



Nassau grouper migration patterns during full moon suggest collapsed historic fish spawning aggregation and evidence of an undocumented aggregation

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ABSTRACT.—Many fish species migrate to form fish spawning aggregations. The temporal and spatial predictability of these migrations and spawning aggregation locations makes species vulnerable to overfishing, as the majority of an adult population within a large region may be harvested quickly with minimal effort. Historically, the Nassau grouper, *Epinephelus striatus* (Bloch, 1792), was an important fishery species throughout its range, but due to spawning aggregation overfishing, it is now rare in many reef ecosystems. In The Bahamas, stocks continue to decline despite the implementation of spawning aggregation protections. While more Nassau grouper spawning aggregations have been reported in The Bahamas than any other country, very few have been validated, and the dynamics of spawning migrations to and from these sites is poorly understood. Here, we used acoustic telemetry to describe, for the first time, Nassau grouper migrations along Andros Island, The Bahamas, which is bordered by one of the longest barrier reefs in the world. We report the likely extirpation of a historically important spawning aggregation and suggest Nassau grouper are migrating to a previously undocumented spawning location. Fish migrated in groups during the January 2015 full moon along the barrier reef shelf edge traveling roundtrip distances of 71.5–260.3 km [\bar{x} = 164.5 (SD 65.7) km, n = 9]. These results are critical to assess the efficacy of current management strategies in The Bahamas. Thus far, all known spawning aggregations have been reported to the scientific community by fishers. Data from our study, however, suggest the presence of a potential spawning aggregation informed by passive telemetry and warrants further investigation.

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In marine ecosystems, the formation of fish spawning aggregations—transient gatherings of a large number of individuals for reproductive purposes—is a widespread reproductive strategy (Domeier 2012). While the formation of spawning aggregations is reproductively advantageous for species distributed in reef habitats at low densities across large spatial scales, the behavior makes them particularly

vulnerable to overfishing (Coleman et al. 1996). Indeed, predictable aggregations of commercially-fished species allow fishers to maximize catch and profit with minimal effort (Sadovy and Domeier 2005, Erisman et al. 2012).

The ecological effects of overfishing spawning aggregations can be significant given that for many species, spawning aggregations can attract individuals from across broad regions (Sadovy de Mitcheson and Erisman 2012). Furthermore, the ostensible benefits for fish inhabiting no-take marine protected areas are negated if species reliant on spawning aggregations are fished outside protected area boundaries during migrations (Bolden 2000, Sadovy de Mitcheson and Erisman 2012). Overfishing spawning aggregations, therefore, can have profound impacts at local and regional scales across multiple jurisdictions and management regimes (Erisman et al. 2012, Green et al. 2015).

One of the best known examples of a fishery collapse from spawning aggregation overfishing is the Nassau grouper, *Epinephelus striatus* (Bloch, 1792), which was once one of the most important fishery species in the wider Caribbean (Sadovy and Eklund 1999). However, due to heavy exploitation, it is now rare in many coral reef ecosystems throughout its native range (Sadovy de Mitcheson et al. 2008), and the majority of its spawning aggregations no longer form (Sadovy and Eklund 1999, Sadovy de Mitcheson et al. 2013). As such, the Nassau grouper is classified as endangered by the International Union for the Conservation of Nature (IUCN) (Cornish and Eklund 2003) and is listed as threatened under the US Endangered Species Act (81 FR 42268, June 29, 2016).

Nassau grouper are important ecologically as predators on reef fish and invertebrates (e.g., Eggleston et al. 1997, Mumby et al. 2006, 2011), and are also economically and culturally significant. For example, Bahamians have fished grouper for centuries, and the fishery supports thousands of livelihoods, saturating the social fabric of the country (Cushion and Sullivan-Sealey 2008). Landings of Nassau grouper in The Bahamas were valued in excess of US \$1.08 million in 2014 and represent a substantial contribution to revenue generated by fisheries (Sherman et al. 2016). The Bahamas is one of the few remaining countries where Nassau grouper populations still support many active spawning aggregations, but declines in abundance even within marine reserves, and the collapse of historical spawning aggregations have been noted (Sadovy and Eklund 1999, Sherman et al. 2016; C Dahlgren, Bahamas National Trust, unpubl data). Approximately 40 Nassau grouper spawning aggregations are reported in The Bahamas, elucidated through anecdotal accounts and local knowledge (Sadovy and Eklund 1999, Sherman et al. 2016). Very few, however, have been validated or studied scientifically, and thus the historic and current status of Nassau grouper spawning aggregations in The Bahamas is largely unknown.

Research focused on Nassau grouper spawning migrations has been limited in geographic scope throughout The Bahamas, with a narrow understanding of migrations and spawning aggregations from Andros Island. Andros, the largest island in The Bahamas, is bordered along the east coast by one of the longest barrier reefs in the world (Lopez et al. 2000), and is reported to support two Nassau grouper spawning aggregations. One spawning aggregation is reported off South Andros Island at Tinker Rocks, but no stock or migration information exists for this location except that fishing occurred historically (anonymous fisher, South Andros, pers comm). Two studies attempted to describe spawning stock sizes at the other Nassau grouper spawning aggregation located at High Cay, Andros (Fig. 1). A 1999–2001

hydroacoustic survey resulted in spawning stock size estimates between 9300 and 12,500 individuals (Ehrhardt and Deleveau 2007). Those estimates, however, were not empirically validated in situ and starkly contrasted to diver surveys of the same area at the same time, which reported approximately 500 Nassau grouper during the January 1999 spawning period (Ray et al. 2000). Anecdotal accounts from local fishers also support the lower abundance estimates from the early 2000s (Park Warden, Bahamas National Trust, pers comm; anonymous fisher, South Andros, pers comm). There is no current information regarding stock assessments or migration patterns for the spawning aggregation at High Cay, Andros Island.

The lack of information concerning current stock assessments and associated migratory behavior at any Andros spawning aggregation is unfortunate, especially given that the Bahamas Department of Marine Resources implemented a targeted fishing closure of the High Cay aggregation for four 5-d periods around the full moons in November through February starting in 1998 (Ray et al. 2000). Since 2004, a national seasonal closure of Nassau grouper spawning aggregations has been implemented for up to 3 mo during the spawning season, though exact dates were announced annually and subjected to change. More recently in October 2015, The Fisheries Resources (Jurisdiction and Conservation) Act (<http://laws.bahamas.gov.bs>) was amended to include a fixed seasonal closure of the Nassau grouper fishery, making it illegal to take, land, process or sell Nassau grouper during the spawning season from 1 December through 28 February (Bahamas Ministry of Agriculture and Fisheries 2015). A similar strategy has been implemented by the Cayman Islands Department of the Environment, and several studies suggest that such management measures are effective for stock recovery and stability (e.g., Whaylen et al. 2007). However, in The Bahamas, Nassau grouper populations continue to decline since spawning aggregation protections were implemented (Cheung et al. 2013, Sherman et al. 2016), underscoring the need to better understand the extent, variance, and current state of spawning migrations within the country.

Revisiting the High Cay spawning aggregation from Andros Island offers an opportunity to assess the efficacy of a closed season management strategy since this aggregation was the first targeted spawning aggregation for closed-season management in 1998. The extensive reef system off Andros Island also offers the opportunity to study migratory behavior across a large system to better understand the ecology of the species and apply data to management. In the present study, we used diver surveys and acoustic telemetry to assess the current state of the High Cay spawning aggregation, and describe the migratory behavior of Nassau grouper within the Andros Island barrier reef system during a winter spawning period. Our specific objectives were to: (1) assess the current state of the High Cay Nassau grouper spawning aggregation, (2) describe timing of migrations with respect to the full moon, (3) determine if Nassau grouper migration pathways follow the Andros barrier reef shelf edge, and (4) estimate distance traveled and speed during migrations.

METHODS

SITE DESCRIPTION.—In total, 16 adult Nassau grouper were tracked passively from December 2014 through March 2015 along the approximately 217 km long barrier reef running parallel to the east coast of Andros Island, The Bahamas. The reef edge is characterized by steep drop-offs and dramatic underwater cliffs at depths from

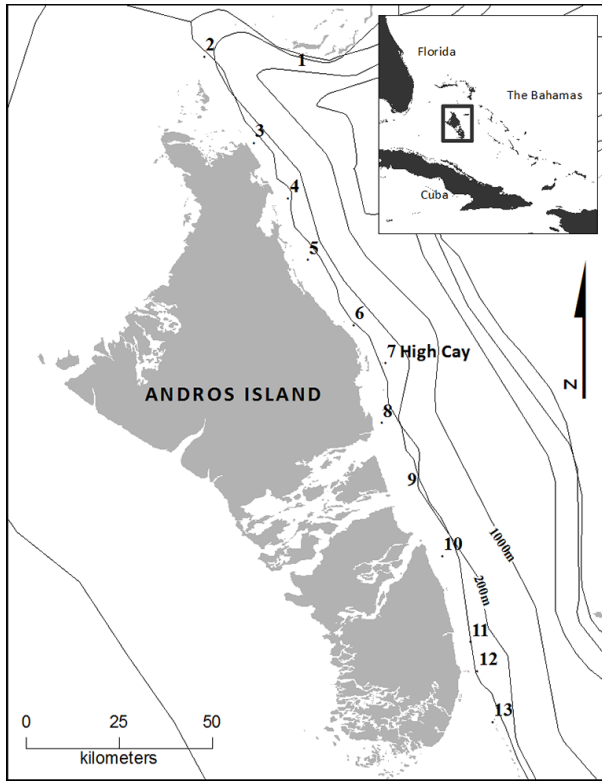


Figure 1. Map of study area (Andros, The Bahamas). Numbers indicate locations of the 13 acoustic receivers deployed along the barrier reef shelf edge. The two historically reported Nassau Grouper spawning aggregations, High Cay and Tinker Rocks, are located at receivers 7 and 11, respectively.

20–35 m before sloping steeply into the Tongue of the Ocean, a deep (1500–1800 m) cul-de-sac-shaped trench (Buchan 2000). We focused our fish capture efforts at the historical spawning aggregation reported near High Cay, a rocky outcrop about 3 km east of Andros (Fig. 1). The aggregation has been reported to form east of High Cay at depths of 25–45 m, along the barrier reef shelf edge (Ray et al. 2000). It is worth noting that a second aggregation site with similar bathymetric features is reported farther south near Tinker Rocks, though there is no scientific information regarding the past or present status of Nassau grouper spawning stocks at that area.

ACOUSTIC ARRAY.—Prior to deploying the acoustic array, the detection range for receivers was assessed at a representative reef site. During range testing, a receiver paired with a range test tag was deployed, and subsequent receivers were spaced at increasing distances from the first receiver and tag from 100 to 325 m away. Receivers were uploaded after 24 hrs. The number of range test tag detections on each receiver was compared to the number of detections by the receiver paired with the range test tag and reported as percent detections (Table 1).

Based on previous research demonstrating that Nassau grouper spawning migrations occur along shelf edges (Bolden 2000, Dahlgren et al. 2016a), an array of 13 Vemco™ VR2W acoustic monitoring receivers (Vemco, Ltd., Nova Scotia, Canada), was placed along the Andros barrier reef shelf edge in April 2014 (Fig. 1). Placement

Table 1. Results of VR2W acoustic receiver range testing at a representative reef site in The Bahamas.

Distance (m)	Detections (%)	Depth (m)
0	100.0	24.1
100	98.8	18.6
150	96.4	22.9
175	53.5	23.5
200	50.3	26.2
225	12.6	27.1
250	4.1	22.9
275	2.0	23.5
300	0.2	26.2
325	0.2	26.2

along the reef edge was predicted to detect any Nassau grouper migrating to and from the High Cay spawning aggregation. Receivers in the Andros array were spaced approximately 15 km apart, and the array extended from Chub Cay, Berry Islands, in the north to Grassy Cay, Andros, in the south (Fig. 1). Each VR2W was oriented facing upward, attached to a line approximately 3 m above the substrate, and each rig was anchored in place by two concrete blocks (Fig. 2). Floatation was provided by up to three styrofoam floats (depending on depth) and receivers were attached to the mooring line with four plastic ties (Fig. 2). Once a general deployment location was chosen, divers used a lift bag to slowly lower each rig onto an optimal location to minimize signal interference from nearby reef structure. Receivers remained in place through March 2015 when they were downloaded and redeployed for continued detection of Nassau grouper migrations during the 2015–2016 spawning season.

FISH TAGGING.—Before deploying baited fish traps in December 2014, the research team dove at the reported High Cay spawning aggregation to confirm the presence of the aggregation. For 2 d before the full moon, divers reported seeing no Nassau grouper aggregation at the site described by Ray et al. (2000). This timeframe is consistent with peak numbers of aggregating fish at other sites in The Bahamas (Dahlgren et al. 2016a). Because exact spawning aggregation locations are known to shift slightly (Colin 1992, 2012), rotating teams of divers searched for aggregating Nassau grouper along the shelf edge (approximately 25–35 m depth) from 1 km south to 1 km north of the reported site.

To capture fish for tagging, baited fish traps were deployed within 100 m of the reported High Cay spawning aggregation. Trapped Nassau grouper were brought slowly to the surface to minimize barotrauma, and fish were kept in a 6745 L aerated, open-circulation live well on board the research vessel before processing. Each fish was transferred to a 100-L tricaine methanesulfonate (MS-222, 75 ppm) buffered seawater bath for anesthesia prior to transmitter surgery. While in the MS-222 bath, standard length (SL) and total length (TL) were recorded to the nearest 0.1 cm. Once anesthetized, each fish was weighed to the nearest 0.1 kg and then transferred to a 144-L aerated seawater bath for transmitter surgery. Each fish was held in a sling in the bath, ventral side up, and a small (2 cm) incision was made along the centerline, posterior to the pelvic fins. A Vemco™ V13 transmitter (13 × 36 mm, 6.5 g in water; Vemco, Ltd., Nova Scotia, Canada) with an estimated life span of 622 d was inserted

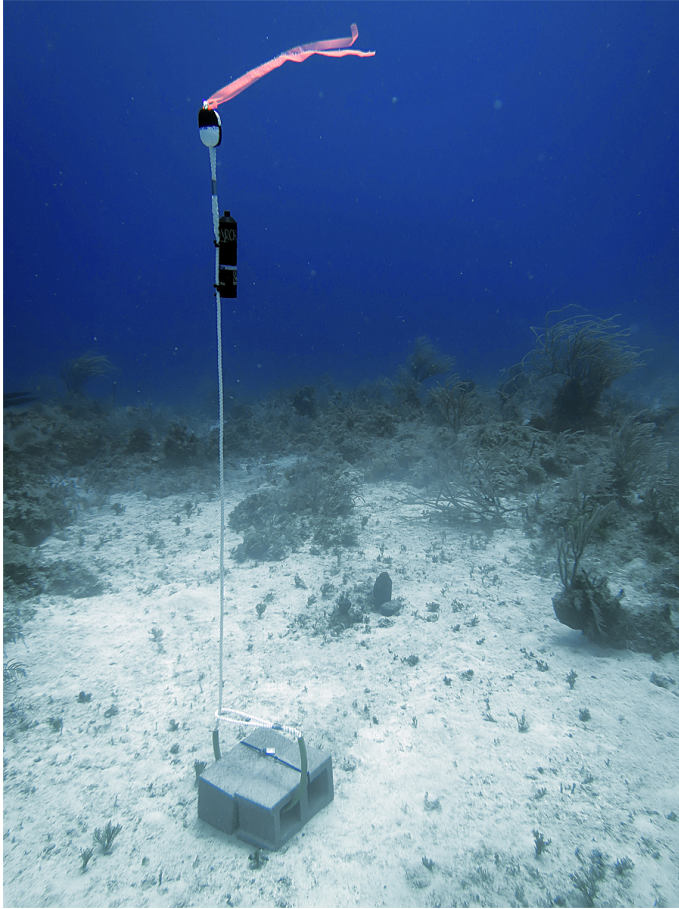


Figure 2. VR2W acoustic receiver deployed along the barrier reef shelf edge at approximately 25 m depth.

into the body cavity, and the incision closed with two to three cruciate sutures using Monosorb™ 3-0 absorbable monofilament. Following surgery, fish were transferred back to the 6745-L aerated, open-circulation live well to recover for 30–45 min prior to release. Once an individual maintained equilibrium and exhibited normal swimming behaviors, it was transferred to a mesh bag, brought to its original capture site, and released at depth by divers who monitored each individual for at least 1 min to ensure the fish continued to exhibit normal swimming behavior and was able to safely reach refuge.

RESULTS

MIGRATION PATHWAY AND TIMING.—Despite an exhaustive search, dive teams did not encounter an aggregation at the High Cay spawning aggregation during the full moon period of December 2014, when fish would be expected to arrive several days prior to the full moon based on other studies in The Bahamas (e.g., Colin 1992). Nevertheless, within 2 d prior to the full moon, 26 adult Nassau grouper [\bar{x} = 62.7 (SD 3.7) cm TL] were captured in baited traps deployed within ≤ 100 m of the reported

Table 2. Summary of Nassau grouper, *Epinephelus striatus*, tagged at High Cay in December 2014. TL = total length. Number of detections indicates the total number of times an individual was detected across all receivers in the array during the January 2015 migration period. Northernmost detection corresponds to receiver numbers in Figure 1. Minimum distance traveled within the array is calculated from an individual's full set of detections and known distances between receivers.

Fish ID	TL (cm)	Number of detections	January 2015 migration	Northernmost detection	Swimming speed (km hr ⁻¹)	Minimum distance traveled within array (km)
152	66.0	11	North	4	1.91	103.9
157	59.2	15	North	4	1.08	105.6
159	62.0	11	North	4	1.52	103.9
161	64.1	32	North	2	2.02	260.3
162	59.0	15	North	2	1.30	154.7
164	63.0	6	North	1	1.30	95.2
166	61.4	15	North	3	1.73	208.0
170	67.5	25	North	3	2.34	208.0
174	63.0	10	North	2	2.02	241.3
192	63.0	8	South	–	1.67	71.5
151	61.0	17	No pattern	–	–	–
155	65.0	10	No pattern	–	–	–
153	52.5	0	Not detected	–	–	–
163	66.0	0	Not detected	–	–	–
168	63.0	0	Not detected	–	–	–
175	67.5	0	Not detected	–	–	–

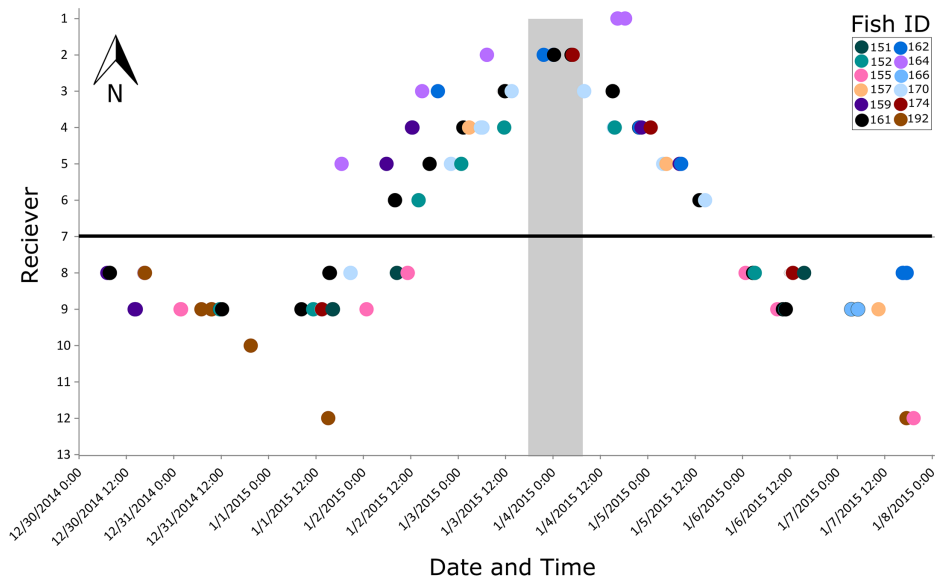


Figure 3. Detections in chronological order on each receiver for all grouper detected within the array during the migration period (4 d before to 4 d after the full moon; $n = 12$). Receivers are in order of increasing latitude (south to north), and numbers correspond to receiver numbers in Figure 1. The solid line along receiver 7 represents the location of the reported High Cay spawning aggregation. There are no data from this station because the receiver was lost. Note that distances between receivers are not uniform (see Fig. 1 for relative locations). The shaded area indicates the night of the January 2015 full moon.

spawning aggregation. Of those, 16 fish ranging in size from 52.5 to 67.5 cm TL [$\bar{x} = 62.7$ (SD 3.7) cm TL] were surgically implanted with acoustic transmitters on 6 and 7 December, 2014 (Table 2). Following their release, none of the 16 grouper were detected for the remainder of the expected December full moon migratory period. However, 12 were detected moving north and south along the array during the expected full moon migratory period the following month in January 2015 (Table 2). Nine showed northward migrations, one made a southward journey, and two were detected, but exhibited no clear movement pattern (and thus removed from further analysis). As prior range testing produced reliable VR2W detection distances of up to 200 m (Table 1), Nassau grouper migratory movements were confirmed to occur along the edge of the Andros barrier reef tract. Detections for these 12 fish were synchronous with the full moon phase. That is, all of the grouper moving north ($n = 9$) began their directed northward movements 3 d before the night of the full moon, and all were detected at their northernmost point on the day of ($n = 8$) or the day after ($n = 1$) the full moon (Fig. 3). All grouper were once again detected at their southernmost point by 2 d after the full moon (Fig. 3). During northward and southward migrations, grouper were often detected within minutes of each other, suggesting synchronized group migrations to and from their destination along the barrier reef shelf edge.

Although nearly two thirds of all detections were recorded during the day, multiple detections (per night) over nine nights before and after the morning and evening astronomical twilight (approximately 05:30 and 19:00 hrs, respectively) were recorded for seven grouper. These detections (2–4 per fish) were limited to one receiver for

each fish. Six multiple nighttime detections (from five fish) were recorded over a 3–8 min time period and appeared consistent with fish moving past the receiver. Three multiple nighttime detections (from three fish) were recorded over a 1 hr 37 min to 4 hrs 23 min time period and may suggest a slowing or stopping individual. These prolonged periods between nighttime detections were recorded by two fish (161 and 162) on the night of the January 2015 full moon at receiver 2 in the north (Fig. 3), and the third fish (170) was detected over a prolonged period three nights after the full moon at receiver 9 in the south (Fig. 3).

When receivers were retrieved in March 2015, the VR2W at the reported High Cay spawning aggregation was missing. However, of the remaining 12 receivers along the barrier reef shelf, 10 detected tagged Nassau grouper during the spawning period. Many of the detections occurred sequentially in time along neighboring receivers, showing south to north movements (Fig. 3) in advance of, and just after, the January 2015 full moon. Surprisingly, however, these trajectories indicated that fish did not stop for an extended time near High Cay. Rather, all grouper migrating northward bypassed High Cay and continued toward the north end of Andros before the full moon and south toward central island latitudes after the night of the full moon (Fig. 3).

MIGRATION SPEED AND DISTANCE.—Of the 12 grouper detected within the array during the January 2015 migration, 10 were detected on sequential receivers, allowing for calculation of distance traveled within the array and migration speed (e.g., Starr et al. 2007, Rowell et al. 2015). The nine grouper migrating northward did so at an average speed of 1.69 (SD 0.41) km hr⁻¹. The one grouper traveling southward moved at 1.67 km hr⁻¹. One-way northward migrators averaged 104.0 (SD 18.7) km along the barrier reef shelf edge. Minimum roundtrip distances tracked within the array by northward migrating fish ranged from 95.2 to 260.3 km [\bar{x} = 164.5 (SD 65.7) km, n = 9]. The southward migrating fish traveled a minimum distance of 71.5 km.

DISCUSSION

Here, we provide evidence of a spawning aggregation collapse, as well as the first description of Nassau grouper spawning movements along the Andros barrier reef system, one of the world's largest reef tracts. Telemetry data show clear movement patterns tightly synchronized to the full moon. The likely extirpation of the historically-fished High Cay spawning aggregation is supported in part by telemetry data that demonstrate Nassau grouper migrations during the expected spawning period bypass the High Cay site en route to a more northern destination.

Despite an exhaustive search at the High Cay spawning aggregation site described both by local fishers and Ray et al. (2000), no Nassau grouper spawning aggregation was seen during the December 2014 spawning period. The diver-confirmed abundance estimate of the spawning stock size in 1999 was only 500, and the extirpation of even larger Nassau grouper spawning aggregations in a similar time span is not unprecedented in The Bahamas (Smith 1972, Colin 1992). However, adult Nassau grouper were indeed captured for the present study 1–2 d prior to the December full moon within 100 m of the reported aggregation site.

Prior to examining the telemetry data, the assumption was that dive teams missed the aggregation. However, detection data clearly demonstrate that in the following

month, grouper bypassed High Cay on northward migrations days before the night of the January full moon (Fig. 3). Potentially, the 16 grouper caught and tagged for the present study in December 2014 were all residents of the High Cay area. This is unlikely, however, as previously-collected survey data suggest extremely low densities for all *Epinephelus* spp. and *Mycteroperca* spp. in the Andros reef tract (<0.1 grouper per 100 m^2) (Dahlgren et al. 2016b). Additionally, only sexually-mature, adult Nassau grouper were captured in the baited traps. If the traps were sampling High Cay residents, we would expect to capture a range of sizes representative of the resident population instead of only adults.

In the absence of an observed spawning aggregation at High Cay, a plausible explanation for capturing so many adult Nassau grouper of sizes comparable to experienced migrators in The Bahamas (Dahlgren et al. 2016a) is that the grouper were captured during a northward migration to a different location. Telemetry data reveal that in January 2015, most grouper migrated $>100 \text{ km}$ along the barrier reef shelf edge to locations near the north end of the island (Fig. 3). Due to the loss of the receiver at High Cay, there are no detection data for that location. However, neighboring receivers to the north and south show that grouper were traveling in groups along the barrier reef shelf edge and passed through the High Cay area without slowing down.

Smith (1972) hypothesized that Nassau grouper migrated together along shelf edges to a spawning aggregation near Cat Cay in the northwest Bahamas, and suggested that there may be staging areas where grouper assemble before migrating en masse. This hypothesis was later corroborated by Colin (1992), who described migratory group movements along shelf edges south of Long Island, The Bahamas. In addition, telemetry data from the Exuma Cays to Long Island indicate that adult Nassau grouper tagged several kilometers apart passed receivers on shelf edges within hours of each other on the way to spawning aggregations in the days before the full moon (Dahlgren et al. 2016a). Similarly, telemetry data from the present study show that grouper migrating north along the Andros barrier reef shelf edge were frequently detected within minutes of each other along the length of the array. All but two of the grouper making northward migrations were first detected by receivers south of High Cay. In addition, on the return southward after the night of the full moon, all but one grouper with roundtrip detections swam past High Cay to receivers 8 and 9, 16.2 and 35.1 km south of High Cay, respectively (Fig. 3). Therefore, it is possible that baited traps used in our study captured adult Nassau grouper along their migration pathway rather than at their aggregation.

Our visual observations suggest that the historical Nassau grouper spawning aggregation at High Cay did not occur during the 2014–2015 spawning season. This is further supported by observations of fish migrating south to north along the Andros barrier reef past the High Cay location during the expected January 2015 spawning period. For several reasons, we believe the observed movement in January 2015 may represent a spawning migration to a location at the north end of the Andros barrier reef. First, none of the tagged grouper were detected at times other than during an expected migration period around the January full moon. During non-spawning periods, Nassau grouper are solitary reef dwellers with small home ranges on the order of 0.02 km^2 (Bolden 2001). If the home range of a tagged grouper overlapped with the detection range of one of our receivers, the individual would be detected over an extended time (e.g., Bolden 2000, Dahlgren et al. 2016a) and not just within 1 wk of the full moon. Second, based on a tested 200 m detection range for the receivers (Table 1),

long distance movements were confirmed to occur along the barrier reef edge. This movement is consistent with spawning migration movement pathways confirmed elsewhere in The Bahamas and in other parts of the Caribbean Sea (Bolden 2000, Starr et al. 2007, Colin 2012, Dahlgren et al. 2016a). Third, January 2015 movements were tightly synchronized to the full moon, as is characteristic of Nassau grouper spawning migrations in The Bahamas and elsewhere (e.g., Colin 2012). All grouper migrating north were first detected on their northward movement 3 d before the full moon, reached the northern peak of their journey on the full moon ($n = 8$) or the day after the full moon ($n = 1$), began southward movements immediately thereafter, and reached their southernmost detection point by 3 d after the night of the full moon (Fig. 3). Fourth, long-distance migratory fish moved in groups, a behavior that has been described previously (e.g., Colin 1992, Carter et al. 1994, Aguilar-Perera 2006). Finally, swimming speeds along the telemetry array during the migratory period averaged 1.69 (SD 0.41) km hr^{-1} , a value consistent with other telemetry studies (Starr et al. 2007, Dahlgren et al. 2016a), while six fish appeared to be migrating at night based on multiple detections made over a short nocturnal time period. Finally, nocturnal detections over a prolonged period up to 4 hrs and 23 min by two fish on the night of the full moon were recorded at receiver 2 in the northern extent of the array, suggesting that these fish stopped migrating during the time of expected spawning before making a migration back south. The relatively prolonged nocturnal detections at the southern extent of our detection range (receiver 9) for the remaining fish (170, Fig. 3) 3 d after the full moon (7 January, 2015) suggests that the fish reached the vicinity of its home range and stopped its migration.

If the grouper tagged in December 2014 and subsequently detected in January 2015 were indeed on spawning migrations during both periods, then the combination of capture and detection data suggest two migrations within one spawning season for 10 of the 16 tagged fish. Multiple migrations of individual Nassau grouper within one spawning season are common in other parts of the species' range, such as the Cayman Islands and Belize, where migratory distances between home reefs and spawning aggregations are generally 30 km or less (Semmens et al. 2006, Starr et al. 2007). In The Bahamas, however, where one-way spawning migrations have been shown to exceed 200 km (Bolden 2000, Dahlgren et al. 2016a), acoustic telemetry has revealed a rarity of multiple migrations by individual fish within one winter spawning period, with only a single fish observed to do so over several years of tracking multiple fish (Dahlgren et al. 2016a). Multiple intraseasonal migrations by an individual in The Bahamas have been recorded only when the second full moon after the autumnal equinox falls early in the spawning season (i.e., either the last week of November or first week of December) (Dahlgren et al. 2016a). When this occurs, during the first migration fish may not travel all the way to the intended spawning aggregation or return to home reefs in between full moons (Dahlgren et al. 2016a). The December 2014 full moon was indeed during the first week of the month and its timing may be related to the unexpected movement patterns. The relationship between migration distance, full moon timing, and intraseasonal migration occurrence warrants further investigation, as there may be intraspecific differences not only throughout the wider Caribbean region but also in The Bahamas.

Without in situ confirmation of an aggregation with concurrent spawning behavior, it is impossible to state with certainty that the January 2015 telemetry data reveal a previously unknown spawning aggregation in the northern Andros barrier reef,

or whether the observed migration is a response to the collapse of the historical High Cay spawning aggregation and subsequent exploratory movements in search of a non-existent spawning aggregation. The mechanisms by which fish learn migration routes and spawning aggregation locations are not fully understood. Some suggest learning through experienced migrators may play a key role, including sound production by experienced migrators guiding first-time spawners to spawning aggregations (e.g., Schärer et al. 2012, Rowell et al. 2015, but see Bernard et al. 2016). The consequences of harvesting the majority of adults from a spawning aggregation may lead to a dearth of experienced individuals to lead first-time cohorts (Sadovy de Mitcheson and Erisman 2012). Overharvest of adult Nassau grouper at High Cay, for example, could not only result in the extirpation of a season's spawning stock, but also prevent future migrators from learning both the pathway and destination. Recent evidence suggests, however, that aggregation recovery is possible. The US Virgin Islands, which experienced the loss of a Nassau grouper spawning aggregation due to overfishing, has experienced a slow reappearance of aggregations that may be the result of Nassau grouper mimicking the migration of yellowfin grouper, *Mycteroperca venenosa* (Linnaeus, 1758) (Nemeth et al. 2006, Kadison et al. 2009, Rowell et al. 2015). Therefore, if Nassau grouper are still in a region following the loss of a spawning aggregation, aggregation recovery may be possible at alternate locations.

Our results suggest both the collapse of a known spawning aggregation despite seasonal protection of the site, as well as a potentially unrecorded spawning aggregation located north of High Cay. Thus far, all known Nassau grouper spawning aggregations in The Bahamas have been reported and made known to the scientific community through fisher reports. If future visual observations confirm the presence of an unrecorded spawning aggregation, it will be the first time a spawning aggregation has been discovered using passive telemetry and underscores the versatility and importance of using this technology for monitoring and studying migratory fishes.

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LITERATURE CITED

Aguilar-Perera A. 2006. Disappearance of a Nassau grouper spawning aggregation off the southern Mexican Caribbean coast. *Mar Ecol Prog Ser.* 327:289–296. <http://dx.doi.org/10.3354/meps327289>

- Bahamas Ministry of Agriculture and Fisheries. 2015. Fisheries resources (jurisdiction and conservation) (amendment) regulations. Available from: http://laws.bahamas.gov.bs/cms/images/LEGISLATION/SUBORDINATE/2015/2015-00717/FisheriesResourcesJurisdictionandConservationAmendmentRegulations2015_1.pdf
- Bernard A, Feldheim KA, Nemeth R, Kadison E, Blondeau F, Semmens BX, Shivji MS. 2016. The ups and downs of coral reef fishes: the genetic characteristics of a formerly severely overfished but currently recovering Nassau grouper fish spawning aggregation. *Coral Reefs*. 35(1):273–284. <http://dx.doi.org/10.1007/s00338-015-1370-3>
- Bolden SK. 2000. Long-distance movement of a Nassau grouper (*Epinephelus striatus*) to a spawning aggregation in the central Bahamas. *Fish Bull*. 98:642–645.
- Bolden SK. 2001. Nassau Grouper (*Epinephelus striatus*, Pisces: Serranidae) movement in The Bahamas, as determined by ultrasonic telemetry. PhD dissertation. University of Miami, Miami.
- Buchan KC. 2000. The Bahamas. *Mar Pollut Bull*. 41(1–6):94–111. [http://dx.doi.org/10.1016/S0025-326X\(00\)00104-1](http://dx.doi.org/10.1016/S0025-326X(00)00104-1)
- Carter J, Marrow GJ, Pryor V. 1994. Aspects of the ecology and reproduction of Nassau grouper, *Epinephelus striatus*, off the coast of Belize, Central America. *Proc Gulf Caribb Fish Inst*. 43:65–111.
- Cheung WL, Sadovy de Mitcheson Y, Braynen MT, Gittens LG. 2013. Are the last remaining Nassau grouper *Epinephelus striatus* fisheries sustainable? Status quo in The Bahamas. *Endanger Species Res*. 20:27–39. <http://dx.doi.org/10.3354/esr00472>
- Coleman FC, Koenig CC, Collins LA. 1996. Reproductive styles of shallow-water groupers (Pisces Serranidae) in the eastern Gulf of Mexico and the consequences of fishing spawning aggregations. *Environ Biol Fishes*. 47(2):129–141. <http://dx.doi.org/10.1007/BF00005035>
- Colin PL. 1992. Reproduction of the Nassau grouper, *Epinephelus striatus* (Pisces: Serranidae) and its relationship to environmental conditions. *Environ Biol Fishes*. 34:357–377. <http://dx.doi.org/10.1007/BF00004740>
- Colin PL. 2012. Timing and location of aggregation and spawning. *In*: Sadovy de Mitcheson Y, Colin PL, editors. Reef fish spawning aggregations: biology, research and management. London, UK: Springer. p. 117–158.
- Cornish A, Eklund AM. 2003. *Epinephelus striatus*. The IUCN Red List of Threatened Species: e.T7862A12858266. Available from: <http://www.iucnredlist.org/details/7862/0>
- Cushion N, Sullivan-Sealey K. 2008. Landings, effort and socio-economics of a small scale commercial fishery in The Bahamas. *Proc Gulf Caribb Fish Inst*. 60:162–166.
- Dahlgren CP, Buch KL, Rechisky E, Hixon M. 2016a. Multi-year tracking of Nassau grouper (*Epinephelus striatus*) spawning migrations. *Mar Coastal Fish*. 8(1):522–535. <http://dx.doi.org/10.1080/19425120.2016.1223233>
- Dahlgren C, Sherman K, Lang J, Kramer PR, Marks K. 2016b. Bahamas coral reef report card. Volume 1:2011–2013. 24 p.
- Domeier ML. 2012. Revisiting spawning aggregations: definitions and challenges. *In*: Sadovy de Mitcheson Y, Colin PL, editors. Reef fish spawning aggregations: biology, research and management. London, UK: Springer. p. 1–21.
- Eggleston DB, Lipcius RN, Grover JJ. 1997. Predator and shelter-size effects on coral reef fish and spiny lobster prey. *Mar Ecol Prog Ser*. 149:43–59. <http://dx.doi.org/10.3354/meps149043>
- Ehrhardt NM, Deleveaux VKW. 2007. The Bahamas's Nassau grouper (*Epinephelus striatus*) fishery—two assessment methods applied to a data-deficient coastal population. *Fish Res*. 87:17–27. <http://dx.doi.org/10.1016/j.fishres.2007.06.020>
- Erismán BE, Aburto-Oropeza O, Gonzalez-Abraham C, Mascareñas-Osorio I, Moreno-Baez M, Hastings PA. 2012. Spatio-temporal dynamics of a fish spawning aggregation and its fishery in the gulf of California. *Sci Rep*. 2. <http://dx.doi.org/10.1038/srep00284>
- Green AL, Maypa AP, Almany GR, Rhodes KL, Weeks R, Abesamis RA, Gleason MG, Mumby PJ, White AT. 2015. Larval dispersal and movement patterns of coral reef fishes, and

- implications for marine reserve network design. *Biol Rev Camb Philos Soc.* 90:1215–1247. <http://dx.doi.org/10.1111/brv.12155>
- Kadison E, Nemeth RS, Blondeau J, Smith T, Calnan J. 2009. Nassau grouper (*Epinephelus striatus*) in St. Thomas, US Virgin Islands, with evidence for a spawning aggregation site recover. *Proc Gulf Caribb Fish Inst.* 62:273–273.
- Lopez JV, Peterson CL, Morales F, Brown L. 2000. Andros Island flora and fauna in the new millennium. *Bahamas J Sci.* 8(1):32–41.
- Mumby PJ, Dahlgren CP, Harborne AR, Kappel CV, Micheli F, Brumbaugh DR, Holmes KE, Mendes JM, Broad K, Sanchirico JN, et al. 2006. Fishing, trophic cascades, and the process of grazing on coral reefs. *Science.* 311(5757):98–101. <http://dx.doi.org/10.1126/science.1121129>
- Mumby PJ, Harborne AR, Brumbaugh DR. 2011. Grouper as a natural biocontrol of invasive lionfish. *PLoS One.* 6(6):e21510. <http://dx.doi.org/10.1371/journal.pone.0021510>
- Nemeth RS, Kadison E, Herzlieb S, Blondeau J, Whiteman WA. 2006. Status of a yellowfin grouper (*Mycteroperca venenosa*) grouper spawning aggregation in the US Virgin Island with notes on other species. *Proc Gulf Caribb Fish Inst.* 57:543–558.
- Ray GC, McCormick-Ray MG, Layman CA, Silliman BR. 2000. Investigations of Nassau grouper breeding aggregations at High Cay, Andros: implications for a conservation strategy. Final Report for the Department of Fisheries. Nassau, Bahamas. p. 13.
- Rowell TJ, Nemeth RS, Schärer MT, Appeldoorn RS. 2015. Fish sound production and acoustic telemetry reveal behaviors and spatial patterns associated with spawning aggregations of two Caribbean groupers. *Mar Ecol Prog Ser.* 518:239–254. <http://dx.doi.org/10.3354/meps11060>
- Sadovy Y, Domeier M. 2005. Are aggregation-fisheries sustainable? Reef fish fisheries as a case study. *Coral Reefs.* 24:254–262. <http://dx.doi.org/10.1007/s00338-005-0474-6>
- Sadovy Y, Eklund AM. 1999. Synopsis of biological data on the Nassau grouper, *Epinephelus striatus* (Bloch, 1792), and the jewfish, *E. itajara* (Lichtenstein, 1822). NOAA Technical Report NMFS No. 146. NOAA/National Marine Fisheries Service, Seattle, WA. p. 65.
- Sadovy de Mitcheson, Cornish A, Domeier M, Colin PL, Russel M, Lindeman KC. 2008. A global baseline for spawning aggregations of reef fishes. *Conserv Biol.* 22(5):1233–1244. <http://dx.doi.org/10.1111/j.1523-1739.2008.01020.x>
- Sadovy de Mitcheson Y, Craig MT, Bertoincini AA, Carpenter KE, Cheung WWL, Choat JH, Cornish AS, Fennessy ST, Ferreira BP, Heemstra PC, et al. 2013. Fishing groupers towards extinction: a global assessment of threats and extinction risks in a billion dollar fishery. *Fish Fish.* 14:119–136. <http://dx.doi.org/10.1111/j.1467-2979.2011.00455.x>
- Sadovy de Mitcheson Y, Erisman B. 2012. Fishery and biological implications of fishing spawning aggregations, and the social and economic importance of aggregating fishes. In: Sadovy de Mitcheson Y, Colin PL, editors. Reef fish spawning aggregations: biology, research and management. London, UK: Springer. p. 225–284.
- Schärer MT, Rowell TJ, Nemeth MI, Appeldoorn RS. 2012. Sound production associated with reproductive behavior of Nassau grouper *Epinephelus striatus* at spawning aggregations. *Endanger Species Res.* 19:29–38. <http://dx.doi.org/10.3354/esr00457>
- Semmens BX, Bush PG, Heppell SA, Johnson BC, McCoy CMK, Luke SKE, Pattengill-Semmens CV, Heppell S, Whaylen L. 2006. Defining the biogeography of a spawning aggregation to inform marine reserve planning and evaluation in the Cayman Islands. *Proc Gulf Caribb Fish Inst.* 59:638.
- Sherman KD, Dahlgren CP, Stevens JR, Tyler CR. 2016. Integrating population biology into conservation management for endangered Nassau grouper *Epinephelus striatus*. *Mar Ecol Prog Ser.* 554:263–280. <http://dx.doi.org/10.3354/meps11771>
- Smith CL. 1972. A spawning aggregation of Nassau grouper, *Epinephelus striatus* (Bloch). *Trans Amer Fish Soc.* 2:257–261. [https://doi.org/10.1577/1548-8659\(1972\)101%3C257:ASAONG%3E2.0.CO;2](https://doi.org/10.1577/1548-8659(1972)101%3C257:ASAONG%3E2.0.CO;2)

- Starr RM, Sala E, Balesteros E, Zabala M. 2007. Spatial dynamics of Nassau grouper *Epinephelus striatus* in a Caribbean atoll. *Mar Ecol Prog Ser.* 343:239–249. <http://dx.doi.org/10.3354/meps06897>
- Whaylen L, Bush P, Johnson B, Luke KE, McCoy C, Heppell S, Semmes B, Boardman M. 2007. Aggregation dynamics and lessons learned from five years of monitoring a Nassau grouper (*Epinephelus striatus*) spawning aggregation in Little Cayman, Cayman Island, BWI. *Proc Gulf Caribb Fish Inst.* 59:413–422.

