

Spatial and Temporal Dynamics of a Nassau Grouper Fish Spawning Aggregation Located on an Isolated Seamount in Puerto Rico

Evan Tuohy^{1*}, Michelle Schärer¹, Louis Penrod², Richard Appeldoorn¹

¹Department of Marine Science, Universidad de Puerto Rico, Recinto de Mayagüez, Mayagüez, Puerto Rico, 00681

²Department of Ocean Engineering and Marine Sciences, Florida Institute of Technology, Melbourne, Florida, 32901

*Corresponding Author

E-mail: evan.tuohy@upr.edu

Abstract

1. The Nassau grouper, *Epinephelus striatus*, is a slow-growing, late-maturing, long-lived reef fish widely distributed throughout the south-western North Atlantic. Known for forming large spawning aggregations numbering in the tens of thousands, they are now listed as Critically Endangered by the IUCN. Recently, the only Nassau grouper spawning aggregation in Puerto Rico was documented at Bajo de Sico, a seamount and seasonally closed marine protected area.
2. Studies elsewhere on the spatio-temporal dynamics of Nassau grouper aggregations have documented how, and how far, fish move from home sites to the spawning site and have shown the tight link between aggregation formation and the lunar cycle. However, these have not evaluated the potential impacts of a reduces spatial extent represented by a seamount, nor can they address the impacts of local seasonal protection relative to the size of the closed area and the timing of aggregation formation.
3. Acoustic telemetry was used to quantify the spatio-temporal dynamics of spawning aggregation formation of Nassau grouper at Bajo de Sico. Twenty-six individuals were tagged and tracked over three consecutive spawning seasons.

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4. Nassau grouper formed 3-4 aggregations per season corresponding to the January through April lunar cycles. Individuals displayed high visitation rates to the aggregation site: 98% visited at least two peaks per season; 80% visited multiple seasons. The timing of arrival, departure, and residency at the site were significantly different among individuals and lunar months, indicating significant variability in aggregation formation. Nassau grouper occupied a relatively small staging area (2.7 km²) and courtship arena (0.67 km²) compared to aggregations occurring on continental/insular platforms or large atolls; movements off the seamount may occur but were not detected. Results indicate the current seasonal closure inadequately protects the spawning population on Bajo de Sico and should be extended through June.

Keywords: Nassau grouper, Fish Spawning Aggregations, Acoustic telemetry, Management, Puerto Rico

1. Introduction

Many commercially and ecologically important coral reef fishes are reported to aggregate *en masse* for the purpose of reproduction (Sadovy de Mitcheson et al., 2008; Grüss et al., 2014). Transient fish spawning aggregations (FSAs) occur at specific times and locations, comprise hundreds to thousands of conspecifics, and individuals migrate long distances from their respective home reef sites (Domeier & Colin, 1997). Ephemeral in nature, FSAs represent most, if not all, of the reproductive effort for a given population and are thus essential for population maintenance and persistence. Historically, many FSAs are the target of direct and intense fishing pressure since they are predictable in space in time. Traditionally recognized as periods for immediate economic gain rather than long-term biological stability, many of the FSAs have been fished to the point of collapse, with the remaining ones reported to occur at a fraction of the historical population levels (Sadovy de Mitcheson et al., 2008). However, studies have shown that grouper spawning aggregations can recover following the implementation of concerted management and conservation action combined with effective enforcement and compliance (Nemeth, 2005; Waterhouse et al., 2020).

The Nassau grouper, *Epinephelus striatus* (Bloch, 1792), is a large-bodied (max. length 120 cm), ecologically, and commercially important reef fish inhabiting the tropical Western Atlantic (Sadovy & Eklund, 1999). Occurring on shallow (<100 m) high relief coral reef habitats, Nassau grouper are responsible for maintaining trophic integrity, biological diversity, and contribute to ecosystem connectivity via ontogenetic and reproductive migrations (Sadovy & Eklund, 1999; Stalling, 2008; Nemeth, 2012; Sadovy de Mitcheson, Heppel & Colin, 2012). Like most other epinephelids, the Nassau grouper's slow growth, late age at maturity and formation of large reproductive aggregations have made them particularly susceptible to overfishing. However, Nassau groupers are gonochoristic, which differs from the dominant sexual pattern of protogynous hermaphroditism displayed by most groupers (Sadovy & Eklund, 1999). Once considered the most commercially important reef fish species throughout their

range, Nassau grouper are severely overfished (Sadovy & Eklund 1999; Sala et al., 2001; Aguilar-Perera, 2006; Sadovy de Mitcheson et al., 2008; Stallings, 2009; Cheung et al., 2013, Sadovy de Mitcheson et al., 2013; Waterhouse et al., 2019), currently listed by the International Union for Conservation of Nature (IUCN) as Critically Endangered (Sadovy, Aguilar-Perera & Sosa-Cordero, 2018), and designated as threatened under the U.S. Endangered Species Act (NOAA 2016). Puerto Rico is no exception, where despite 30 years of management regulations their population remains low (NOAA, 2016), and almost all known Nassau grouper FSAs are considered extirpated. (Sadovy, 1997; Garcia-Sais et al., 2007; Garcia-Sais et al., 2020).

Nassau grouper are transient spawners capable of travelling hundreds of kilometres across contiguous reef systems to join aggregations (Bolden, 2000; Dahlgren et al., 2016). Documented FSA sites occur on large atolls and/or continental shelves with distinct geomorphological characteristics shared between these locations (Kobara et al., 2013). Prior to spawning, Nassau grouper are reported to migrate in groups from home reefs to an aggregation site (Colin, 1992; Carter, Marrow & Pryor, 1994; Aguilar-Perera & Aguilar-Davila, 1996). Once at the aggregation site, individuals exhibit complex reproductive behaviours associated with courtship and territoriality, occupying different areas within discrete temporal scales leading up to peak spawning (Nemeth, 2012). Previously thought to travel to and remain at the core FSA site for the duration of spawning, recent tagging studies have shown that Nassau grouper make multiple periodic, short-term migrations to and from their spawning site throughout the spawning season (Starr et al., 2007; Nemeth, 2012; Kobara et al., 2013; Rowell et al., 2015).

The spawning season for Nassau grouper is reported to occur from November to July throughout the tropical north-western Atlantic, however, at most locations, spawning is reported to occur over a three-to-four consecutive months period (Sadovy & Eklund, 1999; Rowell et al., 2015). Aggregation formation is reported as remarkably synchronous (Starr et al., 2007), with Nassau grouper forming FSAs over a seven-to-ten-day period with peak spawning occurring over a two-to-four-day period (Colin, 1992; Whaylen et al., 2004; Heyman & Kjerfve, 2008; Rowell et al., 2015). The specific timing of these aggregations occurs in conjunction with distinct lunar periodicity. Although variability in the timing and duration of these FSAs is observed between locations, the periodicity is assumed to be fixed at the site level (Rowell et al., 2015).

In this study, acoustic telemetry was used to track Nassau grouper over multiple years to describe the aggregation dynamics of a documented FSA at a submerged seamount off western Puerto Rico located within a seasonal marine protected area (MPA; Schärer et al., 2014). This is the only known Nassau grouper spawning aggregation within the waters surrounding Puerto Rico and occurs on a deep, semi-isolated seamount, potentially differing in spatial scale to other Nassau grouper spawning sites in the region. The specific objectives were to characterize: 1) the temporal and spatial dynamics of Nassau grouper at the FSA site, 2) the movement patterns and migrations off the seamount, and 3) the timing of FSA formation relative to the months of protection in the seasonal MPA. This multi-year study provides valuable insight into Nassau grouper spawning dynamics, particularly as it relates to a unique geomorphological setting.

2. Material and Methods

2.1. Study Area

Nassau grouper movements were monitored at Bajo de Sico (BDS), an isolated seamount 27 km off the west coast of Puerto Rico (Figure 1). Bathymetry is characterized by a ridge of highly rugose rock promontories on the top of the submerged seamount, ranging in depth from 25 to 50 m, which rises from a mostly flat, gradually sloping shelf covered in rhodolith habitat that extends to 100 m in depth and encompasses an area of 11.1 km². Beyond 100 m depth the shelf slopes steeply into a vertical wall that reaches depths of 200–300 m to the south east and over 1,000 m to the north and north west. The dominant oceanographic features and their location within the Mona Passage make this area subject to periods of strong (> 2.0 kts), persistent northerly currents (Garcia-Sais et al., 2007; Garcia-Sais et al., 2020).

Bajo de Sico is characterized by highly diverse and taxonomically complex fish assemblages (Garcia-Sais et al., 2007; Garcia-Sais et al., 2020) and is known to harbour multiple spawning aggregation sites in addition to that of Nassau grouper (Sadovy et al., 1994; Schärer et al., 2012; Sanchez et al., 2017). The spawning season for Nassau grouper at this location is documented to occur during January through April, corresponding with the January-March lunar cycles (Scharer et al., 2014). In the US exclusive economic zone (EEZ) jurisdiction of the seasonal MPA around BDS there is a six-month closure to reef fish fishing from October 1 to March 31 to protect coral reef habitats and reef fish species during spawning. Management measures were first designated at this MPA to protect the spawning stock of red hind, *Epinephelus guttatus*, (December 1 through February 28/29) and later expanded (October 1 through March 31) to provide protection for spawning stocks of additional species of snappers and groupers and to avoid damage to coral reef habitat (Crabtree, 2009). Although the possession of and fishing for reef fish species, managed by the Caribbean Fishery Management Council fisheries management plans, are prohibited during the six months' seasonal closure, the regulation does not prohibit fishing, scuba diving, or the possession of highly migratory species (HMS) and lobster throughout the entire year. The use of anchors, traps, longlines and nets is prohibited year-round. Despite these regulations, monitoring efforts have indicated consistently low population densities of Nassau grouper at BDS (Garcia-Sais et al., 2007; Schärer et al., 2014; Garcia-Sais et al., 2020).

2.2. Fish Tagging

Ethics Statement: At the time of this study there was no ethical review as the Institutional Review Board of the University of Puerto Rico at Mayagüez did not have a policy that covered research on wild-caught fishes.

Acoustic tagging of multiple groupers was conducted at the spawning aggregation site during two reproductive seasons. Due to the deeper depths at which this aggregation occurs (> 40 m), an *in situ* tagging approach using closed-circuit rebreathers was developed to decrease barotrauma impacts and increase tagging efficiency (Tuohy et al., 2015). Nassau groupers were captured using Antillean arrowhead fish traps (n=4) baited daily with squid and canned cat food. Technical divers with rebreathers descended to the traps and removed the individuals selected for tagging by coercing them into a mesh catch bag with a 30-cm zipper designed for this task. Once in the bag, fish were restrained in an inverted position, inducing a tonic immobility state, and the zipper was positioned over the abdomen to access the ventral abdomen's incision site. Transmitters (V16-4h or V16p-4h, 69 Hz; dimensions = 16 mm diameter X 54 mm length, 19 g weight in air; nominal delay = 60-90 sec; battery life = 1,250-1,580 days; Vemco (now Innovasea), Halifax, NS, Canada) were inserted into the body cavity via a 2-cm incision made 5 cm posterior to the pelvic girdle. After tag insertion the incision was closed with 2-3 stainless steel surgical staples (Reflex one skin stapler with 5.7 mm staples). Following each surgical procedure, total length (TL) measurements and a fin clip were taken and a numbered external tag (Hallprint T-bar anchor tag type TBA; 7 cm) was inserted into the dorsal musculature. The duration of the tagging procedure lasted 12 ± 2.2 min, and individuals were released at the site and depth of capture. Each fish was observed by divers upon release to ensure that there were no immediate adverse effects following tagging (Tuohy et al., 2015).

2.3. Acoustic Receiver Array

Tags were monitored with an array of 16 omni-directional acoustic receivers (VR2 and VR2W, 69kHz; Vemco) deployed at depths ranging from 30 – 75 m (mean \pm SD = 48.05 ± 12.16) covering approximately 2.2 km² of the study area (Figure 1). Given the depth constraints to safe diving, limited number of receivers, and challenging environmental conditions at Bajo de Sico, it was not possible to deploy or maintain an array that encompassed the entire seamount. Therefore, the array was designed to surround the main high relief habitats (promontories and areas of high rugosity) that are the preferred habitat for the species (Sadovy & Eklund, 1999). At BDS, receivers were located primarily along the east-west ridge that encompasses the shallowest habitats of the seamount (Figure 2), the eastern-most receiver was located at a raised area, referred to as the eastern satellite, separated from the main ridge by deeper habitats. The southernmost receivers were located on or adjacent to a separate raised area, defined as the southern satellite. Additional receivers, covering an area of 0.21 km², were deployed at the aggregation site to track fine scale movements of individuals while aggregated. Each receiver was deployed on the sea floor moored to a cement base deployed in open sandy areas. One receiver was attached to a subsurface buoy; however, this anchoring system was generally avoided due to frequent periods of strong currents.

Efforts were undertaken in 2015 and 2016 to explore the presence of tagged grouper along a potential migration corridor between BDS and the insular shelf off western Puerto Rico (PR). The area, known as Little Sico, is a smaller, deeper seamount located to the south west of

BDS at a depth of 120 m at its shallowest point and provides habitat within the reported depth range of the species (Starr et al., 2007; Sadovy de Mitcheson et al., 2012). Two receivers were attached to subsurface buoys (hard plastic trawl floats) between depths of 40-50 m oriented in the downward position. Two additional receivers were placed on the PR shelf next to the suspected migration corridor to track movements of individuals onto the main island's insular platform.

Range testing was conducted using two different methodologies. First, given the mean depth of receivers (48.05 m) and distance from shore, an *in situ* range testing at the study site was logistically difficult, so fine-scale range testing was conducted at a shallower (20 m) location of similar habitat. The range test involved mooring a VR2W to a cement base at a depth of 20 m, identical to the mooring used at the study site. A tripod with a range test tag (V16-4h; transmission rate = 5 sec; Vemco) attached 50 cm from the substrate was positioned at 30 m increments away from the acoustic receiver. The range tag remained in place for a period of 10 minutes before being moved to the next distance for a total distance of 300 m. Second, to confirm these results, boat-based drift range tests were conducted by suspending the range test tag from a weighted line attached to the vessel. The weighted line was deployed at the location and depth of an acoustic receiver and the trajectory, distance from the acoustic receiver and time of day were tracked with a handheld GPS as the vessel drifted away from the receiver. A total of 15 drifts were conducted from one receiver during periods of minimal current velocity so that the weighted line remained directly under the vessel. A 70% probability of detection corresponding to distance of 150 m was used for further analysis (Farmer et al., 2013).

2.4. Data Analysis

Space use characteristics were calculated for each tagged Nassau grouper with detection records within the array during each spawning season. Acoustic receivers were retrieved at intervals of six months to one year, depending on the location. Data were downloaded using VUE software (Vemco) and directly imported into R (R core team, 2018). Prior to any analysis, data were filtered to remove false or spurious detections defined as single detections within a 24-hour period (Aspillaga et al., 2018; Keller et al., 2020). These detections may occur when two tags emit a signal simultaneously and collide within the detection range of a receiver. Additionally, tag detection records were considered unreliable when a stationary characteristic of the signal or irregular depth were observed, indicating tag loss, mortality, or predation, at which point the tag was eliminated from the analysis.

2.5. Space use during Aggregation Formation

Brownian bridge movement models (BBMM) were used to calculate the utilization distribution (UD) for each tagged individual. The UD is defined as the probability distribution defining an animal's use of space. The BBMM is a temporally explicit method for estimating the UD based on the probability of an individual being at a location along the movement path

conditional to the distance and elapsed time between successive locations. The model not only accounts for the spatial distribution between locations, but also considers their time dependency and assumes a conditional random walk movement pattern between pairs of locations dependent on step length and time interval between successive steps (Horne et al., 2007). Brownian bridge UD estimates also consider the error associated with a given position, which is represented by the estimated detection radius of the acoustic receivers (Horne et al., 2007). The location error used for the models was based on the 70% probability of detection at 150 m and the time step 720 minutes (Farmer et al., 2013).

Each individual's core area (CA) was defined as the minimum area encompassing the 50% UD volume, and the home range (HR) area was calculated as the minimum area encompassing the 95% UD volume, with CA and HR considered to be the area where individuals spend up to 50% and 95% of their time, respectively. Annual spawning Brownian bridge HR estimates were calculated for the entire tracking period using the "adehabitatHR" package in R (Calenge, 2006). Kruskal-Wallis H tests were used to test for significant differences in spawning habitat use (50% and 95% UD) between years. A Wilcoxon Rank-Sum test was used to test for difference in spawning and non-spawning habitat use (Tuohy et al., in press) between years.

2.6. Timing of Arrival, Departure and Residency at the Aggregation Site

The timing of FSA formation was analysed by recording the number of detections and number of tags present at the aggregation site. Monthly and daily detection rates and tag presence were graphed to indicate periods of peak presence at the FSA site. Spawning site visitation rate refers to the proportion of tags present at the aggregation site and was calculated by dividing the total number of tags present at the FSA site by the total number of tags used in the analysis. Spawning site visitation rates were calculated for each spawning season ($n = 3$) and spawning peak with each season ($n = 10$). The timing of arrival at and departure from the FSA site were recorded as the first and last tag detection record at any of the receivers deployed at the main FSA site and were recorded in decimal days after the full moon (DAFM) and lunar illuminations (daily proportion of the lunar disk illuminated). Kruskal-Wallis H tests were used to assess differences in the arrival and departure timing between individuals and lunar months. Residency was calculated by subtracting the timing of departure from the timing of arrival and recorded as decimal days (DD) spent at the aggregation site for each spawning peak. Differences in residency time at the FSA both within and between spawning months were assessed using Kruskal-Wallis H tests. The relationship between residence time and fish total length (TL) were tested using a linear regression.

2.7. Vertical Distribution

For tags that contained pressure sensors (2014, $n = 13$; 2015, $n = 11$; 2016, $n = 7$; V16p-4h), depth measurements were averaged into daily (24 hrs) periods for spawning and non-spawning times. During peak spawning periods, diurnal and nocturnal depth values were calculated (relative times reported between sunrise and sunset) to assess differences between diel depth profiles. Mean depths between spawning and non-spawning periods were compared using Wilcoxon Rank-Sum test. A Wilcoxon Signed-Rank test was used to assess differences between diel depths recorded during peak spawning periods.

3. Results

A total of 29 Nassau grouper were tagged at the main spawning area during the 2013 ($n=10$) and 2014 ($n=19$) spawning seasons, of which 26 were included in subsequent analyses given their detection records (Table 1). These 26 individuals ranged in size from 52 to 80 cm TL and were detected for periods ranging between 18 and 1,580 days (mean \pm SD = $1,192.57 \pm 332.63$). No significant differences were found between the fish length (TL in cm) of tagged (Mean \pm SD = 67.21 ± 9.29) and untagged individuals (length estimates obtained from paired-laser video surveys; Mean \pm SD = 70.37 ± 9.73 ; $t(267) = -1.65$, $P > 0.05$). The acoustic receiver array continuously collected data from tagged Nassau grouper over a 4.5-year period (March 2013 to September 2017). Only the tagging data collected during 3-4 spawning months from years 2014-2016 were used as this provided the largest sample size of tags. Differences in the months of analysis related to temporal differences in the observed spawning periodicity of those years (Tuohy et al., 2016). Since tagging was conducted during January and February 2014 spawning peaks, only data recorded from subsequent peaks following tagging was considered for the analysis. Three of the 29 tags (10%) were detected for a period greater than four years, ten (35%) were detected between three and four years, two tags (6%) were detected between two and three years, eight (28%) were detected between one and two years, and six (21%) were detected during less than one year (Table 1).

3.1. Timing of Aggregation Formation and Spawning Site Visitation Rate

Tagged Nassau grouper aggregated during the lunar months of January to April with variability between years (Figure 2). In 2014 and 2016 aggregation formation occurred during the January to March moons ($n=3$) and in 2015 during the January to April moons ($n=4$). Increased numbers of tagged individuals were detected at the aggregation site, as defined by four receivers that accounted for 93% of all spawning season detections, from 5.74 ± 1.31 to 13.53 ± 1.01 DAFM (range = -3-23 DAFM; 0.75-0.00 lunar illuminations) with peak formation (highest number of detections and tags present) between 9.3 ± 2.45 - 11.4 ± 1.5 DAFM (range = 6-15; 0.6

to 0.08 lunar illuminations). Population level spawning site visitation rates for all peaks and years was 0.75 ± 0.17 (range = 0.44-1.00). The February moon had the highest mean site visitation rate with 0.87 ± 0.12 of tag presence, followed by January (0.81 ± 0.18) and then March (0.7 ± 0.06). Individual spawning site visitation rate was 0.79 ± 0.18 (range = 0.33-1.00), with 63% of tags present for all spawning peaks within a given season, 35% present for two spawning peaks and 2% present for only one spawning peak.

3.2. Timing of Arrival, Departure and Residency at the Aggregation Site

The timing of arrival and departure to the FSA site for each lunar month varied considerably (Figure 3). The mean timing of arrival and departure for each lunar month was 5.29 ± 2.52 and 13.73 ± 1.65 DAFM for January, 3.92 ± 2.03 and 14.06 ± 1.04 DAFM for February, and 6.96 ± 0.99 and 13.16 ± 1.64 DAFM for March. Significant differences in the timing of arrival and departure were found between individuals (Arrival: $\chi^2(3) = 15.366$, $P = 0.00$; Departure: $\chi^2(3) = 14.803$, $P = 0.00$) and lunar months (Arrival: $\chi^2(3) = 15.366$, $P = 0.00$; Departure: $\chi^2(3) = 14.803$, $P = 0.00$).

Tagged Nassau groupers remained at the FSA site for 7.83 ± 1.1 DD (mean \pm SD; range = 0.1-17.98 DD) per season. The mean residency for each lunar month was 8.34 ± 3.04 DD for January, 9.98 ± 0.97 DD for February, and 6.61 ± 0.99 DD in March. Mean residency for April was 4.51 ± 3.37 in 2015. Significant differences in residency time at the FSA site were found between spawning peaks ($\chi^2(6) = 26.001$, $P = 0.00$) and within lunar months ($\chi^2(3) = 19.471$, $P = 0.00$). A linear regression showed no significant relationship between residency time (DD) and fish total length (TL in cm; $F(1,99) = 1.88$, $P = 0.174$), with an $R^2 = 0.009$.

3.3. Aggregation Formation in Relation to Seasonal MPA

Aggregation formation, defined as the increased detection of tagged individuals at the FSA site, occurred outside of the seasonal MPAs closed season in 2015 and 2016. In 2015, aggregations occurred associated with the January-March moons, however, an increased number of tagged fish were detected at the FSA site during the April moon. Indications of aggregation formation were not observed, neither in tag presence nor visual census, to be associated with the April moon in other years studied with acoustic tags (Tuohy et al., in press). In 2016, the aggregation observed in April was associated with the expected timing of the lunar cycle, but with the March full moon occurring late in the month (March 23/24), the subsequent timing of the aggregation formed in April (Figure 2). Additionally, during the 2014 and 2016 tracking periods, three tagged fish migrated to the FSA site in relation to the April and May moons that corresponded to the spawning lunar periodicity observed for this location (Tuohy et al., in press).

All these latter migrations resulted in less than 24 hrs spent at the aggregation site and fish migrated separately.

3.4. Space use during Aggregation Formation

The BBMM annual spawning season core area utilization distribution (50% UD) for tagged Nassau grouper ranged from 0.1 to 0.22 km² with a mean \pm SD of 0.11 \pm 0.01 km². The annual home range utilization distribution (95% UD) ranged from 0.33 to 1.2 km² with a mean \pm SD of 0.47 \pm 0.07 km² (Table 1). Kruskal-Wallis H tests indicated no significant differences in space use during aggregation formation among individuals (50% UD; $\chi^2(9) = 8.4, P = 0.59$ and 95% UD; $\chi^2(9) = 8.25, P = 0.61$) or among lunar months (50% UD; $\chi^2(3) = 1.15, P = 0.77$ and 95% UD; $\chi^2(3) = 1.76, P = 0.62$). The total combined spawning core area (50% UD) and home range (95% UD) for all tagged fish detected within the array during the spawning season were 0.87 km² and 2.31 km² respectively (Figure 4A).

Fourteen (54%) tagged fish were detected within the array outside of the spawning season and had annual residency within the array on BDS. Seven of these individuals resided at the aggregation site for the duration of the year. The remaining seven migrated from home reef sites on BDS to the FSA site during peak spawning periods (mean \pm SD = 8.44 \pm 1.42 DD; range = 5.82-10.03 DD). Following the spawning season, all fish returned to their respective home reef locations (Tuohy et al. in press). The total combined spawning core area (50% UD) and home range (95% UD) encompassing all 14 resident tagged fish detected within the full array during the spawning season were 0.79 km² and 1.86 km², respectively, with no significant differences between core area (50% UD; $W(2) = 64.0, P = 0.12$) and home range (95% UD; $W(2) = 73.0, P = 0.27$) utilization distributions between the spawning and non-spawning seasons.

Twelve (46%) of the tagged fish were only detected during the spawning season (mean \pm SD = 7.52 \pm 1.00 DD; range = 6.39-8.93 DD). Seven (27%) of those individuals (Tag # 001,003, 004, 012, 015, 027, 030) were only detected at the FSA site during peak spawning periods and were not detected within the array for the remainder of the spawning season. All seven fish were detected at subsequent aggregations for the duration of the study and visited 2.4 \pm 0.63 aggregations per year. The total combined spawning core area (50% UD) and home range (95% UD) for these seven tagged individuals were 0.23 km² and 0.67 km² respectively (Figure 4B).

The remaining five (19%) fish (Tag # 017, 020, 021, 025, and 029) were only detected for a single spawning season and were not detected in subsequent years (Figure 5). Tag# 017, 020 and 021 were all tagged during the January 2014 aggregation and were detected at the aggregation site for the remainder of month. These fish departed the FSA site in accordance with the remaining tagged population. Tag# 017 left the FSA site 15 DAFM and travelled throughout the array, subsequently detected at 11 receivers during the 23-day tracking period. Movement in the easterly direction was observed and the last detection was at the eastern satellite (Figure 5). The remaining four tagged fish returned to the FSA site for multiple

spawning peaks and were detected throughout the array during the spawning season. Tag# 020 departed the FSA site and moved to the southern satellite location where it remained for 7 days. Subsequently, it returned to the FSA site 4 days before the February moon and remained there until the peak aggregation time. This grouper remained at the main spawning site for 30 days and was not detected elsewhere within the array. Its last detections were recorded at the eastern-most receiver deployed within the main spawning area before disappearing from the detection record after a 56-day tracking period. Tag# 021 departed the FSA following the January peak aggregation period and moved to and remained near one of the receivers on the main promontory ridge until the following peak aggregation period. The fish then returned to the main spawning core area for the duration of the February aggregation, after which it migrated back to the same location on the main promontory as previously detected. This fish returned to the main site for the March peak period however, after it departed from the aggregation site it was not detected for the remainder of the study. Tag# 025 was implanted in February 2014, and the grouper resided at the same site for the remainder of the aggregation peak period corresponding to the February moon. In March (22 DAFM), it undertook a southerly migration to the southern satellite receiver location where it was detected over a period of 89 days, after which it disappeared (Figure 5). Tag# 029 was inserted during the February 2014 aggregation and the fish departed the FSA site on 17 DAFM. This fish moved considerably throughout the array and was detected at 12 different receivers including both the eastern and southern satellites. During its 19-day tracking period, detections indicated movements towards an easterly direction until its last detection was recorded at the eastern satellite receiver.

3.5. Small-scale Movements

Tagged Nassau groupers made multiple forays to the FSA area for the duration of peak spawning periods. This behaviour was detected for nine (48%, excluding residents within the FSA area) tagged fish, including all resident individuals with home reefs on BDS but outside of the FSA area ($N = 7$). Individuals made 3.45 ± 1.88 (mean \pm SD; range = 1-12 trips per moon) trips to the FSA site per moon and travelled a mean minimum distance of 1.01 ± 0.05 km (mean \pm SD; range = 0.04 – 1.6 km) per trip between home reef and spawning site. Movement speed to and from home reefs was 0.31 ± 0.25 m/s mean \pm SD; range = 0.03-2.1 m/s) with no significant difference in the swim speeds to and from the aggregation area (Median = 0.23, Wilcoxon Rank-Sum test: $W(2) = 1415.5$, $P = 0.38$).

3.6. Large-scale migrations

No detections were recorded from receivers deployed on the suspected migration corridor connecting BDS to the PR insular shelf. Due to the logistical difficulties and the nature of the deployments, only one of the receivers deployed on subsurface buoys at Little Sico was recovered. The depth of deployments coupled with periods of prolonged strong currents hindered deployment and recovery attempts for these receivers.

3.7. Vertical Distribution

During the spawning season tagged fish resided at depths between 16.38 and 100.07 m (mean \pm SD = 39.81 ± 2.89 ; Table 1 and Figure 6). Mean depth during peak aggregation formation was 42.77 ± 2.27 m (range = 16.38 – 100.07) compared to 38.46 ± 1.73 m (range = 16.68 – 81.88) during the non-aggregation season. A Wilcoxon Rank-Sum test indicated that daily depth during aggregations (Median = 43.37 m) was significantly deeper from daily depth during non-aggregation times (Median = 37.6 m), $W(2) = 8469$, $P < 0.05$. Mean maximum depth of fish during the aggregations was 54.38 ± 5.64 m (range = 42.3 – 100.07) compared to 44.01 ± 3.24 m (range = 38.85 – 58.51) when they were not aggregated to spawn. A Wilcoxon Rank-Sum test indicated that mean maximum depth during aggregation periods (Median = 55.57 m) was significantly deeper to the mean maximum depth during non-aggregation times (Median = 43.58 m), $W(2) = 1845$, $P < 0.05$. Diurnal mean depth during peak aggregation times was 41.13 ± 3.08 m compared to 42.76 ± 3.45 m nocturnal mean depth. A Wilcoxon Signed-Rank test indicated that nocturnal depth (Median=42.82m) was significantly deeper than diurnal depths (Median = 42.41m) during aggregation periods, $W(2) = 27265$, $P < 0.05$.

4. Discussion

Nassau grouper at Bajo de Sico (BDS) aggregated during three to four periods per year corresponding to the January through April lunar cycles. A peak aggregation associated with the April moon was observed in 2015, but not in 2014 or 2016. No aggregation formed in December as previously reported in the region for this species (Colin, 1992). The aggregation peak period associated with the February moons displayed the greatest spawning site visitation rate and residency of tagged individuals followed by the January, March, and April moons, respectively. Tagged fish displayed high spawning site visitation rates to the FSA site, with the majority (98%) visiting at least two peaks per season. The timing of arrival, departure, and residency to the FSA were significantly different among individuals and lunar months, and residency times had no relation with fish total length. The combination of these factors indicates, that although spawning aggregation formation is reported as highly synchronous for this species (Starr et al., 2007), at BDS some inter- and intra-annual variability of FSA formation was detected.

Previous studies have reported the migratory dynamics of Nassau grouper associated with reproduction to be complex and of variable scale (Colin, 1992; Carter, Marrow & Pryor, 1994; Aguilar-Perera & Aguilar-Davila, 1996; Bolden, 2000; Starr et al., 2007; Nemeth, 2012; Kobara et al., 2013; Rowell et al., 2015; Dahlgren et al., 2016). Of the 26 tagged Nassau grouper included in this study, 14 were detected to reside year-round on BDS, half of the resident fish resided at home reefs outside of the FSA area ($n = 7$). Two that were only detected at the spawning site during the aggregations, underwent multiple small-scale, daily movements to and from the FSA site during the aggregation periods. Tagged fish with defined home reefs migrated 2 - 12 times during an aggregation peak with the minimum distance travelled ranging from 0.04 to 1.6 km per trip for individuals with defined home reef sites.

Migrations of tagged Nassau grouper off the seamount and onto the PR insular shelf were not detected, but indirect evidence suggests that larger-scale migrations to the PR shelf may be occurring. First, a fisher reported the catch of a grouper on the PR shelf bearing a transmitter that corresponded to the timeline of a tag missing from the array (Tag #008). When questioned further regarding the report, the fisher was reluctant to provide further information, presumably because the possession of Nassau grouper is prohibited in both local and federal water surrounding Puerto Rico (Tuohy et al., 2015). Second, the southerly migration of Tag #025 observed after the February 2014 aggregation was toward a suspected migration corridor, and the tag then disappeared from the detection record for the remainder of the tracking period. This suggests a possible migration to the PR shelf, but these movements occurred prior to the deployment of additional receivers along the suspected migration corridor.

Nassau grouper occupied significantly different depth profiles within the water column during aggregation formation. Both the deepest and shallowest depths recorded during the peak aggregation period indicating that individuals use a larger volume of habitat while aggregated at BDS. Nassau grouper occupied deeper depth during the nocturnal periods, which supports the observation of fish moving to deeper shelf edge habitats during crepuscular periods to participate in courtship and spawning (Whaylen et al., 2004; Starr et al., 2007; Nemeth, 2012). Starr et al. (2007) reported Nassau grouper making deep vertical migrations in excess of 250 m in the months following spawning. However, this was not observed with tagged fish on BDS, where the deepest depths were associated with peak aggregation formation, after which, the fish migrated back to the shallower non-spawning depth profiles.

Characteristics unique to this location (an isolated bank) and limitations of the array resulted in a relatively smaller spatial scale when compared to other studies (Nemeth, 2009; Nemeth, 2012; Rhodes et al., 2012; Feeley et al., 2018). While this may prevent the quantification of some traditional space use metrics associated with transient FSAs (Nemeth, 2012), it offers the potential for understanding how differing spatial scales may affect these metrics. During the spawning season, species that form reproductive aggregations exhibit patterns in the spatio-temporal scale of habitat use as fish migrate from home reef to spawning aggregation sites. Nemeth (2012) defined these spatial patterns of migration relative to movements and behaviour during the spawning season. The functional migration area (FMA) includes all biological processes and interactions that occur as fish move along migratory pathways from home reefs to spawning sites. The FMA can be subdivided into four spatio-temporal scales and are defined as follows, in descending order: 1) the *catchment area* encompasses all of the home ranges of a spawning population using a single aggregation site during an annual reproductive cycle, 2) the *staging area* is the larger area surrounding the spawning site where individuals congregate in groups prior to spawning or for several weeks between spawning peaks, 3) the *courtship arena* is the area of increased densities where courtship behaviours and interactions occur in close proximity to the spawning site during the specific reproductive period or lunar phase, and 4) the *spawning site*, where the act of spawning occurs and is occupied for a few hours during specific days of the aggregation. These metrics

have been quantified for Nassau grouper aggregations that occur on extensive reef systems where individuals occupied a catchment area on the scale of 7,500 km², staging areas of 15 km², courtship arena of < 10 km², and spawning site of < 1 km² (Nemeth, 2009; Nemeth, 2012). However, the spatial scale of these areas is highly dependent on the complexity of the reef system and the amount of contiguous habitat available for their migration and varies depending on the location. For example, for a Nassau grouper aggregation reported to occur on small, isolated islands with extensive barriers to migration, the catchment area was limited to 30 - 100 km² (Colin, Shapiro & Weiler, 1987; Semmens et al., 2005; Starr et al., 2007; Nemeth, 2012).

The FMA and catchment area can be estimated when enough information is available on home sites, spawning sites and migration pathways and distances (Nemeth, 2009). These conditions were not met at BDS due to the limited spatial coverage and lack of receiver overlap of the array. If all fish resided on BDS, the FMA and catchment areas would be limited to approximately 11.1 km² (total area shallower than the 100 m bathymetric contour). However, if individuals migrate to BDS from the PR insular shelf, the FMA and catchment areas would be substantially larger. For example, calculating this area for a single fish with a minimum migration distance to an area of the PR shelf immediately adjacent to BDS would yield a catchment area of 16 km². The staging area on BDS was estimated as the total area encompassed by the combined areas of the BBMM UD for the five single season and 14 resident fish. Nassau groupers are reported to visit the spawning area multiple times per year and roam actively on a daily basis within large staging areas of at least 15 km² (Starr et al., 2007; Nemeth, 2012). Fish occupy this area prior to aggregation formation and for several weeks between peaks (Starr et al., 2007; Nemeth, 2012). This behaviour was observed with the five single season tagged fish before their permanent absence from the detection record at BDS. The resident fish occupied home reefs sites within this same area, and either resided at the FSA site or actively migrated between home reefs and the spawning site, therefore their habitat use was included in the estimation of the staging area. Based on these movements a staging area was estimated at of 2.7 km² (Figure 4A). As the peak aggregation period approached, tag detection records indicated a concentration of tags at the area surrounding the presumed spawning site. This was also supported by the seven tagged fish with home reefs on BDS outside of the array, where these individuals migrated to the FSA site and were not detected elsewhere within the array or at times other than the peak aggregation period. The total area encompassed by the BBMM UD estimates was 0.67 km² and represents the courtship arena at BDS. The spawning area is embedded in the courtship arena and could not be defined.

Seasonal fishing restrictions that span the entire reproductive period, or spatial closures that encompasses the entire staging area are measures that have been shown to be effective for protecting spawning stocks (Nemeth et al., 2005; Russel et al., 2012; Sadovy de Mitcheson et al., 2012; Waterhouse et al., 2020). Therefore, understanding animal spatial ecology is a critical step to designing effective MPAs or seasonal closure regulations that offer adequate protection during the periods they are most vulnerable to incidental capture or poaching events. Current management strategies for Nassau grouper in the Greater Caribbean region have largely focused

on protecting FSA sites and spawning populations through seasonal closures and MPAs focused on spawning times and locations, respectively (Starr et al., 2007; Sadovy de Mitcheson et al., 2008; Sadovy de Mitcheson et al., 2012; Scharer et al., 2012; Dahlgren et al., 2016). Incorporating spatial buffers around FSA sites large enough to account for the variability and uncertainty in spatial dynamics are well documented (Nemeth, 2012; Russell, Luckhurst & Lindeman, 2012; Rowell et al., 2015), however, less attention has been given to the variability observed in the temporal context. At BDS, Nassau grouper displayed significant inter-annual variability in FSA formation and were recorded not only aggregating after the March 31 end of the closed season, but also making frequent visits to the FSA area after of the aggregation periods observed at BDS (Tuohy et al., in press). Annual protection of FSA sites and their migratory corridors offer the necessary protection for individual fish and to the spawning stock (Nemeth, 2012; Dahlgren et al., 2016). However, in locations where governance and socio-economic factors limit implementation of the necessary protective measures, the incorporation of a seasonal MPA with an adequate temporal buffer (i.e. expanding the closure period before and/or after the known aggregation period) based on local scientific information is warranted. For species whose aggregation season borders the limits of a seasonal closure, a temporal buffer would account for shifts in lunar phase within a synodic month causing the FSA's aggregation period to extend into the following month and leaving the spawning population susceptible to fishing mortality or by-catch impacts like barotrauma. Employing temporal buffers in seasonal closures would be a minimum application of the precautionary principle, especially in data-limited situations or for species already overfished, both of which pertain to Nassau grouper.

Bajo de Sico differs in spatial scale to the other known Nassau grouper FSAs that occur on continental shelves or large atolls. The small population size (Scharer et al., 2014; Garcia-Sais et al., 2020), temporal variability in FSA formation, relative isolation, depth of spawning aggregation formations and reduced spatial scale of habitat use increase the vulnerability of this spawning stock to fishing pressure, whether deliberate or incidental. A recent survey of landings in Puerto Rico (Gedamke et al., 2020) found Nassau grouper to be present in the catch reports for the island indicating the species is currently landed despite regulations banning its year-round capture since 1990 in the EEZ and 2004 in the Puerto Rico territorial waters. Thus, although there is a year-round ban on the fishing and possession of Nassau grouper, a spatial closure at the known spawning area during the complete spawning season would provide protection at a time when aggregated fish are most vulnerable and during their movements back and forth to their home range. The current seasonal closure at BDS (October 1 to March 31) inadequately protects Nassau grouper during the reproductive season, and data suggest it should be extended through June or shifted to encompass the months of December through June. However, the annual closure of BDS would offer the highest level of protection to this highly vulnerable population, in addition to secondarily protecting the spawning and recruitment dynamics of the highly diverse and taxonomically complex fish species assemblages reported for this location (Garcia-Sais et al., 2007; Garcia-Sais et al., 2020)

Equally important to the designation of appropriate protection is that an adequate enforcement strategy exists increased compliance with the regulations. Enforcement has proven exceedingly challenging in Puerto Rico and other remote locations where limited political will, resources and technologies are implemented for adequate surveillance (Aguilar-Perera & Aguilar-Davila, 1996; Sadovy & Eklund, 1999; Sala, Ballesteros & Starr, 2001; Whaylen et al., 2004; Sadovy de Mitcheson et al., 2008; Sadovy de Mitcheson et al., 2012). Consolidating enforcement efforts to focus on reproductive periods would benefit and ensure the optimal use of limited resources. Furthermore, the current multi-use designation of the seasonal MPA at BDS could limit the ecosystem benefits of protection, as multi-use MPAs are more difficult to enforce, and increased anthropogenic activity has been shown to disrupt FSA dynamics (Sadovy de Mitcheson et al., 2012). The prioritization of training workshops for enforcement officials and stakeholders could prove beneficial in enhancing compliance with the regulations designed for the conservation of this species. Positive indications of successful management implementation would be a reduction in landings of Nassau grouper observed from catch reports and/or increase in densities observed from fisheries independent monitoring. Our results not only expand the knowledge of critical habitats used by this species, but also contribute to the knowledge of spawning dynamics at smaller spatial scales and population sizes. Management could use this scientific information to further refine or target enforcement efforts with respect to the specific spawning season and especially, to predicted periods of higher vulnerability. The continuation and expansion of standardized monitoring efforts is essential to further characterize the larger-scale space use metrics, migration corridors and characterizing potential drivers of seasonal variability of temporal dynamics for this FSA.

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Table 1. Summary of acoustic telemetry data from tagged *Epinephelus striatus* detected across all sites during the spawning season. Data are Length (TL in cm), Days Detected (DD), Tracking Period (TP, days), Core Area (CA 50%) and Home Range (HR 95%).

Trans. ID	Length (cm)	Capture Date	DD	TP	No. Detections	Depth Range	CA 50%	HR 95%
1	51	3/2/13	149	1486	14,534	22.74-84.6	0.10	0.46
2	61	3/2/13	1579	1579	137,298	22.75-70.96	0.11	0.47
3	52	3/4/13	89	1484	7,668	20.01-70.05	0.10	0.45
4	60	3/4/13	117	1079	9,950	16.65-80.05	0.10	0.45
6	63	3/6/13	1044	1450	82,760	22.75-94.0	0.11	0.41
7	60	3/4/13	470	1427	12,616	21.23-80-36	0.13	0.62
9	53	4/7/13	1580	1580	139,789	24.26-84.91	0.11	0.46
10	60	4/7/13	1538	1538	146,238	25.47-76.45	0.11	0.46
11	78	1/20/14	117	808	27,195		0.10	0.46
12	71	1/22/14	97	1160	34,974		0.10	0.43
13	73	1/22/14	399	508	72,301		0.10	0.43
14	75	1/24/14	615	1235	104,692		0.10	0.42
15	76	1/25/14	115	1157	27,182		0.10	0.43

16	77	1/25/14	758	774	44,559		0.12	0.51
17	65	1/27/14	19	23	2,315		0.13	0.86
19	63	1/28/14	747	1153	40,375		0.11	0.60
20	75	1/24/14	43	56	9,649	18.52-74.29	0.11	0.48
21	79	1/25/14	66	66	8,556	22.75-69.75	0.13	0.52
22	72	1/25/14	740	912	113,713	33.56-80.36	0.10	0.42
23	76	1/27/14	970	1329	49,550	25.78-77.33	0.13	0.52
24	80	1/28/14	600	1151	26,428	16.68-100.07	0.11	0.48
25	60	2/22/14	20	109	9,196		0.11	0.45
26	52	2/22/14	1250	1250	133,886		0.11	0.47
27	76	2/23/14	84	1128	14,905		0.10	0.43
29	65	2/23/14	18	18	4,796		0.11	0.57
30	76	2/23/14	86	1126	19,123		0.10	0.43

Figure 1. Study area at the Bajo de Sico Seamount, Puerto Rico. (A) Acoustic receiver array at Bajo de Sico with depth contour in 10 m increments (30-100 m). White circles indicate relative location of acoustic receivers with receivers (B) Bajo de Sico in relation to Puerto Rico, Little Sico and the north-west Puerto Rico shelf.

Figure 2. Daily frequency of detection for *E. striatus* during the spawning seasons at Bajo de Sico for (A) 2014, (B) 2015 and (C) 2016. Data are number of detections (blue bars) and number of tags detected (orange dots), and open circle represent the timing of full moons.

Figure 3. Timing of arrival and departure of tagged *E. striatus* to the aggregation site relative to the full moon. Data are mean \pm SD days before or after the full moon of arrival (blue bars) and departure (orange bars) of *E. striatus* at the aggregation site. Black lines indicate the standard deviation.

Figure 4. Spawning space use estimates of tagged *E. striatus* at BDS for (A) all tagged individuals during the spawning season, and (B) seven resident individuals at peak spawning aggregation formation. Orange polygons represent Core Area (50% utilization distribution), green polygons represent Home Range (95% utilization distribution), and white polygon denotes the staging area.

Figure 5. Movements of tagged *E. striatus* that were only detected during the 2014 spawning season. Black lines represent relative migratory pathways used by tagged individuals.

Figure 6. Spawning season depth profile of tagged *E. striatus* containing pressure sensors in years (A) 2014, (B) 2015, and (C) 2016. Data are daily average minimum (orange), mean (blue) and maximum (grey) depths.

