips to the spawning grounds than did females. This pattern is similar to ours showing that males were more frequent visitors than females to the spawning site. However, Zeller (1998b) found that males spent 8 times longer at the spawning site than females. Similarly, Johannes et al. (1999) reported a difference between male and female squaretail coral groupers *Plectropomus areolatus* in the timing of arrival and departure to/from a spawning site; in our study, female and male Nassau groupers arrived and left at the same time.

Our interpretation of Nassau grouper movement behavior at Glover's Reef is that individuals live alone in small home ranges, except during winter full moons when they carry out population-wide synchronous migrations to their spawning site. This seems to be typical of the Nassau grouper throughout the Caribbean, as several researchers have reported only limited movements of groupers over most of the year (Randall 1967, Bolden 2000) and strong site fidelity to a home range (Beets & Hixon 1994, Carter et al. 1994, Bolden 2000). In addition to site fidelity to a home base, our results show strong fidelity to the Glover's Reef spawning site. All tagged groupers returned to the same spawning site every year, although not all fish visited on every winter full moon. Our previous study (Sala et al. 2001) and numerous interviews with fishers over time revealed no additional Nassau grouper spawning sites at Glover's Reef. To test whether this high degree of spawning site fidelity is general to the Caribbean, similar studies tagging a large number of groupers over time should be conducted on contiguous reefs harboring more than one spawning site. We tagged groupers at the spawning site; it would also be valuable to tag groupers at other times and locations at Glover's Reef to verify that all groupers inhabiting this area travel to the same spawning site.

Strong fidelity to spawning sites has been shown for small reef fishes. In Panama, the bluehead wrasse *Thalassoma bifasciatum* used the same spawning sites on patch reefs over at least 4 generations (Warner 1988). Warner (1988) conducted experimental studies indicating that this intergenerational fidelity to spawning sites implies cultural transmission. It has been suggested that Nassau groupers also learn the routes to spawning sites by social transmission (Bolden 2000). We know that Nassau groupers have used the same spawning sites for more than 100 yr (Colin 1992, Carter et al. 1994), whereas their average life span is 16 yr, and that none of the spawning aggregations eliminated by fishing has returned (Sadovy & Eklund 1999). Eliminating a spawning aggregation by fishing is similar to Warner's experimental removals of bluehead wrasses from patch reefs. In both cases, an abandoned spawning site is not used again, indicating that there is a cultural transmission associated with spawning. We do not know the minimum number of individuals needed for cultural transmission to be effective, but we know that Nassau grouper aggregations harboring less than 1000 individuals have not been sustainable over time (Sadovy & Eklund 1999). This Allee effect may exacerbate the decline of the Nassau grouper populations (Gascoigne & Lipcius 2004).

There seems to be a complex relationship between the timing of the full moon, the number of full moons in a year, and the size of the spawning aggregation. Local fishermen have told us that when there are 13 moons in a year, fishing is good during the last full moon in December, indicative of a large aggregation. Our results add reason to investigate this traditional knowledge. When the full moon was late in December, on a year with 13 moons, 60% of the tagged fish returned to the spawning site in December. On other years with 12 moons, and an earlier full moon, none of the tagged groupers was detected at the spawning site around the full moon in December. Also, when the full moon was late in January, the timing of arrival and the number of groupers occurring at the spawning aggregation were more similar to our observations in February of other years. There are interesting consequences for population structure and temporal recruitment patterns if this relationship between timing of the full moon and abundance of spawning groupers is robust, because every few years when there is a 13th moon, there may be higher larval production. This could lead to high recruitment in those years and, if populations are recruitment limited, then stronger year classes should result. This is a subject that deserves additional research.

Implications for grouper conservation

The spatial dynamics described here have strong implications for fisheries management and conservation of the Nassau grouper. There has not yet been a recovery of a depleted spawning aggregation of Nassau groupers in sections of the Caribbean that have been closed to fishing (Sadovy & Eklund 1999), indicating that there may be distinct reproductive populations in the Caribbean. Our results support this hypothesis, and indicate that the complex spatial dynamics of Nassau groupers need to be incorporated into fisheries management strategies based on a metapopulation approach. This may involve stratified management schemes across spatial scales. For example, Glover's Reef may be best managed as separate units because the eastern side of the atoll contributed more individuals to the spawning aggregations than did the western side. In addition, a marine reserve would be better placed on the windward fore-reef, should the preservation of the Nassau grouper population be a major conservation goal.

Our results underscore the need for more information about adult movements to use in metapopulation models and population viability analyses, and indicate that adult migration may play an important role in the connectivity between patches or populations. Fisheries closures and marine reserves have been created in Belize and the Bahamas to protect Nassau grouper spawning sites, but these measures ignore adult migration patterns. Our results indicate that the preservation of the Nassau grouper in the Caribbean requires that fisheries closures be maintained during the predictable window of time when all individuals migrate to spawning grounds, that deeper reefs be included in this protection, and that closures be long enough to account for the 4 spawning events realized by individual groupers. As suggested by Fulton et al. (1999), protecting a spawning aggregation may not sufficiently protect groupers if they are caught as they migrate, or if fishing rates are too high outside the spawning season.

Interestingly, the movements reported here and in previous studies are across spatial scales similar to those involved in the dispersal of reef fish larvae (on the order of 50 to 100 km; Cowen et al. 2006). Our results indicate that replenishment of depleted populations may not occur via adult migration between isolated atolls or reefs, and that repopulation would be entirely dependent upon larval recruitment. Because there are reef fish larval dispersal barriers in the Caribbean, and the degree of connectivity between populations is spatially very heterogeneous (Cowen et al. 2006), we would expect that some Nassau grouper populations isolated by deep waters that do not contain any spawning aggregations are doomed to extinction, or at least will be depleted for a very long time. In any case, the repopulation of overfished spawning aggregations will be slow and largely dependent on the rate of dispersal of adults between spawning sites (presently unknown for contiguous reef systems). These findings support the call for protection of all Nassau grouper spawning aggregations in the Caribbean as a necessary action, although perhaps not sufficient for the preservation of the species.

CONCLUSIONS

Our data provide the most extensive record to date of the migratory movements of an endangered coral reef fish. Before this study, the accepted paradigm was that Nassau groupers inhabited mostly shallow reefs and, in Belize, spawned exclusively in December and January. Our study demonstrated that both male and female Nassau groupers travel to the spawning site up to 4 times from December through March. Additionally, our results revealed an unexpected complexity in the migration of adult Nassau groupers between habitats and indicate that their population-wide migration is remarkably synchronous and predictable. For the first time, we provide evidence that Nassau groupers move as a group to deep water after spawning. It is unclear, however, whether the deep dives and aggregations represent spawning events. Increased underwater observations using manned submarines or remotely operated vehicles will provide more data on the activities of the groupers in deep water. Our results indicate that effective conservation of the Nassau grouper requires the inclusion of migratory routes and deep reefs, in addition to the existing protection of shallow spawning sites.

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