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ARTICLE

# Multiyear Tracking of Nassau Grouper Spawning Migrations

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***Abstract***
**An understanding of temporal patterns of migration and spatial connectivity between home ranges and spawning sites is necessary for effective management of species that form transient spawning aggregations. The Nassau Grouper *Epinephelus striatus* is a Caribbean coral reef fish that displays such spawning aggregations, which have been overfished to the point of threatening the species. Using acoustic telemetry, we examined the size at which Nassau Grouper migrate to spawning aggregations, the timing of migrations, and the distance of migration routes used by Nassau Grouper from within and outside of a large, no-take marine reserve in the central Bahamas. Fish (total *n* = 19) were tagged in 2004 (*n* = 6) and 2005 (*n* = 13) and were tracked for one to four spawning seasons. Fish that were 54 cm TL or greater made spawning migrations, with all but one migrating southward along the shelf edge of Exuma Sound for a distance of 70 km to over 200 km, usually during the December full moon. Fish typically made one migration annually, which lasted from 1 to 3 weeks, with fish remaining at spawning sites for only 1–2 d; however, when the full moon was early in the spawning season, several fish remained away from their home reefs through two lunar cycles or delayed their migrations by a month, and one fish made two migrations. Fish that were migrating for the first time had slower swimming speeds to spawning sites than did experienced fish, but swimming speeds were similar between the two groups during return migrations, suggesting that their migration behavior was learned. Our results demonstrate that spawning migration patterns for this species may be more variable in The Bahamas than at other Caribbean locations. The present findings also have important implications for the management of the species, including increasing the minimum size limit to 54 cm or larger and the use of both marine protected areas and seasonal closures to rebuild the spawning stock.**

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Spawning aggregations are predictable, repeated concentrations of conspecific marine animals that are gathered for spawning at densities at least four times greater than outside aggregations (Domeier 2012). This reproductive strategy has been confirmed for at least 85 reef fish species globally (Domeier 2012) and may also be the strategy used by at least another 80 marine species (Claydon 2004; Sadovy de Mitcheson and Colin 2012). Many of these species form transient spawning aggregations characterized by migrations that take animals to established sites well outside of their normal home ranges for short periods of time only once or a few times annually (Domeier 2012). Spawning aggregations are a common reproductive strategy used by many commercially important species in coral reef systems, such as groupers (Epinephelidae) and snappers (Lutjanidae).

Because snappers and groupers are typically long-lived and late-maturing species, their life histories make them vulnerable to overfishing (Coleman et al. 2000). Their reproductive strategy exacerbates this vulnerability. The abundance of large fish at predictable times and locations attracts increased fishing effort on spawning aggregations and produces landings that greatly exceed those at other times of the year (Sadovy de Mitcheson and Erisman 2012). As transient aggregations draw fish from large areas, concentrated fishing at aggregation sites can have dramatic effects on fish populations. Furthermore, these spawning aggregations can comprise the single time and place for all annual reproductive activity of a species in a region; therefore, concentrated fishing on spawning sites can dramatically reduce reproductive success. As a result, fishing at spawning aggregations is unlikely to be sustainable (Sadovy and Domeier 2005), and there are numerous examples of transient spawning aggregations in decline (Sadovy de Mitcheson et al. 2008)—or worse, being fished to the point where they no longer form (Olsen and LaPlace 1979; Aguilar-Perera 2006; Cheung et al. 2013), thus putting the species at risk of local or global extinction (Dulvy et al. 2003; Cheung et al. 2005; Sadovy de Mitcheson et al. 2013).

One species that typifies the reproductive strategy of transient spawning aggregations is the Nassau Grouper *Epinephelus striatus* (Sadovy de Mitcheson and Colin 2012). Nassau Grouper are considered an endangered species by the International Union for Conservation of Nature (Albins et al. 2009), owing largely to concentrated fishing on their spawning aggregations (Sadovy de Mitcheson 2013). Throughout the Caribbean region, there were once at least 50 spawning aggregations reported, but 32 or more have been fished to the point of commercial extinction (Sadovy de Mitcheson et al. 2008) and may take decades to recover, if at all (e.g., Kadison et al. 2010).

The Bahamas is one of the few regions where viable fisheries for Nassau Grouper still exist, and 20–30 spawning aggregations have been reported (e.g., Sadovy and Eklund 1999; Cheung et al. 2013; Kobara et al. 2013). These aggregations form during the full-moon periods of December, January, and February. Nassau Grouper fisheries in The Bahamas are managed with a minimum size limit of 1.36 kg (3 lb), a network of marine protected areas, and a closed season. Despite these measures, there have been recent declines in Nassau Grouper populations in The Bahamas (Cheung et al. 2013), with an estimated 60% of reported spawning aggregations no longer forming (Sadovy de Mitcheson et al. 2008). Since the 2004–2005 spawning season, the Government of The Bahamas has implemented a closed season for Nassau Grouper fishing during the winter spawning months, but the closure has been inconsistent in its timing from year to year, is often declared within days of the first full moon of the spawning season, and is poorly enforced, particularly in some of the more remote parts of The Bahamas. As a result, there are high levels of poaching during the spawning season (C. P. Dahlgren, personal observation). Furthermore, although populations within the Exuma Cays Land and Sea Park (ECLSP), a large, fully protected marine reserve, have greater abundance and biomass than elsewhere in The Bahamas (Sluka et al. 1997; Dahlgren 2004; Mumby et al. 2006), they have declined from historic levels (C. P. Dahlgren, unpublished data). Thus, there is a need for improved management to protect Nassau Grouper populations and to promote their recovery (Sadovy de Mitcheson et al. 2008; Cheung et al. 2013).

For species that migrate to spawning aggregations, effective management—particularly the design of marine protected areas—requires an understanding of the species' spatial distribution and movement (Green et al. 2015). The use of external tags and acoustic telemetry has greatly improved our ability to determine spatial linkages among fish home ranges, spawning sites, and migration corridors (Zeller 1999; Nanami et al. 2013; Matley et al. 2015). Studies that use externally visible tags have reported a few Nassau Grouper that were tagged at spawning aggregations and subsequently were found anywhere from less than 5 km to more than 200 km from where they were tagged (e.g., Colin 1992; Carter et al. 1994; Starr et al. 2007). In the central Bahamas, one fish that was tagged in the Exuma Cays was subsequently captured by fishers at a spawning aggregation in southern Long Island, traveling a straight distance of 220 km (Bolden 2000). Elsewhere, acoustic telemetry has been used to track long-distance migrations of Nassau Grouper (Whaylen et al. 2004; Semmens et al. 2006; Starr et al. 2007).

Here, we describe two studies that used acoustic telemetry to examine Nassau Grouper movement over spatial scales of tens to hundreds of kilometers in the central Bahamas over multiple years. In 2004–2005, we conducted a pilot study aimed at determining (1) spatial patterns of emigration from a large, no-take reserve (ECLSP), particularly during the spawning season; (2) the timing of spawning migrations; and (3) movement patterns and pathways during migrations. A more extensive study conducted from 2005 to 2008 examined long-term spatial connectivity between Nassau Grouper home ranges and spawning aggregations

within fished and protected areas. Specifically, we examined (1) where, when, and how often fish from different locations go to spawn; (2) annual spatial and temporal migration patterns; and (3) the relationship between body size and migration. These studies provide a better understanding of variability in spatial and temporal patterns in Nassau Grouper spawning migrations and have important implications for the management of the species.

## STUDY AREA

Nassau Grouper movement was monitored throughout the Exuma Cays in the central Bahamas (Figure 1). The Exuma Cays are a chain of over 300 islands extending over 200 km from Great Exuma in the southeast to the Sail Rocks in the northwest. Eastward of the Exuma Cays is Exuma Sound, a semi-enclosed ocean basin that reaches depths of over 3,000 m. Along the eastern shores of the islands are hard-bottom ledges, coral reefs, and sandy habitats that extend for 1–2 km and depths of 20–40 m before dropping off precipitously into the abyssal depths of Exuma Sound. Westward of the Exuma Cays is the Great Bahama Bank, a large, shallow, sandy platform where depths do not exceed 10 m.

In the northern portion of the Exuma Cays lies the ECLSP (Figure 1), a large (409 $km^2$ of marine habitats), no-take area that was established in 1959 and where all fishing has been prohibited since 1986 (Dahlgren 2004). Seventy kilometers south of the park is Lee Stocking Island (LSI), where the Perry Institute for Marine Science's Caribbean Marine Research Center was located. Within the Exuma Cays system, three Nassau Grouper spawning aggregations have been reported, and another five spawning aggregations have been reported to occur farther south at Long Island (Figure 1; Sadovy and Eklund 1999, and unpublished data).

## METHODS

### Fish Tagging

From 2004 to 2005, a total of 19 Nassau Grouper were tagged at least 1 month prior to the expected spawning migrations. In October and November 2004, six Nassau Grouper were tagged within the ECLSP to examine whether fish leave the park, and if so, when they leave and where along the shelf they migrate. In October 2005, an additional five fish were tagged in the ECLSP, and eight fish were tagged in the LSI area to examine migration timing and routes in greater detail (Figure 1). Fish ranging from 35 to 41 cm TL received surgically implanted Vemco V8SC-2L transmitters (9 × 28 mm; 5.0 g in air) with an expected battery life of 903 d. Larger fish were implanted with the V13-1H transmitters (13 × 36 mm; 12 g in air), which had an expected battery life of 809 d. Each transmitter was programmed to emit a unique signal at a frequency of 69 kHz approximately every 225 s (random delay = 150–300 s).

Nassau Grouper were captured in baited traps or by divers using mesh nets and a mixture of equal parts quinaldine and ethanol (95%) that was diluted with seawater at a ratio of 1:200 to help sedate the fish. All fish were slowly brought to the surface, where their condition was assessed before they were anesthetized with tricaine methanesulfonate (MS-222) in buffered seawater at a concentration of 75 mg/L. Once anesthetized, each fish was measured for TL and placed in a sling ventral side up, and a small incision was made in the abdomen posterior to the pelvic fins. The transmitter was inserted into the body cavity, and the incision was closed by using two to four interrupted sutures via procedures used for other tropical grouper species (Zeller 1999). After surgery, fish were placed in a recovery bath of seawater for at least 10 min. Once fish were able to maintain an upright swimming position and exhibited an escape response to handling, they were returned by divers to their place of capture and were released (hereafter, "release sites"). Efforts were made to tag fish near receivers to ensure detection in their home range, but several fish were tagged outside the detection range of receivers and were only detected during spawning migrations.

*Receiver locations.*—Vemco VR2 acoustic telemetry receivers were used to detect tagged fish. Receivers were deployed in water depths of 3–35 m on 1–2-m-long mooring lines buoyed by Styrofoam floats to elevate them above the seafloor and reduce interference in detections from the topography of the seafloor for fish moving along reef structure. Moorings were anchored with a pair of concrete blocks on hard bottom or with a sand anchor in sandy substrates. Range testing on receivers indicated effective detection distances of at least 150 m for V8-4H transmitters and at least 250 m for V13-1H transmitters.

During the winter of 2004–2005, movement out of the ECLSP by Nassau Grouper that were captured and tagged within 10 km of the southern boundary was detected by using six small receiver arrays, which were located near the southern boundary of the ECLSP at 0, 1, 5, and 10 km inside the park and 2.5 and 5 km outside the park (Figure 2). Each array consisted of two to five receivers spaced 200 m apart, extending perpendicular to the shelf edge from islands to the reef drop-off. These arrays were recovered in October 2005 and repositioned for the follow-up study.

After successfully tracking fish movement out of the ECLSP on the offshore-most receivers in 2004 (see Results), a more extensive array of 28 receivers was deployed in October 2005, prior to the spawning season, to track larger-scale spawning migrations in the Exuma Sound region. Individual receivers were placed an average of 10 km apart, extending from the northernmost extent of Exuma Sound between the Exuma Cays and Eleuthera Island to the North Point of Long Island, covering a distance of 280 km (Figure 1). Receivers were placed within 200 m of the reef drop-off in bottom depths of 10–33 m. This array encompassed three of the reported spawning aggregation sites in

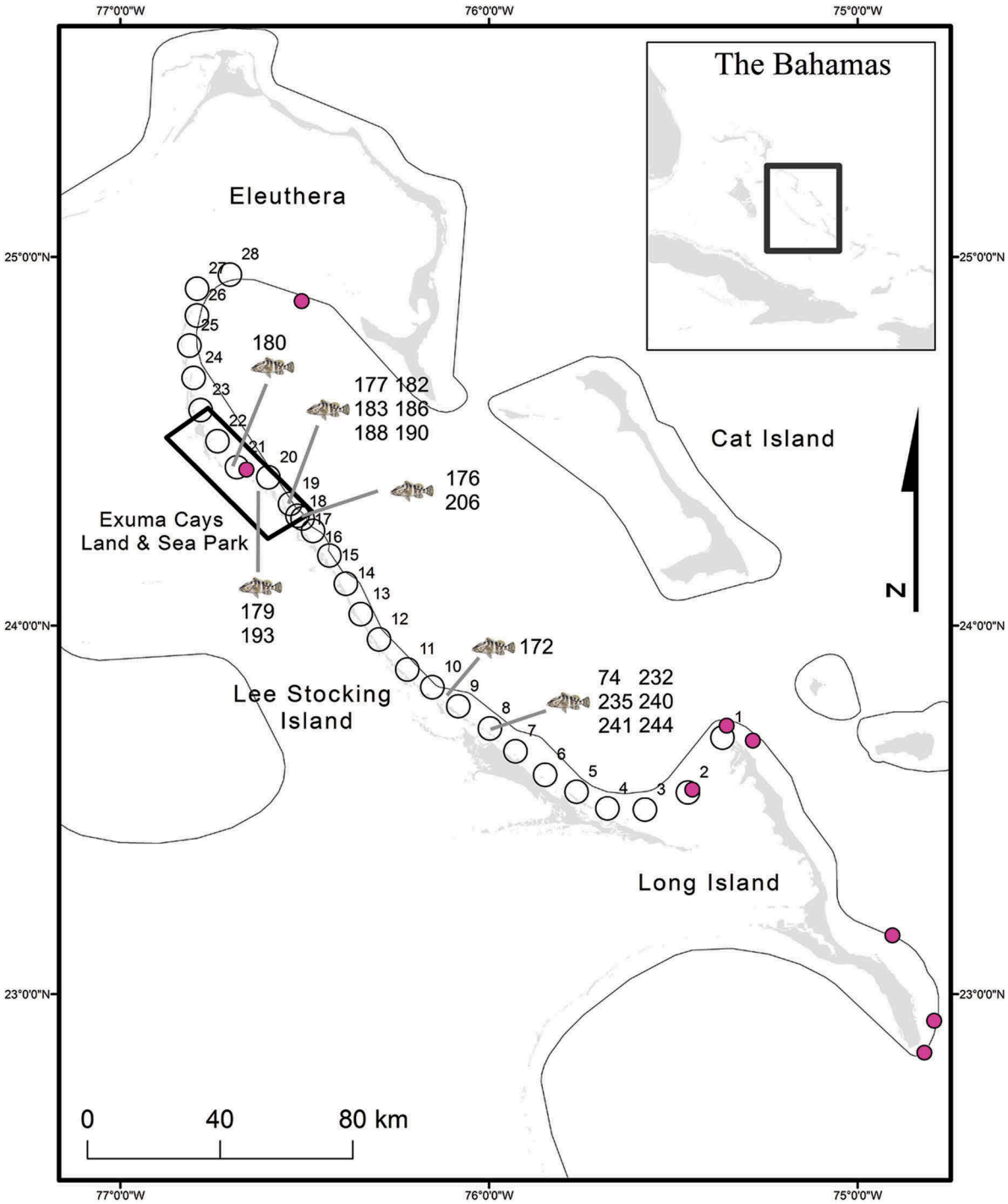


FIGURE 1. Map showing the Nassau Grouper spawning aggregation sites (pink circles) reported for the central Bahamas, along with the receiver locations (numbered open circles) used throughout Exuma Sound from 2005 to 2008. Release locations for individual fish that were tagged in 2005 and 2006 are shown (fish icon); fish that were tagged within 5 km of each other are grouped together. Lines around islands indicate the location of the 200-m depth contour.

the central Bahamas (Sadovy and Eklund 1999). Receivers were downloaded and had their batteries replaced each summer from 2005 until their retrieval in June 2008, which allowed us to track fish through three spawning seasons.

*Data analysis.*—If a fish was detected at a site other than the site where it was tagged during the winter spawning season, we assumed that it migrated to a spawning site even if we did not detect it at any of the spawning sites within the

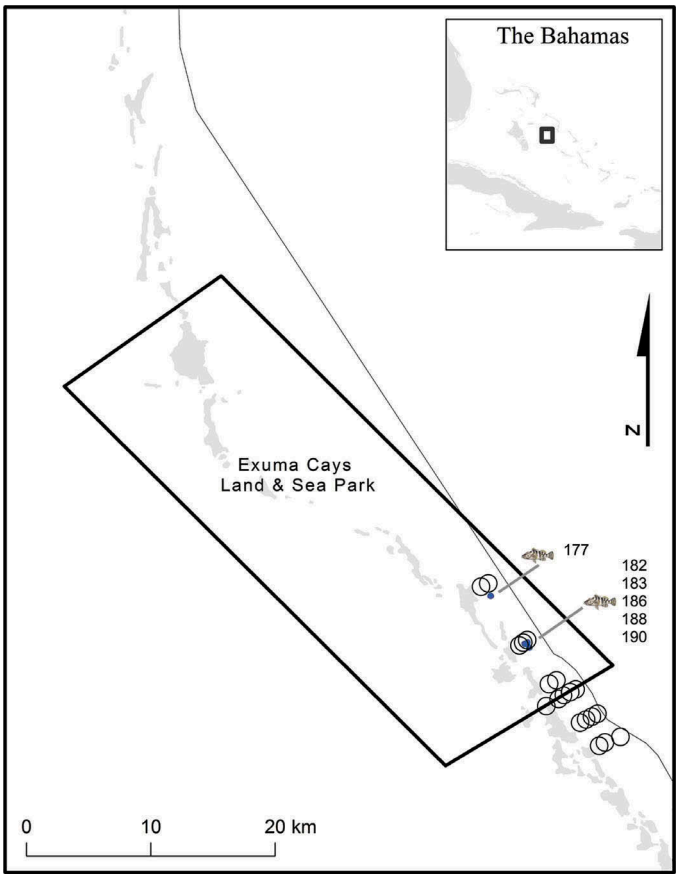


FIGURE 2. Map of receiver locations (open circles) that were used to detect Nassau Grouper spawning migrations in 2004–2005. Receivers extended from the shore to the shelf edge at 1, 5, and 10 km inside and along the southern boundary of the Exuma Cays Land and Sea Park as well as 2.5 and 5.0 km outside of the park in 2004–2005. Circle sizes approximate the average receiver detection range. Release sites are shown for individuals that were tagged in 2004 (blue circles). The bathymetry line indicates the 200-m depth contour.

receiver array (Nanami et al. 2013). Fish that showed distinct directional movement away from release sites through the array but were not detected for several days before being detected again on a return migration were assumed to have migrated outside of the array. For each fish that migrated, the duration of time spent away from the release site was calculated. For fish tagged within the detection range of receivers, the duration away was calculated as the time between the last detection at its release site before a migration and the first detection at its release site after the migration (Nanami et al. 2013). For each fish that was tagged outside the detection range of a receiver, migrations were observed when the fish was detected at more than one receiver away from its release site. In these cases, the duration away was estimated as the time between the first detection and the last detection during the winter spawning season.

Migrating fish size was assumed to be the measured size of fish for those observed to migrate during the first spawning season (1–3 months) after tagging. For subsequent spawning seasons, fish size was estimated using a growth curve generated from the von Bertalanffy growth function,

$$L_a = L_\infty x\left[1 - e^{-K(a-t_0)}\right],$$

where $L_a$ is the length at age $a$; $L_\infty$ is the asymptotic length (94 cm TL); $t_0$ is the theoretical age at a length of zero (–3.27); and $K$ is the growth parameter (0.063) based on values from the published literature (Sadovy and Eklund 1999). Annual increase in size was estimated using this curve based on the measured size of the fish.

For any fish that was detected at more than one receiver away from its release site, migration speeds were calculated for that individual on its migration away from and on the return trip to the release site: the distance along the shelf edge between (1) the receiver detecting the fish closest to its release site and (2) the receiver where it was detected farthest away from its release site over the course of a migration was divided by the time between the two detections. Using a two-way ANOVA, migration speeds were compared for migrations to and from the spawning aggregations and were compared between experienced fish and those making their first migration. Experienced fish included all individuals that had made a confirmed migration. For an experienced fish, migration speed was averaged for all migrations away from or returning to the release site after that individual's first observed migration.

## RESULTS

In total, 385,541 detections were recorded from the 19 tagged Nassau Grouper. Individual fish were detected for 112–1,144 d, with a mean of 482 d between tagging and last detection (Table 1). Six fish were tracked through one spawning season, seven fish were tracked through two spawning seasons, five fish were tracked through three spawning seasons, and one fish was tracked through four spawning seasons (Table 1). Of the 19 tagged fish, 12 individuals made spawning migrations: seven fish were detected as making migrations over multiple years, and five fish were detected during their first spawning migration.

### Movement Out of the Exuma Cays Land and Sea Park during the 2004–2005 Spawning Season

During the 2004–2005 study, all six fish that were tagged in the ECLSP were detected by receivers closest to their release locations at approximately 5 km ($n$ = 3), 1 km ($n$ = 2), and less than 1 km ($n$ = 1) from the park's southern boundary (Figure 2). Fish 182 remained at or near its release site throughout the spawning season. Fish 183 and 186 were detected by the receiver closest to their release site for

TABLE 1. Summary of fish tagged in 2004 and 2005 within the Exuma Cays Land and Sea Park (ECLSP) and in the vicinity of Lee Stocking Island (LSI); individuals are presented in order of size (cm TL) from smallest to largest. Black cells indicate years for which no data exist for individual fish.

| Fish number | TL (cm) | Location | Release date | Last detection | Number of days | Number of detections | Migrated 2004–2005 | Migrated 2005–2006 | Migrated 2006–2007 | Migrated 2007–2008 |
|---|---|---|---|---|---|---|---|---|---|---|
| 183 | 35 | ECLSP | Nov 6, 2004 | Mar 26, 2005 | 140 | 24 | No | | | |
| 186 | 36 | ECLSP | Nov 7, 2004 | Mar 28, 2005 | 132 | 16 | No | | | |
| 74 | 36 | LSI | Oct 17, 2005 | May 12, 2006 | 207 | 27 | | No | | |
| 241 | 39.5 | LSI | Oct 16, 2005 | Apr 9, 2008 | 907 | 2,466 | | No | No | |
| 198 | 40 | LSI | Oct 18, 2005 | Mar 26, 2008 | 890 | 609 | | No | No | |
| 206 | 40.5 | ECLSP | Oct 10, 2005 | Jul 12, 2006 | 275 | 1,523 | | No | | |
| 182 | 41 | ECLSP | Nov 6, 2004 | Jun 15, 2005 | 219 | 8,130 | No | | | |
| 172 | 48.2 | LSI | Oct 17, 2005 | Oct 31, 2007 | 745 | 5 | | No | No | Yes |
| 235 | 49.5 | LSI | Oct 16, 2005 | Jun 15, 2008 | 974 | 214,280 | | No | No | Yes |
| 232 | 51 | LSI | Oct 17, 2005 | Dec 1, 2006 | 410 | 1,060 | | No | Yes | |
| 244 | 52.5 | LSI | Oct 16, 2005 | Jul 15, 2007 | 638 | 101,425 | | No | Yes | |
| 193 | 53.5 | ECLSP | Oct 13, 2005 | Dec 21, 2007 | 800 | 5 | | No | Yes | Yes |
| 177 | 58.5 | ECLSP | Nov 7, 2004 | Jan 17, 2007 | 802 | 78 | Yes | Yes | Yes | |
| 240 | 59 | LSI | Oct 16, 2005 | Nov 4, 2007 | 750 | 53,341 | | Yes | Yes | |
| 188 | 60 | ECLSP | Nov 6, 2004 | Dec 25, 2007 | 1,144 | 232 | Yes | Yes | Yes | Yes |
| 190 | 62 | ECLSP | Oct 25, 2004 | Jan 12, 2007 | 809 | 1,169 | Yes | Yes | Yes | |
| 176 | 63 | ECLSP | Oct 13, 2005 | Feb 21, 2006 | 132 | 1,100 | | Yes | | |
| 179 | 63 | ECLSP | Oct 13, 2005 | Jan 9, 2007 | 454 | 9 | | Yes | Yes | |
| 180 | 71 | ECLSP | Oct 13, 2005 | Feb 6, 2007 | 482 | 42 | | Yes | Yes | |

112–118 d, with several days between detections, but no spawning migrations were detected for those fish. The three largest fish (177, 188, and 190) all left their release sites and were detected within 20–90 min of each other by the offshore receiver at the ECLSP boundary 10 d before the full moon (Figure 3) despite the fact that they were tagged approximately 4.5 km apart (Figure 2). After being detected by the receiver 5 km south of the ECLSP, they were not detected for 13–15 d before returning to the ECLSP along the shelf edge 4–6 d after the full moon (Figure 3). After their return to the ECLSP, each fish was detected by the receiver closest to its release site and was detected for two to three subsequent years (Table 1). The 2004–2005 study determined migration timing and indicated that migration occurred along the shelf edge. We used this information in the 2005–2008 follow-up study to determine where fish were during the 13–15 d of absence in 2004–2005.

## 2005–2006 Spawning Season

During the 2005–2006 season, 16 Nassau Grouper were detected within the expanded receiver array, including the three fish that were tagged and migrated in 2004 (Table 1). During the December–January spawning season, six fish were detected away from their release sites (fish 177, 179, 180, 188, 190, and 240), and one fish that was consistently detected at its release site throughout the year disappeared during the December 2005 full moon (fish 176; Figure 4). All seven (six from ECLSP and one from LSI) of these fish exceeded 58 cm TL at the time of tagging (Table 1) and were detected by the receiver closest to their release site after migrating.

Duration away from the release sites ranged from as little as 7 d to as many as 26 d, with longer durations observed for fish that were tagged in the ECLSP. Five of the six fish (176, 180, 188, 190, and 240; Figure 4) that migrated left their release sites between 5 and 12 d prior to the full moon in December; they returned to the same area where they were released between the day of the full moon and 11 d after the full moon in December. The one exception to this was fish 179, which left its release site 10 d before the January full moon and returned 11 d after the full moon. All individuals but fish 176 migrated southward, and three fish that were tagged up to 100 km apart were detected at the Hail Mary (receiver 2) and North Point (receiver 1) spawning aggregation sites near Long Island but were not at the sites simultaneously (Figure 4). Fish that were detected in the vicinity of a spawning aggregation site were detected there for only 1–2 d before they migrated back to their release sites.

Four Nassau Grouper migrated outside of the receiver array during the 2005–2006 spawning season. Fish 190 moved past receiver 1 off Long Island and out of the receiver array during December 2005 for 12 d before being detected as it moved back north to its release site in the ECLSP. Fish 176 disappeared from its release site in the ECLSP from 3 d before to 5 d after the

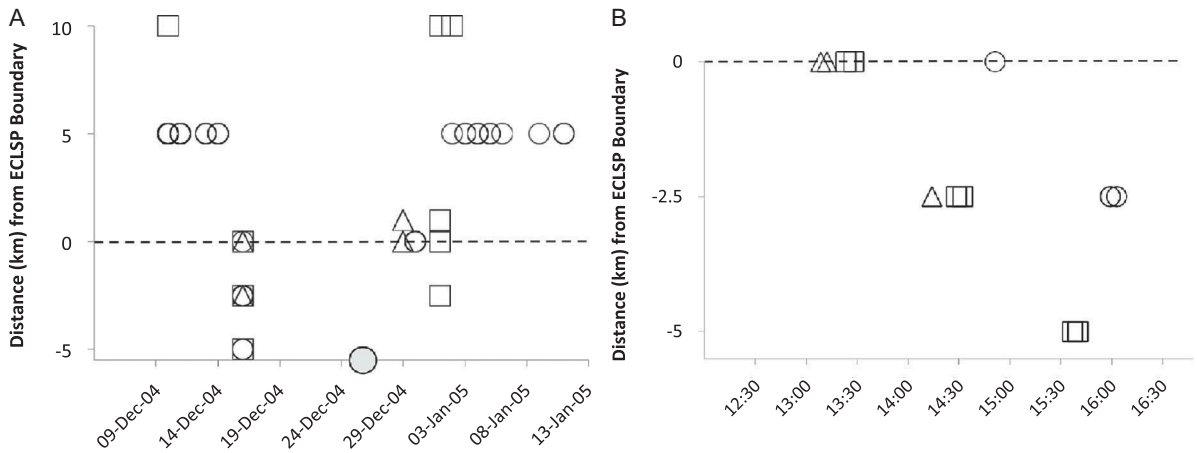


FIGURE 3. **(A)** Daily positions of Nassau Grouper migrating during the winter of 2004–2005 (*x*-axis shows when fish were detected at daily intervals; shaded circles on the *x*-axis indicate the date of the full moon); and **(B)** the timing of the spawning migration out of the Exuma Cays Land and Sea Park (ECLSP) on December 16, 2004 (*x*-axis shows the exact time of detection). The *y*-axis in both panels shows the distance from the southern boundary of the ECLSP, with positive numbers corresponding to receivers located inside the park. Only fish that migrated are shown.

December full moon and was not detected by any receivers at that time. Two other fish (179 and 188) migrated southward but were not detected at known spawning sites (Figure 4).

## 2006–2007 Spawning Season

In the winter of 2006–2007, 13 fish were detected, 9 of which made spawning migrations (6 fish from ECLSP and 3 fish from LSI; Table 1). All fish migrating in 2005–2006 migrated again during the winter of 2006–2007, except for fish 176, which was not detected in 2006–2007. Fish 179, 188, 190, and 240 all migrated several days before the full moon during the same month (either December or January) in which they had previously migrated, but fish 180 migrated 1 month later than during the previous year. The three fish that migrated to a confirmed spawning site in the winter of 2005–2006 (fish 177, 180, and 240) were detected at the same spawning site in 2006–2007.

Three fish that were tagged between sizes of 51.0 and 53.5 cm TL in 2005 but that did not migrate during the 2005–2006 spawning season made their first spawning migration during the 2006–2007 spawning season (Table 1). Based on the von Bertalanffy growth equation, their size at first migration was between 54 and 56 cm TL.

For all migrating Nassau Grouper, the duration away from release sites varied from 10 to 45 d. Up to 9 d before the December full moon, two individuals from the ECLSP (fish 190 and 188) and two fish from the LSI area (fish 232 and 240) migrated south to the Hail Mary (receiver 2) and/or North Point (receiver 1) spawning sites (Figure 5). After being detected at the spawning site, most individuals left the array for an extended period of time (fish 190 and 232) or remained within 20 km of the spawning site (fish 240) and did not return to their release sites for over 1 month. Fish 188, however, returned to its release site after the December full moon and made a second migration just prior to the January 2007 full moon. This was the only time that a fish made more than one spawning migration in a season. In addition to the fish that migrated in December, fish 180 and 244 began migrations 8–10 d before the January full moon. Fish 244 returned to its release site 4 d after the full moon, but fish 180 was not detected in the array again until 3 d after the February full moon (i.e., after a 39-d absence). Fish 179 was detected during a migration for a third year but only twice during a return migration after the January full moon.

## 2007–2008 Spawning Season

In the winter of 2007–2008, six fish were detected within the receiver array, and four of those individuals were detected by receivers away from their release sites (two from ECLSP and two from LSI; Table 1). Fish 188 and 193 had migrated during the previous spawning season, and fish 172 and 235 were detected as migrating for the first time (Table 1). The fish that were detected away from their release sites for the first time were tagged in 2005 (near LSI) at 48.2 cm TL (fish 172) and 49.5 cm TL (fish 235), and the estimated size of those fish during the 2007–2008 spawning season was 54–55 cm TL. Both of the experienced fish (fish 188 and 193) were tagged in the ECLSP but were only detected south of LSI.

During the 2007–2008 spawning season, the duration away from release sites ranged from 11 to 41 d (Figure 6). Fish 172 was detected away from its release site for the first time several months before the other fish migrated, leaving its release area 11 d before the October full moon, and was last detected near the North Point site 5 d after the October full moon. The other first-time migrant

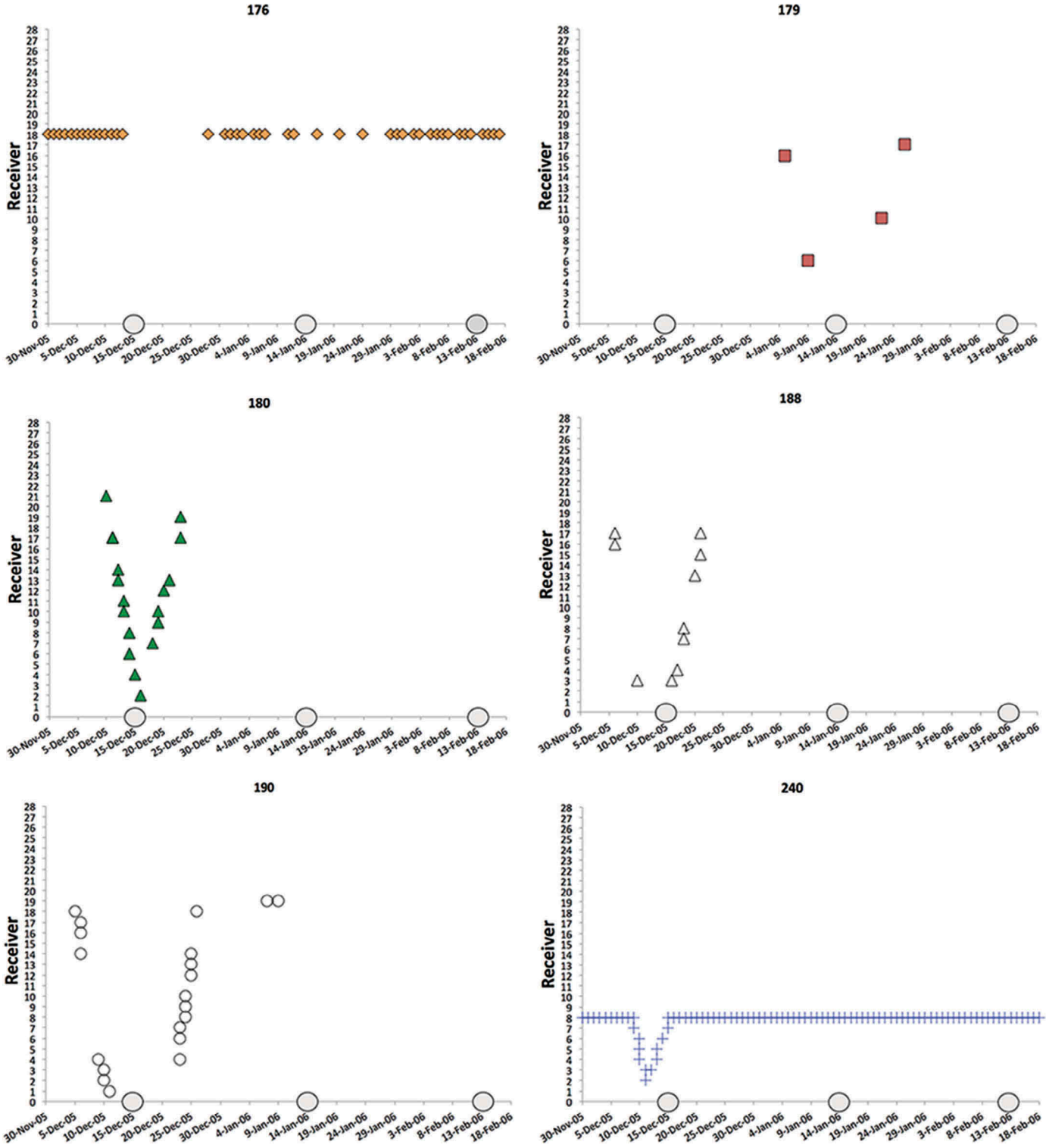


FIGURE 4. Daily positions of individual Nassau Grouper migrating during the winter of 2005–2006. The *x*-axis shows the date, with full moons denoted by shaded circles; the *y*-axis shows the receiver number, roughly from south to north. Only fish that migrated are shown.

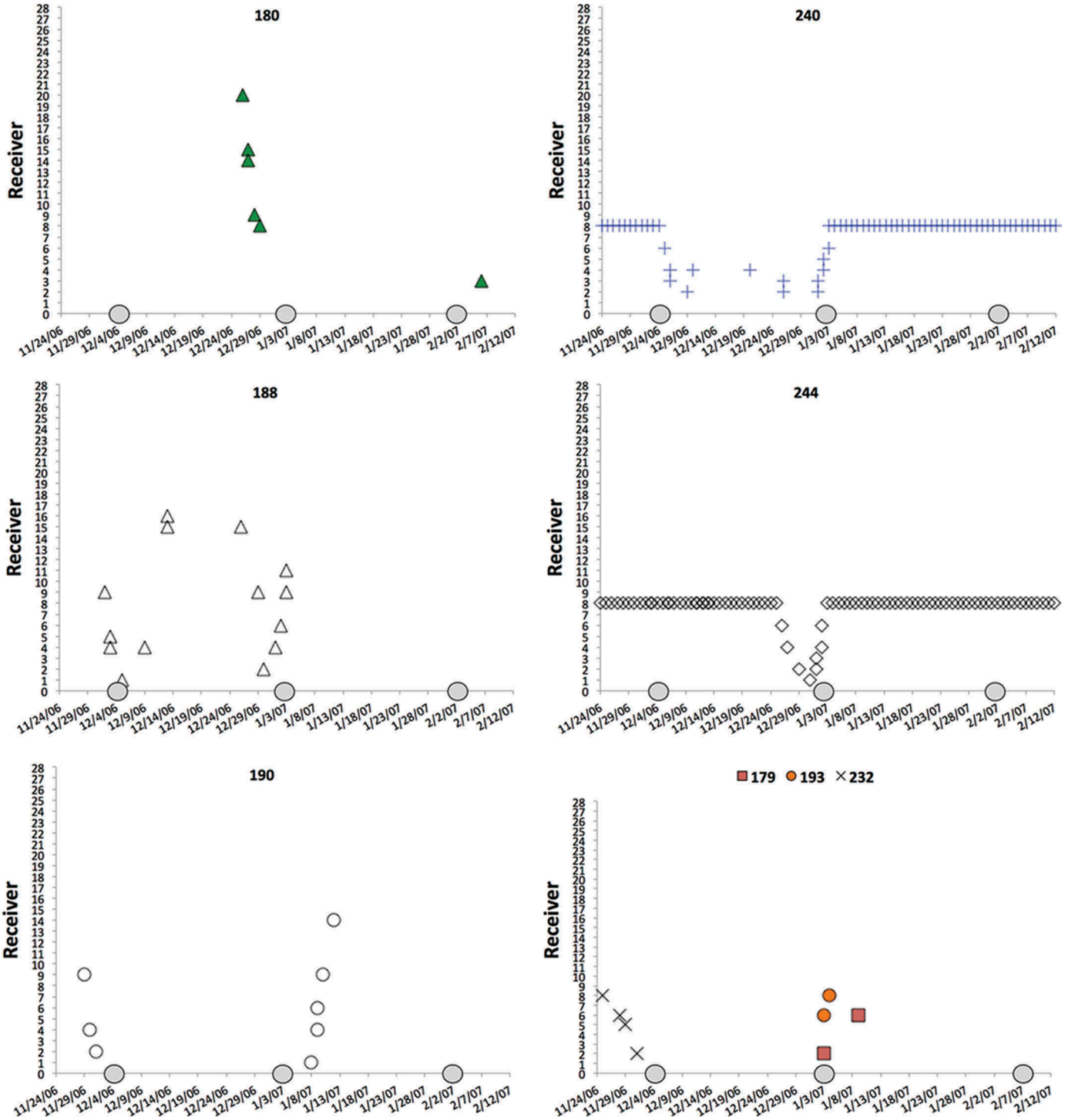


FIGURE 5. Daily positions of individual Nassau Grouper migrating during the winter of 2006–2007. The *x*-axis shows the date, with full moons denoted by shaded circles; the *y*-axis shows the receiver number, roughly from south to north. Three fish that were each only detected five times or less are grouped on one graph. Only fish that migrated are shown.

(fish 235) moved southward through the array and remained outside of the array for over 50 d before returning. Fish 188, an experienced fish, migrated at least 14 d prior to the December full-moon period (Figure 6), the fourth consecutive year in which it was detected as migrating around the December full moon. Fish 193 was only detected once away from its release site around the December full moon (Figure 6).

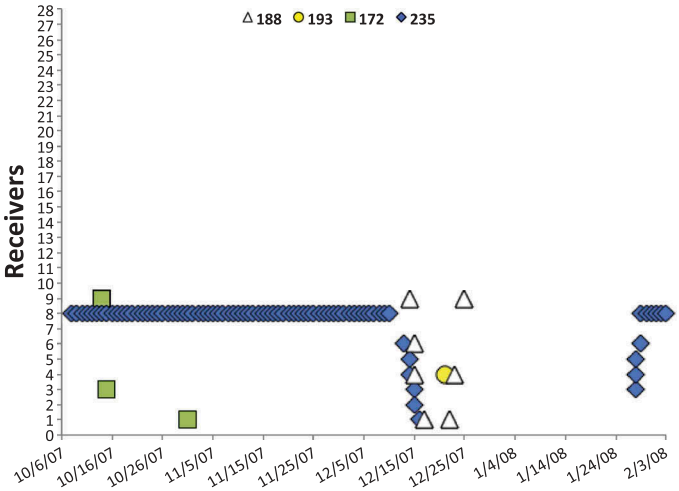


FIGURE 6. Daily positions of Nassau Grouper migrating during the winter of 2007–2008. The *x*-axis shows the date, with full moons denoted by shaded circles; the *y*-axis shows the receiver number, roughly from south to north. Only fish that migrated are shown.

## Migration Speeds

First-time migrations were detected for fish 172 (to the spawning site only), 193 (return from the spawning site only), 232, 235, and 244. When comparing migration speeds for experienced individuals (fish 177, 179, 180, 188, 190, and 240) and those migrating for the first time, there was a significant interaction between the migration speed during outgoing versus return migrations and experience (ANOVA: $P = 0.004$). The speed of fish undergoing first-time migrations to spawning sites was nearly one-third that of experienced fish (ANOVA: $P < 0.001$; Figure 7). First-time migrants and experienced fish did not differ in migration speed during return trips, with both migrating at speeds similar to the outgoing speed of experienced fish (Figure 7).

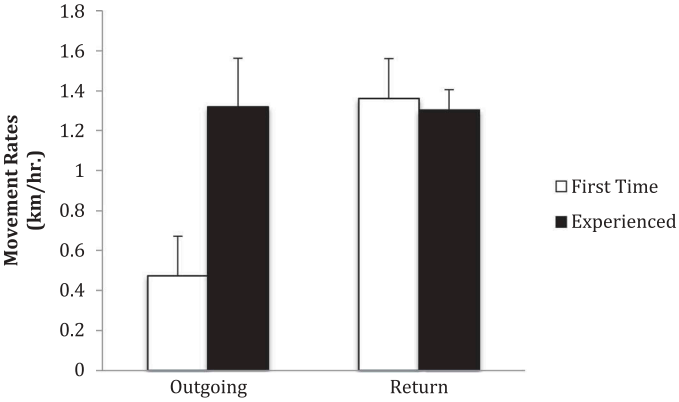


FIGURE 7. Mean (+SE) swimming speed of Nassau Grouper making their first migration or repeated migrations (i.e., experienced fish) to and from spawning sites during 2005–2007.

## DISCUSSION

After determining that Nassau Grouper swim synchronously along the shelf margin as they migrate from a large marine protected area to spawning aggregations, we used a telemetry array extending a distance of 280 km through the central Bahamas to further study their migration behavior. We documented repeated Nassau Grouper spawning migrations over multiple years, determined that fish originating from different areas of the Exuma Cays migrate to the same spawning sites, and estimated the size at first migration in The Bahamas. Spawning sites used by Nassau Grouper were often not the closest areas to the capture and release sites. We also found that fish migrating for the first time did so at a slower speed than experienced fish. Some of our findings are consistent with previous studies; however, Nassau Grouper from The Bahamas appear to have different habits than those studied in other regions of the Caribbean, and therefore our results have important management implications.

Frequent detections of tagged fish throughout the year by receivers that were located within 300 m of an individual's release location were consistent with reported home ranges of adult Nassau Grouper in the ECLSP, averaging 18,305 $m^2$ (Bolden 2001). Individual fish also showed high site fidelity to both spawning sites and home reefs, similar to studies of Nassau Grouper elsewhere (Semmens et al. 2006; Starr et al. 2007). Although some fish were only detected away from their release sites, this may be attributable to (1) being tagged outside of the receiver's range (e.g., fish 193 and 179) or (2) a weakening signal from the transmitters of fish that were tracked over multiple years (e.g., fish 188).

Spatial and temporal patterns of spawning migrations varied from those reported in other studies. In contrast to Glover's Reef, where all tagged Nassau Grouper were tracked to a single spawning site (Starr et al. 2007), Nassau Grouper in The Bahamas were tracked to two spawning sites with receivers, and the movement of several fish past those two sites and outside of the receiver array—as well as a single individual (fish 176) leaving the ECLSP array for over a week—suggests that fish from Exuma Cays used at least two additional spawning sites. Even greater coverage by receivers over an area roughly double that of our array may be necessary to track all Nassau Grouper to potential spawning sites (Figure 1).

The distance over which fish migrated to a spawning aggregation was also greater in The Bahamas than the 20–30-km migration distance reported elsewhere (Semmens et al. 2006; Starr et al. 2007). In our study, Nassau Grouper were tracked as they migrated to aggregations up to 200 km from their release locations (Table 2). The present study was not designed to test hypotheses related to spawning site selection by individuals, but it is worth noting that most of the tagged fish did not migrate to the nearest reported spawning site, often moving past confirmed spawning sites on migrations. The shortest migration detected was 70 km, and

TABLE 2. Summary of key spatial and temporal results for Nassau Grouper migrating to spawning aggregations in The Bahamas (ECLSP = Exuma Cays Land and Sea Park; LSI = Lee Stocking Island).

| Variable | ECLSP | LSI | 2004–2005 | 2005–2006 | 2006–2007 | 2007–2008 |
|---|---|---|---|---|---|---|
| **Spatial results** | | | | | | |
| Migrated to | | | | | | |
| Receiver 2 (Hail Mary) (*n*) | 1 (190 km) | 1 (60 km) | | | | |
| Receiver 1 (North Point) (*n*) | 1 (160 km) | 1 (70 km) | | | | |
| Out of range (*n*) | 3 (>170 km) | 2 (>70 km) | | | | |
| Unknown (*n*) | 2 | 1 | | | | |
| **Temporal results** | | | | | | |
| Month of migration | | | | | | |
| Oct (*n*) | | | 0 | 0 | 0 | 1 |
| Dec (*n*) | | | 3 | 6 | 5 | 0 |
| Jan (*n*) | | | 0 | 1 | 3 | 2 |
| Feb (*n*) | | | 0 | 0 | 0 | 0 |
| Number of migrations in the season | | | | | | |
| One (*n*) | | | 3 | 7 | 8 | 3 |
| Two (*n*) | | | 0 | 0 | 1 | 0 |
| Duration away from the release site (d) | | | | | | |
| *n* | | | 3 | 6 | 6 | 2 |
| $\bar{x}$ | | | 18.3 | 12.3 | 30.3 | 30.5 |
| SE | | | 2.9 | 4.4 | 12.7 | 19.5 |

the maximum migration distance outside of the array was likely to have exceeded 200 km. The greater distance traveled in our study is likely a function of the larger shelf area for the Great Bahama Bank than for Glover's Reef or Little Cayman, suggesting within-species plasticity in migratory behavior to adapt to local conditions. Such plasticity in spawning migrations within a species has also been documented for fish in other systems (e.g., Lucas et al. 2001).

The duration away from the release sites varied annually in this study, ranging from 12 to 30 d. Years of shorter average duration away were similar to observations of Nassau Grouper in Belize (Starr et al. 2007), but the patterns of transit time to and from an aggregation versus the time spent at an aggregation were opposite. The time spent at an aggregation averaged 11.6 d in Belize, with only 1–2 d in transit between home reefs and spawning sites (Starr et al. 2007), whereas fish in The Bahamas typically only spent 1–2 d at spawning sites and were in transit for 1–3 weeks. The reduced time spent by Nassau Grouper at spawning sites in The Bahamas may be attributable to the necessity of traveling two to six times greater distances than the Nassau Grouper in Belize. Energetic requirements associated with swimming greater distances may have also resulted in slower migration speeds in The Bahamas (1.3 km/h) compared with Belize (1.9 km/h; Starr et al. 2007).

Annual variability in the duration away from release sites does not appear to be due to more time spent at migration sites or in transit but rather to the time between monthly full moons, when fish remained at large but were not detected at spawning sites or release sites (e.g., fish 240; Figure 3). The 2006–2007 spawning year, when an extended duration away was common, was also the year in which a single fish (188) was observed to make two migrations during the spawning season—the only time this fish was observed to do so over the 4 years it was tracked. The rare occurrence of multiple spawning migrations by individuals in The Bahamas greatly contrasts with spawning migration studies from Belize and the Cayman Islands, where 50–60% of Nassau Grouper made multiple migrations in a single spawning season and where fish made up to four monthly spawning migrations per year (Semmens et al. 2006; Starr et al. 2007). The predominance of single migrations for individuals in The Bahamas may be another result of longer migration distances.

In 2004–2005 and 2005–2006, there was a consistency of migrations around the second full moon after the autumnal equinox (December), with only one fish migrating around the third full moon (January). Prolonged durations away, delayed migrations, and multiple migrations during the 2006–2007 and 2007–2008 spawning seasons resulted in the majority of fish being away from home reefs during the third full moon after the equinox (January 2007; December 2008). Years in which spawning may have been delayed were ones when the second full moon after the equinox fell early in the spawning season at the beginning of December (2006) or at the end of

November (2007). Colin (1992) suggested that Nassau Grouper in The Bahamas spawn during the winter full-moon period, when water temperatures reach approximately 25°C. Warmer water temperatures may have contributed to a delay in spawning during years when the lunar cycle resulted in full moons early in the spawning season. In December 2006, for example, water temperatures averaged over 26°C during the weeks immediately before and after the full moon, potentially causing a delay in spawning (National Oceanic and Atmospheric Administration, Office of Satellite and Product Operations: www.ospo.noaa.gov/data/cb/TS_vs/vs_ts_LeeStockingIsland_Bahamas.txt). These patterns provide evidence that both temperature and lunar phase may influence spawn timing for Nassau Grouper.

Although there was variability in the month and duration of migrations, the timing of the arrival at spawning sites relative to the moon phase was consistent over time in The Bahamas but differed from the results of other studies conducted throughout the Caribbean. In other locations, the average arrival time of fish was after the full moon (Starr et al. 2007), and peak reproductive activity occurred 1–8 d after the full moon (Tucker et al. 1993; Whaylen et al. 2004, 2006; Archer et al. 2012; Schärer et al. 2012). In contrast, we detected fish at spawning sites from 5 d before to 2 d after the full moon, with most arriving 2–3 d before the full moon. This timing corresponds to peak densities of Nassau Grouper in visual surveys of the Hail Mary and North Point spawning sites from 2010 to 2014 (C. P. Dahlgren, personal observation). Arrival date may have shown some variability in relation to distance traveled, as fish traveling shorter distances arrived and departed earlier than those traveling greater distances, leading to little co-occurrence at spawning sites even when fish from different areas migrated to the same spawning site.

First-time migrators exhibited slower swimming speeds to spawning aggregations but faster return swimming speeds that were similar to those of experienced fish; these results are consistent with the hypothesis that spawning migration behavior has a learned component. Courtship sound production by experienced fish at spawning sites may contribute as a mechanism for attracting first-time fish to specific spawning locations (Rowell et al. 2015). In contrast to this evidence, however, our finding of a fish making its first spawning migration in October 2007, 2 months before any other observed spawning migration by an experienced fish during any year of the study, suggests that factors other than attraction by conspecifics could also influence spawning migrations.

Fish were first observed to migrate to spawning sites at a size of 54 cm TL or greater, which corresponds to the sizes of fish observed at spawning aggregations off Long Island, The Bahamas (C. P. Dahlgren, personal observation), and is greater than (1) the 44–47 cm TL at which Nassau Grouper have first been observed to reach maturity (Sadovy and Colin 1995) and (2) the minimum legal harvest size of 1.36 kg, or approximately 44 cm TL. Increasing the minimum size limit to 54 cm TL or larger would allow more fish to make at least one migration to spawn before entering the fishery.

Results highlighting differences in Nassau Grouper spawning migration patterns between locations in the Caribbean and interannual variability within The Bahamas have important management implications and highlight the need to understand local population dynamics for this species. Annual reproductive activity for an individual Nassau Grouper in The Bahamas is focused on a 1–2-d period, which may make the Bahamian populations even more vulnerable to exploitation than Nassau Grouper populations from other parts of the Caribbean that may spawn several times annually. Furthermore, longer migrations and longer durations away from home reefs during spawning migrations have important implications for spatial management. Although marine protected areas where fishing is prohibited (e.g., ECLSP) may afford important protection to the Nassau Grouper residing within them, our study documents how common it is for fish to migrate out of the ECLSP, as all but one fish greater than 54 cm were detected outside the marine protected area during the spawning season. Furthermore, the distances traveled during spawning migrations were larger than the marine protected areas in the region, making fish vulnerable to fishing during migrations.

Protecting fish at spawning times is essential to protect and rebuild populations of Nassau Grouper (Sadovy de Mitcheson 2013). Protection of individual spawning sites at the time of spawning (or year-round if those sites are used by multiple species) has become a common strategy and was previously used in The Bahamas for some spawning sites. However, results show that fish were at spawning sites for only 1 or 2 d despite being away from their home range for 12–30 d on average. Only protecting at spawning sites may relieve some fishing pressure but still exposes the fish to capture during their prolonged migrations. As such, a complete ban on fishing for Nassau Grouper in The Bahamas during the entire time that fish may be migrating to spawn—from at least the last week of November through February—is necessary, and such a ban would have protected all but one fish in our study. In other parts of The Bahamas, however, different spawning patterns may be prevalent (K. Stump, Shedd Aquarium, personal communication), which may affect the timing of a closed season. Furthermore, as climate change causes ocean temperatures to warm, the timing and duration of spawning migrations may change, which may necessitate changes to the closed season.

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