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Diel movements and space use of *Lutjanus analis* at a spawning aggregation site, examined to evaluate the efficacy of a seasonal closed area for management

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ABSTRACT: Designing place-based management for species that reproduce in transient fish spawning aggregations (FSAs) requires knowledge of movements and space use around aggregation sites. We examined the efficacy of the Mutton Snapper Seasonal Closed Area (MSSCA) in St. Croix, United States Virgin Islands, in protecting *Lutjanus analis* from fishing during the spawning season. We used acoustic telemetry to identify the spatial and temporal patterns of movement of 24 mutton snappers over 3 spawning seasons. *L. analis* aggregated from March to July with peak abundance during April, May, and June. Unlike its congeners, which spawn at sunset, *L. analis* spawns in the early afternoon. We were able to determine that *L. analis* used the MSSCA as a staging area during nighttime hours but migrated daily outside the MSSCA for spawning. We also used data from an acoustic Doppler current profiler to examine the relationship between fish movements and coastal current patterns. Fish migrated west in the morning with the prevailing current, occupied the presumed spawning site at slack tide, and then migrated east, again with the prevailing current, back to the MSSCA. We noted that chronic poaching was highly prevalent during the spawning season, reducing the effectiveness of the MSSCA and market closure. In light of our findings, to improve management of the *L. analis* FSA, we recommend re-evaluating the MSSCA boundaries and timing, improving enforcement, and engaging fishers and the community through co-management efforts. Pro-active management is of particular importance, given that this may be the only *L. analis* FSA site on St. Croix.

KEY WORDS: Fish spawning aggregation · Marine protected area · Acoustic telemetry · Movement ecology · Lutjanidae

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1. INTRODUCTION

Many large-bodied species of coral reef fish participate in transient fish spawning aggregations (FSAs), events that occur at predictable times of year in specific locations during which fish migrate tens of kilometers to spawn in high densities (Domeier & Colin 1997). Because of these traits, concentrated fishing on FSAs provides a high catch per unit effort that can mask dramatic spawning population declines (Sadovy & Domeier 2005, Graham et al. 2008, Rhodes & Tupper 2008, Erisman et al. 2011). The status of FSA

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sites worldwide is mostly unknown (54%), and of those for which the status is known, many are in decline (56%) or extirpated (8%) (Sadovy et al. 2008, SCRFA 2023). FSA populations with active spatial and temporal management, enhanced enforcement, and compliance appear stable (29%) or increasing (8%) (Nemeth 2005, Russell et al. 2014, Grüss et al. 2014a, Waterhouse et al. 2020, Rosemond et al. 2022).

Application of spatial fishery closed areas or harvest restrictions during the spawning season are the most common approaches to FSA management (Grüss et al. 2014b, Erisman et al. 2017) and are an integral part of ecosystem-based fisheries management (Pikitch et al. 2004, Appeldoorn 2008). The effectiveness of these techniques, however, can be variable among FSA sites and species (Rhodes & Sadovy 2002, Burton et al. 2005, Nemeth 2005, Nemeth et al. 2006, Pet et al. 2005). Limited success is partly attributed to gaps in knowledge of the extent and timing of movements of reproductive adults relative to the boundaries or timing of fishery closed areas (Eklund et al. 2000, Nemeth et al. 2006, Rowell et al. 2015). By definition, transient aggregating species migrate large distances from home sites to spawning sites, typically spawning during only a few lunar periods of their respective spawning seasons (Domeier & Colin 1997, Nemeth 2009). Most group-spawning species (i.e. those that do not establish spawning territories) continue to move large distances on a daily basis from the spawning aggregation site to staging areas where they rest, visit cleaning stations, or participate in courtship or other activities (Nemeth 2012, Rowell et al. 2015, Feeley et al. 2018, Nemeth et al. 2023).

Spawning aggregation research has been limited because these broad-scale movements and events occur in remote locations and deep water, often during periods of rough seas or poor weather, and many of these populations have been reduced to low numbers, making research more challenging (Domeier & Colin 1997, Sadovy & Domeier 2005). Passive acoustic telemetry can be a useful tool to supplement direct observation and monitoring of these ephemeral events and is effective in tracking target species for extended periods of time and over multiple spawning seasons (Simpfendorfer et al. 2002, Feeley et al. 2018, Nemeth et al. 2023). Acoustic telemetry has been used to document complex movement patterns of a variety of species that form spawning aggregations, including triggerfish (Bryan et al. 2019), groupers (Rhodes et al. 2012, Rowell et al. 2015, Nemeth et al. 2023), snappers (Biggs & Nemeth 2016, Feeley et al. 2018), and siganids (Bijoux et al. 2013). The studies by Rhodes et al. (2012) and Feeley et al. (2018) in particular documented key elements of spawning aggregation dynamics, including tracking grouper *Epinephelus fuscoguttatus* and snapper *Lutjanus analis* from the FSA to their home sites to determine the functional migration areas (FMAs) of these species at these sites.

Documenting the detailed movement patterns within transient aggregating species' FMAs allows estimates of space use, including spawning migration pathways, staging areas, courtship arenas, and spawning sites (Nemeth 2012). Determining the FMA is a critical step in understanding the spatial dynamics and habitat use of local subpopulations and using ecosystem-based fisheries management approaches that increase the persistence of spawning sites and the regional population. The boundaries of spawning protected areas are often based on limited information gathered from traditional fisher knowledge and fishery-independent sampling and surveys, which can lead to insufficient protection from misplaced marine protected area boundaries or timing of seasonal closed areas (Eklund et al. 2000, Farmer & Ault 2011, Kobara et al. 2013, Rowell et al. 2015, Nemeth et al. 2023). As geomorphology and oceanographic currents are important components determining the location of spawning aggregation sites and the potential for transport and retention of larvae (Nemeth et al. 2008, Kobara & Heyman 2010, Chérubin et al. 2011), the spatiotemporal patterns of aggregating species at each FSA site should be evaluated separately. For species that are difficult to study or spawning sites that are poorly known, spatial information from a well-studied site may be applicable to other data-limited areas (Nemeth 2012, Nemeth et al. 2023).

In the United States Virgin Islands (USVI), as elsewhere in the Caribbean, *L. analis* has shown a decreasing population trend and decline in FSA sites throughout its range, and the species is classified as Near Threatened by the International Union for the Conservation of Nature (Claro & Lindeman 2003, Graham et al. 2008, Lindeman et al. 2016). In St. Croix, USVI, several agencies enacted spatial and temporal regulations to protect *L. analis* during the spawning season. The Mutton Snapper Seasonal Closed Area (MSSCA), an area of 8.81 km^2 on the southwest end of the St. Croix shelf, was established in 1993 from 1 March to 30 June each year to protect an *L. analis* FSA site (Kojis & Quinn 2010). An additional market closure prohibiting possession of the species from 1 April to 30 June became effective in 2005 (NOAA Fisheries 2023). Although *L. analis* populations can respond positively to FSA protection (Burton et al. 2005), available species-specific catch data from 2013 to 2017 show that annual landings have declined in the USVI, especially on St. Croix (USVI Department of Planning and Natural Resources unpubl. data). It is unknown to what degree this trend is due to declining populations or declining fishing effort.

Despite decades of protection, it was unknown whether the MSSCA was serving its intended purpose. The placement of the MSSCA boundaries was based on local ecological knowledge and data-limited scientific information (Kojis & Quinn 2010). The MSSCA is centered on the traditional fishing grounds where fishers targeted the *L. analis* spawning aggregation during night fishing (Kojis & Quinn 2010). Fishing for *L. analis* at night occurs elsewhere in the Caribbean (Heyman et al. 2014) and is preferred in St. Croix because catch rates during the day are greatly reduced due to the high abundance of diurnal black durgon *Melichthys niger*, which eats hook and line bait as it descends to the sea floor (J. Sanchez pers. comm.). Additionally, the strong currents along the steep and deep southwest St. Croix shelf edge discouraged fishing with traps and spear guns (G. Martinez pers. comm.); these natural circumstances may protect *L. analis* from fishing mortality during the daytime. Thus, the placement of the MSSCA seemed logical because large numbers of *L. analis* were caught at night during the spawning season at the traditional fishing grounds (Kojis & Quinn 2010). Moreover, the spawning behaviors of *L. analis* at the time were assumed to be similar to other aggregating lutjanids such as cubera *L. cyanopterus* and dog snapper *L. jocu*, which start spawning at sunset (Heyman & Kjerfve 2008, Biggs & Nemeth 2016). However, research from several locations around the Caribbean, including Belize, Mexico, Florida, and St. John, showed that *L. analis* spawn from early to late afternoon (Heyman & Kjerfve 2008, Heyman et al. 2014, Feeley et al. 2018, Heidmann et al. 2021). Moreover, *L. analis* migrate several kilometers between nighttime staging areas and the daytime spawning site (Heyman et al. 2014, Feeley et al. 2018). Therefore, if *L. analis* in St. Croix follow this pattern, then the MSSCA was placed over the nighttime staging area, and the location of the daytime spawning site is still unknown.

The purpose of this study was to provide a contemporary assessment of the MSSCA and its conservation capacity for protecting the St. Croix *L. analis* spawning population. Acoustic telemetry determined *L. analis* movement patterns in relation to existing MSSCA spatial boundaries and closed season timing. Key metrics included timing of aggregation formation, and residency time and space use within and around the MSSCA to determine the level of vulnerability of *L. analis* to fishing mortality during the spawning season. The results show the importance of FSA location and timing for spatial and temporal management of the fishery as well as for potential self-recruitment of the *L. analis* population.

2. MATERIALS AND METHODS

2.1. Study species

Mutton snapper *Lutjanus analis* are common throughout the greater Caribbean region, ranging from Massachusetts, USA, to southeastern Brazil, and occupy a variety of habitats, including submerged aquatic vegetation, sandy areas, mangroves, and coral reefs (Allen 1985). The primary spawning season for *L. analis* occurs from April to July (Graham et al. 2008, Kojis & Quinn 2010), but in some locations can extend from February to August or September (Claro & Lindeman 2003, Heyman & Kjerfve 2008, Claro et al. 2009). *L. analis* are known to form spawning aggregations in the USVI along the shelf edge at the MSSCA southwest of St. Croix, at Tampo, south of St. John, and at the Grammanik Bank, south of St. Thomas (Fig. 1A,B) (Kojis & Quinn 2010, Heidmann et al. 2021). The spawning population of *L. analis* on the St. Croix shelf is geographically isolated from the other 2 USVI FSA sites on the Puerto Rican shelf by the 4000 m deep Anegada-Jungfern Passage (Fratantoni et al. 1997).

As a transient spawning species, *L. analis* typically swim 20–40 km to their spawning aggregation sites (Pittman et al. 2014, Feeley et al. 2018, Heidmann et al. 2021) and begin to aggregate during the first few days after the full moon (DAFM) (Burton et al. 2005, Feeley et al. 2018). Feeley et al. (2018) calculated catchment area, FMA, and staging areas to be 291, 109, and 4.5 km^2, respectively, for *L. analis* in the Dry Tortugas, Florida, USA. Attempts at observing spawning *L. analis* have generally been unsuccessful in many locations (Domeier & Colin 1997, Kojis & Quinn 2010), so the timing of gamete release is poorly understood and may be location-dependent. For example, spawning in this species has been observed in the late afternoon in the Dry Tortugas (Feeley et al. 2018) but in the early afternoon in Belize (Heyman & Kjerfve 2008).

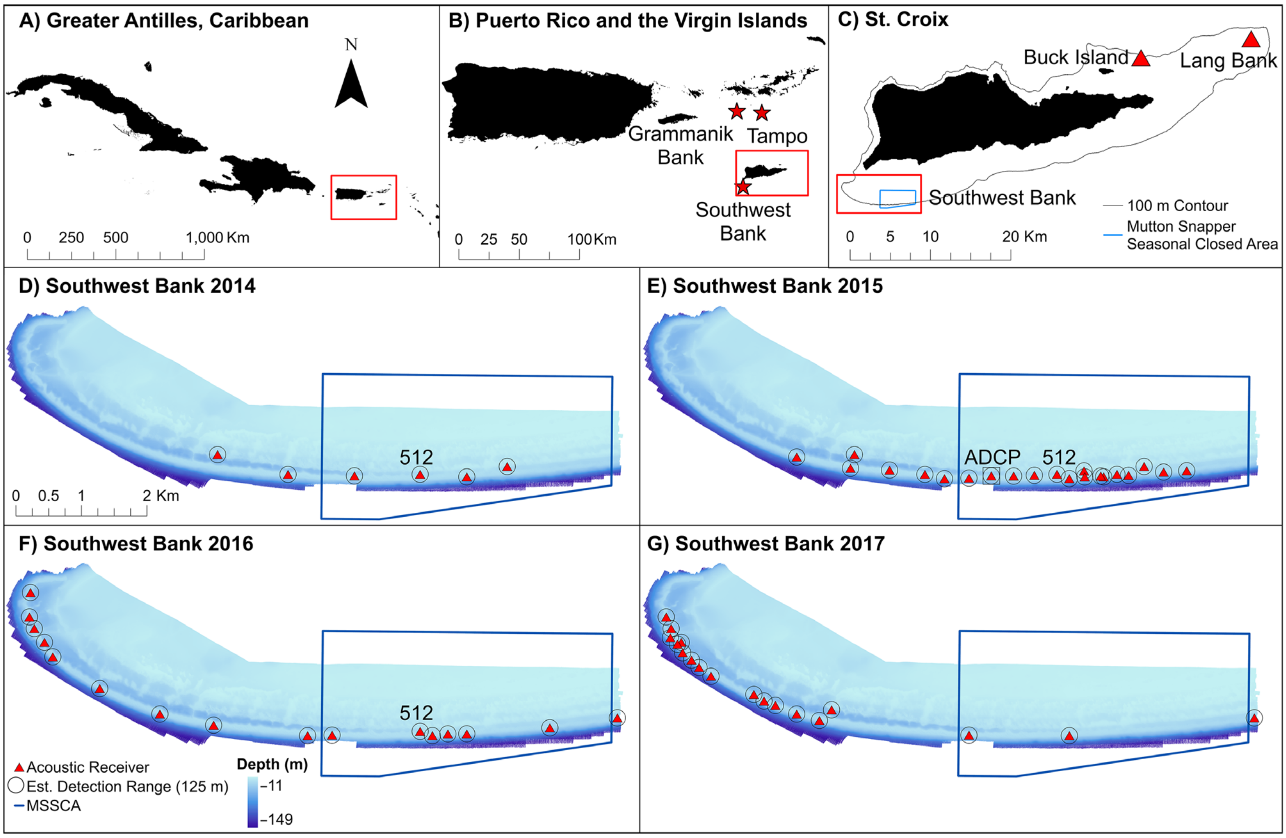

Fig. 1. (A) the Greater Antilles region, (B) Puerto Rico shelf and St. Croix showing locations of 3 known *Lutjanus analis* fish spawning aggregation sites in US Virgin Islands (red stars), and (C) St. Croix, including the Mutton Snapper Seasonal Closed Area (MSSCA) (blue polygon) on the southwest bank and locations of detections for the long-distance migrations of fish no. 59296 (red triangles). Acoustic receiver array during (D) 2014, (E) 2015, (F) 2016, and (G) 2017 spawning seasons. Small red triangles: locations of acoustic receivers, with buffer circles representing 125 m estimated detection range. Location of the acoustic Doppler current profiler (ADCP) during the 2015 season is indicated. Station 512 is where the majority of *L. analis* were caught, tagged, and released. Water depth shown at 10 m resolution (Battista 2015)

2.2. Study sites and underwater visual surveys

This study was conducted within and near the MSSCA, which is located 4 km off the southwestern end of St. Croix (Fig. 1C). The MSSCA is 4.4 km long and 1.7–2.2 km wide, for a total area of 8.81 km^2, and ranges in depth from 12 m to more than 200 m. The benthic habitat along the shelf edge is topographically complex, comprised of spur and groove coral reef and hard bottom habitats dominated by macroalgae cover due to coral bleaching and disease (Quinn & Kojis 2010, Smith et al. 2018). During non-spawning months, *L. analis* are rare within the MSSCA, which is dominated by planktivores such as black durgon *Melichthys niger* and creole wrasse *Clepticus parrae*, followed by herbivores (Scaridae) (Smith et al. 2018).

Underwater visual surveys for *L. analis* during the spawning season were conducted from 2014 to 2017 within the MSSCA and to the west along the shelf edge of St. Croix. A second *L. analis* FSA site (Tampo) located on the shelf edge south of St. John, USVI, composed of sparsely colonized hard bottom habitat, was surveyed opportunistically in May and June of 2015, 2016, and 2017. Surveys at all sites were performed from late morning to late afternoon by divers on open-circuit SCUBA and closed-circuit rebreathers (CCRs), either swimming with the current or using underwater scooters. During surveys, divers towed a surface GPS that was synchronized with a diver's watch and recorded, with timestamps, the number of *L. analis* and behaviors observed. Behaviors that were recorded included group size, direction of swimming, depth and height above the bottom, coloration patterns associated with courtship and spawning, presumed males following females, rapid ascent of groups of fish, and spawning. Videos were also recorded, which were later analyzed for more detailed behavioral and coloration patterns.

2.3. Acoustic array

In May 2014, a small preliminary array of 6 omnidirectional passive acoustic receivers (69 kHz; Model VR2W, Innovasea Systems) were deployed along the shelf edge within the MSSCA where spawning was thought to occur (Fig. 1D). A conservative estimated detection range of 125 m was used to determine receiver spacing (Selby et al. 2016, Bryan et al. 2019), such that the initial array covered 0.3 km^2 (67% inside the MSSCA). Moorings for receivers were constructed using polypropylene line, with the base threaded through a garden hose to prevent chaffing. This protected line was tied to cinder blocks, supported by polystyrene floats, and deployed at 25–42 m depth. Receivers were wrapped in electrical tape and attached to the polypropylene line 1–8 m above the bottom with the hydrophone facing down to maximize detections down the steep slope. SCUBA divers retrieved receivers every year before or early in the spawning season. At this time, receivers and mooring lines were cleaned of biofouling organisms that could grow over the hydrophone and affect detection efficiency (Heupel et al. 2008). Archived data from receivers were downloaded onto a laptop computer into VUE software (Innovasea Systems 2020), and batteries were changed before receivers were rewrapped in electrical tape, initialized, and redeployed.

Each year, the receiver array configuration was adjusted based on spatial patterns found in analysis of the previous year's movements. In 2015, an additional 15 receivers were deployed for a total of 21 receiver stations covering 0.9 km^2, 71% of which were inside the MSSCA (Fig. 1E). Receivers with few detections within the MSSCA in 2015 (Fig. 1E) were relocated to improve fish tracking. In 2016, one receiver was placed on the eastern boundary of the MSSCA to examine when fish left the protected area at the end of each spawning trip. The other receivers were relocated to the west outside of the MMSCA (Fig. 1F), where fish were thought to be spawning based on the timing of spawning observations of *L. analis* at the Tampo FSA site. Observations at Tampo indicated that spawning occurred in the early afternoon and not at sunset as previously thought. Thus, receivers within the MSSCA were relocated to areas where *L. analis* were detected in the early afternoon hours to increase the likelihood of locating the potential spawning aggregation site. Lost and damaged receivers resulted in attrition in 2016 and 2017. In 2016, 16 active receivers covered 0.8 km^2, with 37% inside the MSSCA (Fig. 1F), and in 2017, 13 active receivers were supplemented with 5 additional receivers in May, resulting in 18 stations along the shelf edge covering a total area of 0.7 km^2, 11% of which were inside the MSSCA (Fig. 1G).

2.4. Fish tagging

In 2014, 2015, and 2016, *L. analis* were caught within the MSSCA between March and July from 18:30–22:30 h using hook and line baited with squid, conch guts *Strombus gigas*, scad *Decapterus* sp., or herring *Jekinsia* sp. Prior to insertion of the acoustic transmitter, captured fish were held in flowing seawater tanks, and their airbladder was deflated using a sterilized hypodermic needle (14-gauge, 2.54 cm). Total length (TL) and fork length (FL) were recorded for each fish, a Floy tag was inserted at the base of the dorsal fin, and sex was determined when possible using visual methods (abdominal pressure or canula). Each fish was turned ventral side up to induce tonic immobility without anesthetics, then surgically implanted with an Innovasea acoustic transmitter, either model V13-1L (13 mm diameter, 36 mm long, 6 g; 69 kHz, 147 dB, 110–250 s delay, estimated battery life 1357–1825 d; n = 45) or V13P-1L (13 mm diameter, 48 mm long, 6.5 g; 69 kHz, 147 dB, 30–90 s delay, estimated battery life 565 d; n = 9). A 1.5 cm incision was made approximately 1 cm from and parallel to the ventral midline. The acoustic transmitter was coated in triple antibiotic ointment (Dynarex) and inserted into the peritoneal cavity. The incision was closed using 2–3 chromic gut or nylon surgical sutures (Ethicon, 3-0, cutting FS-1) and covered with triple antibiotic ointment. Fish were observed for at least 2 min to ensure recovery before being released near the bottom using a weighted barbless hook attached to the lower jaw. No IACUC number is available since The University of the Virgin Islands initiated IACUC protocols in 2015, 1 yr after this project began. Fish were tracked from their date of tagging through 22 July 2017, when the array was removed.

2.5. Acoustic data filtering and statistical analysis

Archived transmitter detection data were downloaded from all receivers at approximately 6 mo intervals. Time corrections were calculated for each receiver deployment based on an assumed linear drift using an automatic time-correction function in VUE and applied to the raw detection data. Sensor values from pressure tags were converted to depth (m) using the conversion equation provided by Innovasea for each tag. All data organization and analysis used the R v.4.1 programming language (R Core Team 2022) within the RStudio environment (RStudio Team 2022).

Prior to data analysis, raw detections were filtered to remove potentially erroneous data. Data from the first day of tagging were excluded from analyses in case of behavioral effects of the surgery. Data were also excluded from any fish with less than 10 detections (n = 16) or with irregular activity patterns, such as detections over extended periods at one or two stations, suggesting transmitter loss or fish mortality (n = 11). This quality control process incidentally removed all data from 2014, although one *L. analis* tagged in 2014 (25010) was also detected in 2015, data which were included in the analysis. Detections from the remaining fish that passed filtering criteria (n = 24) were binned into 30 min periods to reduce the potential influence of signal collisions resulting in false detections. Presence or absence was determined for each time bin, and the position for each presence was calculated as the mean latitude and longitude position of the receivers at which each valid detection was recorded within that time bin. All binned spatiotemporal locations were classified into days before full moon (DBFM, negative values) and DAFM (positive values) by counting the days before or after the closest full moon (www.timeanddate.com/moon/us-virgin/saint-thomas?month=6&year=2016), with negative values (i.e. DBFM) greater than 7 d reclassified as positive values (i.e. DAFM) from the previous moon.

Chesson's index was calculated to indicate an overall preference for presence or absence from the full array during the spawning season, accounting for the number of active fish on a daily basis (Chesson 1983). Chesson's indices were also calculated for preference for each month of the spawning season as well as for DBFM and DAFM of the lunar cycle. As not all fish were present during the same months, these variables could not be examined in a single analysis.

To examine movement into and out of the MSSCA, hourly mean longitude of all individuals was examined by time of day, to highlight movement along an east-to-west axis along the shelf edge. A best-fit line was added for each year using LOESS smoothing, pooling all individuals, with days as replicates. The correlation between longitude and time of day (relative to 13:00 h for linearity) was evaluated using Spearman's rank correlation coefficient. The 13:00 h represented the average time of day at which the *L. analis* aggregation reached its western-most position while migrating along the acoustic array. This was corroborated at Tampo, where spawning was most often observed between 12:00 and 15:00 h.

Residence time for all fish was calculated based on the binned locations, such that each half-hour time bin was attributed to a single location and determined to be inside or outside of the MSSCA. Time was standardized by receiver coverage by dividing by the proportion of the array footprint existing inside or outside the MSSCA. This value was converted to a proportion of residence time by dividing by the total standardized residence time.

To examine differences in presence inside or outside the MSSCA at different times of day, a chi-squared test was performed on the frequencies of presence (inside or outside the MSSCA) across time of day from all fish across the entire study. To indicate preference for a specific time, Chesson's index was calculated for inside and outside for each half-hour of the day. This index considers the availability of receivers inside and outside the closed area and reduces the effect of patterns due to variable receiver arrangements.

2.6. Oceanographic patterns

A Nortek Aquadopp acoustic Doppler current profiler (ADCP) was deployed from 4 May 2015 to 2 October 2015 at a depth of 25 m near the western edge of the MSSCA (17.63597° N, 64.87863° W; Fig. 1E). Every hour, temperature was recorded at the head of the instrument (~0.6 m above the substrate), and current speed and direction were recorded in approximately 1 m bins in the water column from the head to the surface. Current speed and direction from each bin were averaged across the lower half of the water column (i.e. 12–24 m) at each time point to obtain the values used to analyze the influence of oceanographic conditions on adult movements.

3. RESULTS

3.1. Spatial and temporal patterns at the FSA site

During 19 d of fishing across 3 spawning seasons in 2014 (n = 9 d in May, June, July), 2015 (n = 6 d in April, May, June), and 2016 (n = 4 d in April, May), 54 *Lutjanus analis* were tagged in the MSSCA: 2014 (n = 5), 2015 (n = 35), and 2016 (n = 14). Five were females, 17 were males, and the remaining 32 were of indeterminable sex. Sizes ranged from 44.0 to 73.2 cm TL, with a mean (±SE) of 55.4 ± 1.0 cm TL (Table 1). In total, 48 of these fish were detected at least once between 15 July 2014 (first detection) and 16 July 2017 (last detection); however, only 24 tagged fish

Table 1. Transmitter number, total length (TL, in cm), sex (male, female, unknown), and detection summary of *Lutjanus analis* tagged in the Mutton Snapper Seasonal Closed Area, St. Croix, sorted by date tagged. † indicates data excluded from analysis and ^{p} indicates pressure transmitter

Transmitter	TL (cm)	Sex	Tag Date (m/dd/yy)	Total number of detections	First detection (m/dd/yy)	Last detection (m/dd/yy)	Days between first and last	Days detected	Total stations detected
25010	53.3	U	7/15/14	558	7/15/14	7/10/15	361	24	20
†25012	73.2	U	7/15/14	8	7/16/14	7/17/14	2	2	4
†25013	44.1	U	7/16/14	174	7/17/14	11/15/16	853	8	3
†24990	45.2	M	4/8/15	1	4/8/15	4/8/15	1	1	1
24991	49.5	U	4/8/15	3621	4/8/15	6/19/17	804	167	36
10832 ^{p}	50.2	U	4/8/15	7896	4/9/15	6/27/16	446	65	26
10833 ^{p}	54.7	U	4/8/15	2767	4/8/15	7/10/15	94	18	20
†10836 ^{p}	66.2	F	4/8/15	13	4/8/15	4/9/15	2	2	4
†10837 ^{p}	65	F	4/8/15	43	4/8/15	4/11/15	4	4	4
24992	59.6	U	4/9/15	441	5/5/15	7/14/17	802	70	34
24993	46.8	U	4/9/15	38	4/10/15	4/11/15	2	2	8
25018	54.5	U	4/9/15	1333	4/9/15	7/16/17	830	69	36
25019	58.7	M	4/9/15	647	4/9/15	6/15/17	799	36	33
25020	48.2	F	4/9/15	853	5/1/15	4/30/16	366	61	25
25007	45.5	M	4/10/15	19	4/10/15	4/12/15	3	3	6
†24994	56.1	U	5/5/15	3	5/5/15	5/5/15	1	1	3
24995	59	M	5/6/15	49	5/6/15	5/10/15	5	5	15
24996	46.5	M	5/6/15	219	5/6/15	5/22/15	17	17	11
24997	54.5	U	5/6/15	95	5/7/15	5/11/15	5	5	15
24998	48	U	5/6/15	105	5/6/15	5/12/15	7	7	14
†24999	52.5	U	5/6/15	369	5/6/15	5/17/15	12	12	3
25000	52	U	5/6/15	33	5/6/15	5/12/15	7	7	10
†25002	47.5	M	5/6/15	1	5/7/15	5/7/15	1	1	1
25004	50	M	5/6/15	34	5/7/15	5/11/15	5	5	13
†25001	44	M	5/7/15	647	6/8/15	5/12/16	340	43	1
†25005	57	M	5/7/15	2	5/7/15	5/8/15	2	2	2
25006	53	M	5/7/15	29	5/7/15	5/12/15	6	6	10
†59300	64.5	U	5/7/15	20552	5/7/15	3/11/16	310	94	3
59301	50	U	5/7/15	71	5/7/15	5/10/15	4	4	7
†10835 ^{p}	65.2	U	5/7/15	2	5/8/15	5/10/15	3	2	2
†10838 ^{p}	58.5	U	5/7/15	130608	5/7/15	11/1/16	545	372	2
†10839 ^{p}	54.5	M	5/7/15	526	5/7/15	5/15/15	9	9	6
†59263	50	U	5/8/15	224	10/19/15	4/16/16	181	26	1
†59264	52	M	5/8/15	7	5/8/15	5/9/15	2	2	2
†59298	52.5	M	5/8/15	99	5/8/15	5/9/15	2	2	5
59283	57.2	U	4/23/16	19	4/24/16	4/28/16	5	4	7
59284	63.8	M	4/23/16	12	4/24/16	4/28/16	5	5	7
†59285	62	U	4/23/16	7	4/23/16	3/18/17	330	7	6
†59286	47.9	U	4/23/16	18	4/24/16	4/27/16	4	2	3
59287	61.4	U	4/23/16	12	4/23/16	5/1/16	9	6	8
†59288	55.3	U	4/23/16	3	4/24/16	5/5/16	12	2	2
†59289	67	U	4/23/16	5	4/23/16	4/27/16	5	2	4
†59290	59.8	U	4/24/16	2	4/28/16	4/28/16	1	1	1
†59291	58	F	4/24/16	3	4/24/16	4/24/16	1	1	1
59292	55	F	4/24/16	123	4/24/16	5/16/17	388	22	18
†59293	58.8	M	4/24/16	7	4/27/16	4/28/16	2	2	5
59295	57.7	U	4/24/16	1126	4/24/16	9/24/16	154	19	15
59296	72.4	U	4/24/16	35	4/24/16	4/29/16	6	5	12

(male: 7; female: 2; unknown: 15) met data-filtering criteria to be included in further analyses (2014, n = 1; 2015, n = 17; 2016, n = 6) (Table 1). Over the course of the entire study, tagged *L. analis* were detected at 38 of the 39 receiver stations on the dynamic acoustic array (6–20 receivers per year) (Fig. 1).

Fish arrived at the MSSCA as early as February and stayed as late as November. Peak spawning months, based on the largest number of fish detected each day, occurred in April, May, and June (Fig. 2). These seasonal patterns were supported by Chesson's index, which showed a higher value for absence from the full array (0.97) than presence (0.03), highlighting the episodic nature of FSA sites. The monthly Chesson's index for inside the MSSCA was highest in May (0.17), April (0.17), and June (0.15), followed by March (0.12) and July (0.11).

Arrival of tagged *L. analis* synchronized around the lunar cycle during the spawning season. From March through July each year, tagged *L. analis* first appeared at the full array 2 DBFM, peaked at 5 DAFM, and most individuals were no longer detected at the full array by 9–10 DAFM. A consistent annual pattern emerged in which fish arrived, on average, 0–2 DAFM during peak spawning months, then arrived successively later in the lunar cycle each

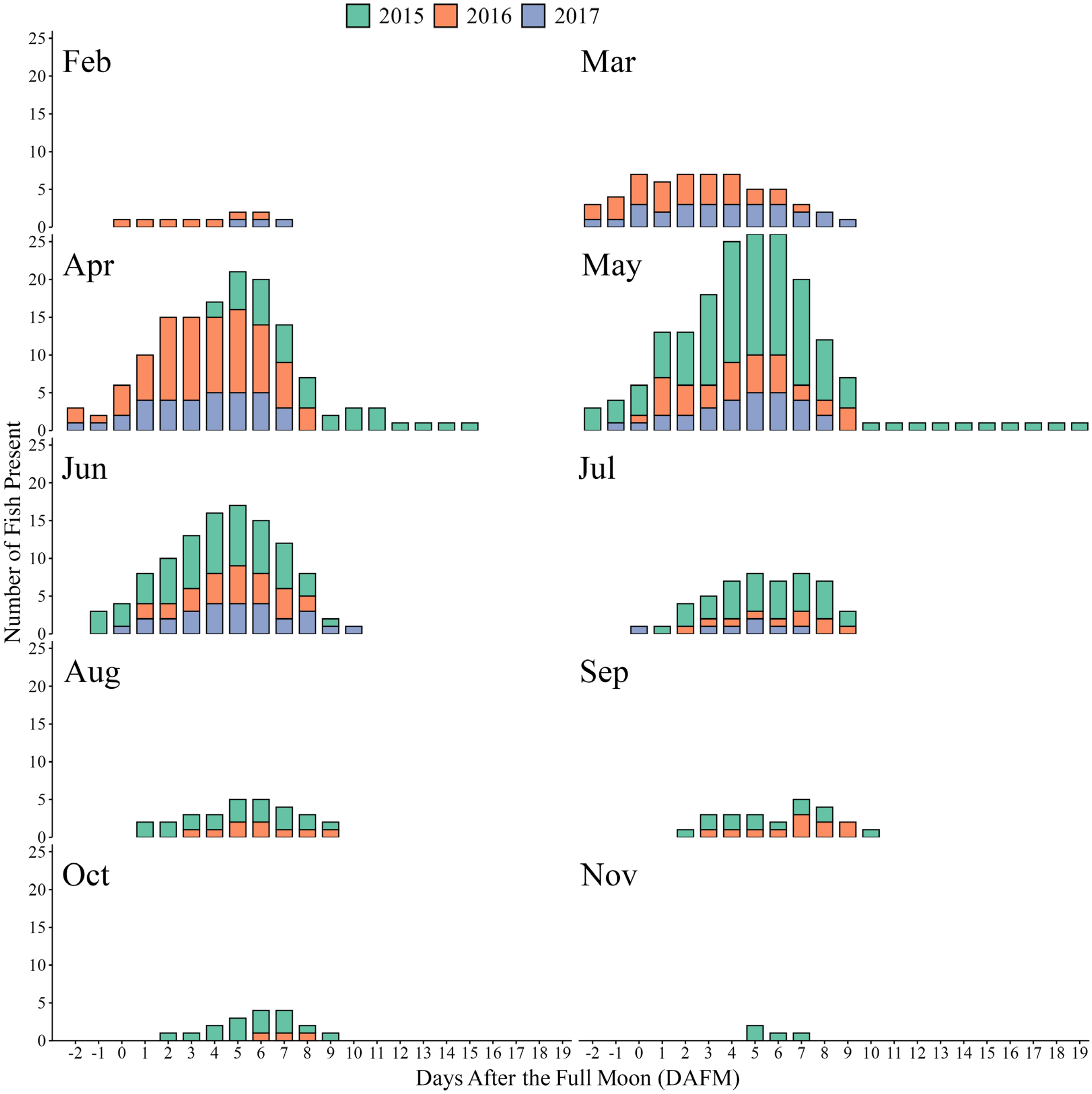

Fig. 2. Number of tagged *Lutjanus analis* detected at the southwest bank array throughout the spawning season each year, in relation to the full moon each month. Color indicates year in which the individuals were detected. No *L. analis* were detected in December or January

month of the spawning season (Fig. 3). Residency time within the full acoustic array was between 1 and 12 d, with a mean of 6.0 ± 0.3 d. Residency time was highest in May and steadily declined through the rest of the spawning season. Chesson's index for DAFM was greater than the expected value for 0–8 DAFM, with 5 DAFM being the highest, closely followed by 4 and 6 DAFM (Fig. 4A). Only 2 fish (24991 and 24996) were present during the new moon, in April and May 2015, respectively, being detected within the full array after other fish had left.

Over half of tagged fish (n = 14, 58.3%) were present at the full array for only one lunar cycle, 10 (41.7%) returned for multiple months (mean: 4 ± 2.0; range: 2–9 mo), and 8 (33%) returned to the aggregation for multiple seasons (4 returned for 2 seasons; 4 returned for 3 seasons). Over the entire tracking period, the mean number of trips into and out of the full array for fish that left the full array for more than 7 d before returning was 9.2 ± 1.7 trips. Within a spawning season, migrating fish took on average 3.9 ± 0.5 trips per year (median: 3 trips; range: 1–9 trips) into and out of the full array. Duration of absence between trips into and out of the full array within a season was between 12 and 31 d, and the median length of absence was 24 d. Between seasons, the duration of absence was between 112 and 322 d, and the median length of absence was 233 d. When fish left the full array for a long absence after the lunar spawning period, the location of the last detection depended on the time of departure: afternoon departures occurred from the western end of the full array, and nighttime departures occurred from the MSSCA.

3.2. Protection efficacy

Overall mean residence time of *L. analis* inside the MSSCA (mean: 49.3%) was highly homogeneous when standardized to the relative distribution of receivers each year. Despite the acoustic receiver area coverage inside the MSSCA declining from 69 to 37 to 13% in 2015, 2016, and 2017 (Fig. 1E,F,G), the standardized residence time inside the MSSCA remained relatively stable at 49, 46, and 53%, respectively. A frequency analysis determined that presence inside relative to presence outside the MSSCA was significantly different than expected across time of day (χ^2_{47} = 1846.8, p < 0.001). Chesson's index for

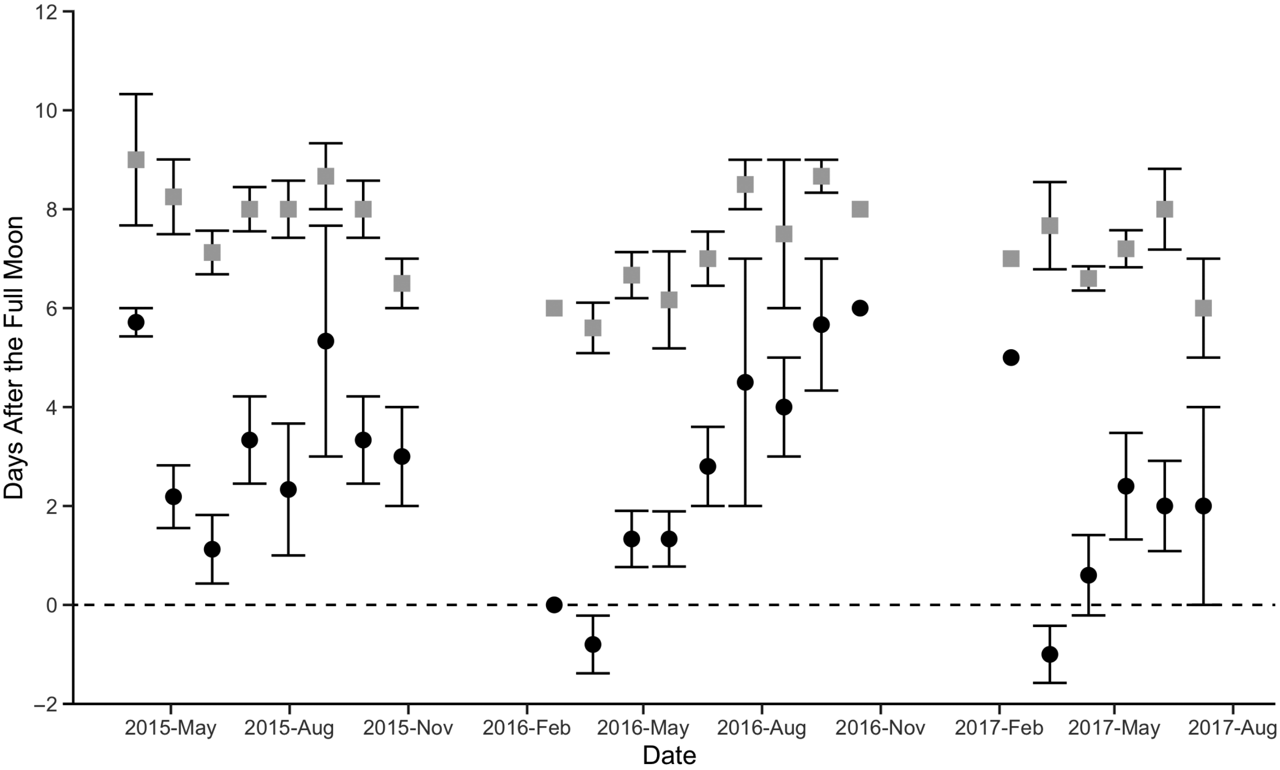

Fig. 3. Average arrival (black circles) and departure (gray squares) dates of tagged *Lutjanus analis* at the acoustic array each month, presented relative to the full moon for 3 consecutive spawning seasons. Error bars: ± SE; lack of error bars means only one tagged fish was present at the array that month. Horizontal dashed line: date of the full moon

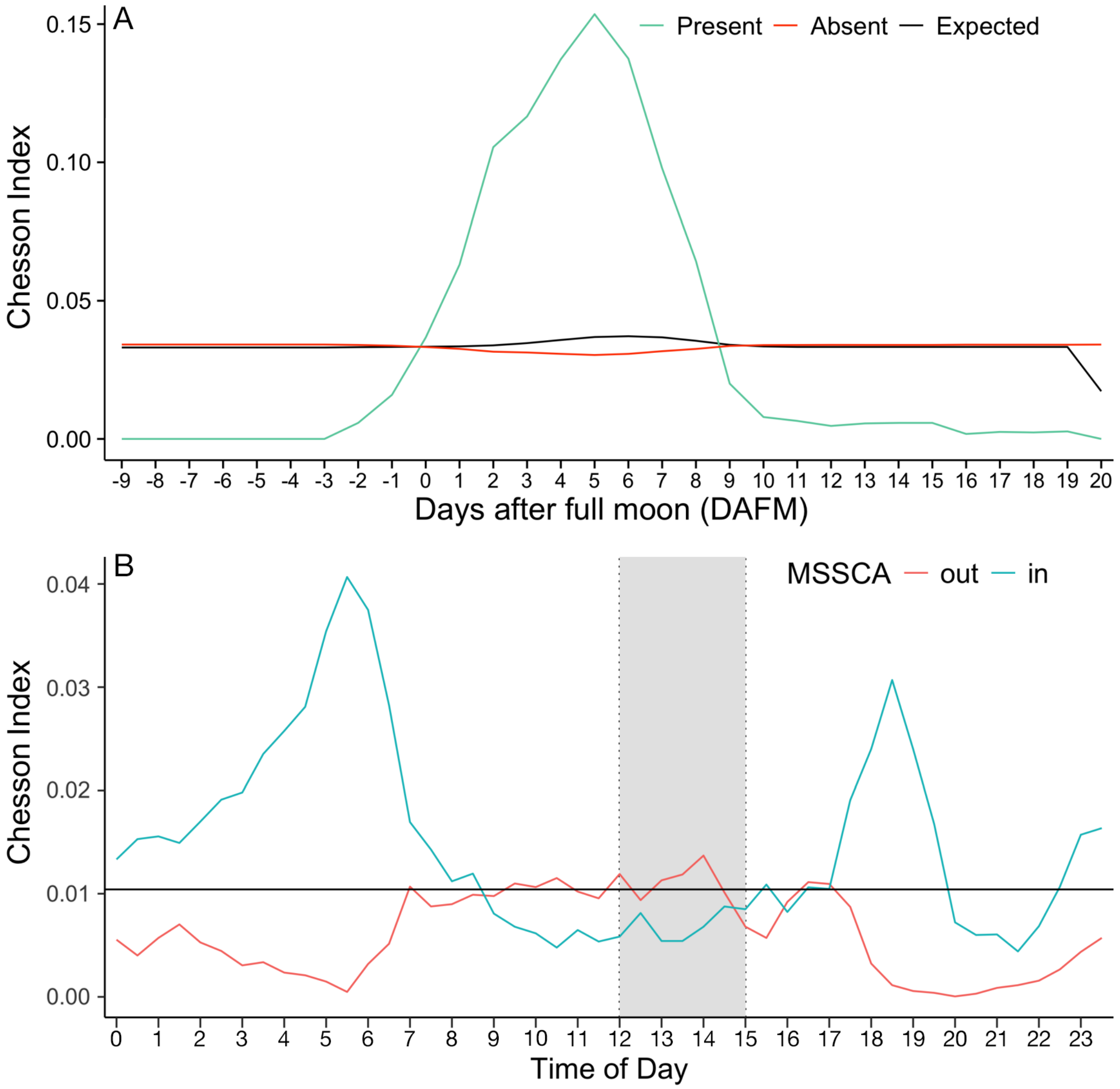

Fig. 4. Chesson's index showing *Lutjanus analis* (A) presence (blue line) or absence (red line) at the full acoustic array during each day after the full moon and (B) inside (blue line) and outside (red line) the Mutton Snapper Seasonal Closed Area (MSSCA) by time of day showing approximate spawning time (gray shaded region). The expected value for each index is shown by the horizontal black line

preference varied greatly throughout the day. Preference for being inside the MSSCA peaked at 05:30 h (high range from 03:00–07:00 h) and 18:30 h (high range from 17:30–19:30 h) (Fig. 4B). Preference for being outside the MSSCA was between 07:00 and 17:30 h, except for a drop in the index between 14:30 and 16:00 h, which may represent fish descending to depths outside receiver detection ranges (see below). The lower detection rates from 14:30 to 16:30 h on peak spawning days (4–6 DAFM) dropped from an average of 179.2 ± 12.8 detections per half hour to 104.8 ± 8.8, a 41.5% decrease. Further examination of this period showed that before absences of longer than a half hour, fish were most often detected at Stn 540 (Fig. 5). Detection rates also showed a 74% decline (46.5 ± 7.2 detections per half hour) from 20:00 to 22:00 h, indicating that fish either left the array or descended to depths outside receiver detection range. This large drop in detections most often occurred at Stns 512 and 537, near the center of the MSSCA. These diel patterns of distribution of tagged *L. analis* are evident for fish during the period of migration (Fig. 6; 06:00–09:00 h), while aggregating at the presumed spawning site (Fig. 6; 12:00–15:00 h) and at their nighttime staging areas within the MSSCA (Fig. 6; 20:00–23:00 h).

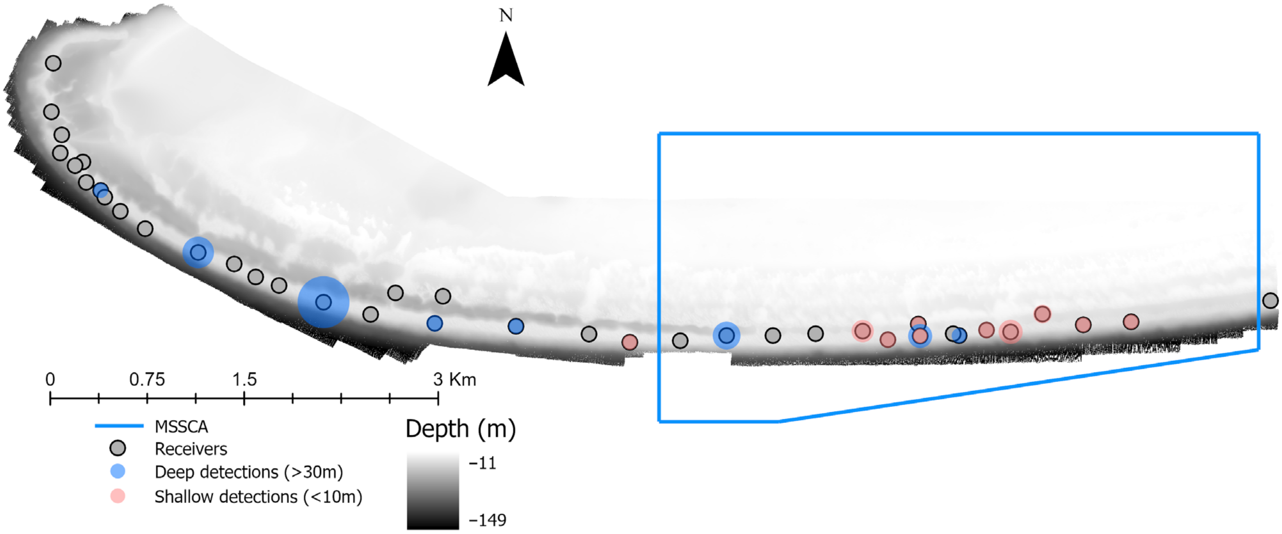

Fig. 5. Receiver stations where *Lutjanus analis* with pressure tags were detected deeper (>30 m, blue) or shallower (<10 m, pink) than normal. Size of the point represents the frequency of deep or shallow detection depths. Gray circles: receivers; largest blue point: receiver station 540. Blue polygon: Mutton Snapper Seasonal Closed Area (MSSCA)

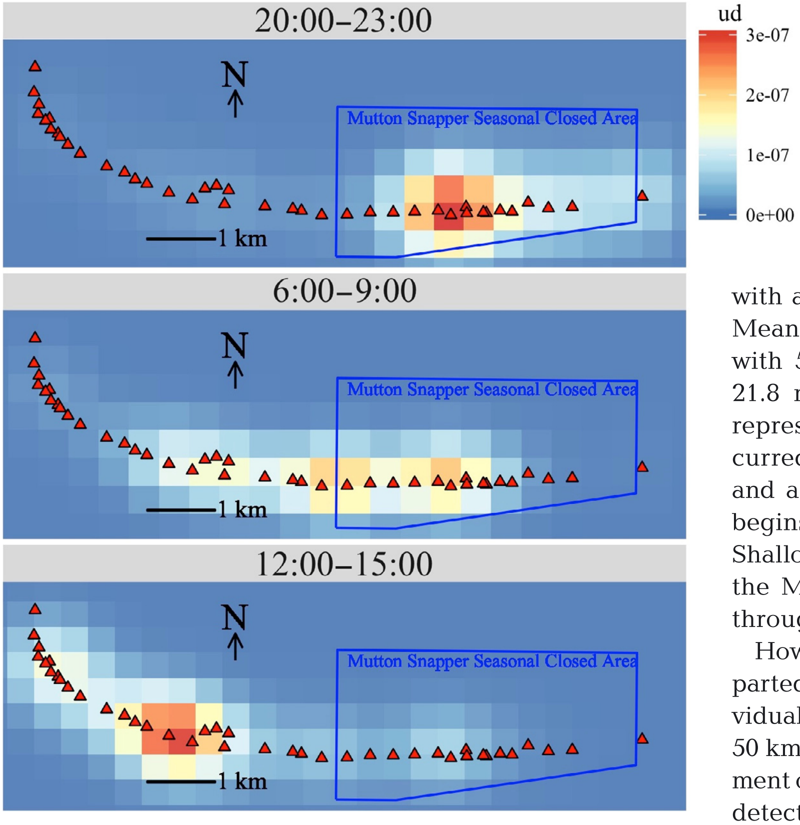

Fig. 6. Kernel utilization distribution (KUD) of all *Lutjanus analis* detected along the southwest bank of St. Croix in 2015–2017, from 06:00–09:00, 12:00–15:00, and 20:00–23:00 h. Red pixels: areas with the greatest densities of fish presence during each time period; dark blue: areas with the lowest densities. Red triangles: receiver locations throughout the study; blue polygon: Mutton Snapper Seasonal Closed Area

Changes in detections at specific times and locations corresponded to vertical movement patterns of the 2 *L. analis* with pressure tags. One of the 2 fish with pressure tags (10832) was detected at between 3.6 and 48.2 m, with a mean detected depth of 19.5 ± 0.03 m. The other (10833) was detected at between 8.2 and 51.9 m, with a mean detected depth of 21.6 ± 0.05 m. Mean depth for both fish was 20.0 ± 0.03 m, with 50% of all detections between 18.2 and 21.8 m. Deep ventures by both fish (>30 m represented 0.5% of all depth detections) occurred most often between 14:00 and 16:00 h and at Stn 540 (Fig. 5), where the shelf edge begins to curve more sharply to the northwest. Shallow ventures (<10 m) tended to be inside the MSSCA and occurred in low frequencies throughout the night and morning.

How far or where fish went when they departed the MSSCA was uncertain, but one individual (59296) traveled a minimum distance of 50 km with a calculated minimum rate of movement of 500 m h^{-1} (13.9 cm s^{-1}). This fish was last detected in the MSSCA on 29 April 2016 (7 DAFM), then detected on 3 May 2016 (11 DAFM) at Lang Bank, and finally detected on 18 and 28 November 2016 within the Buck Island Reef National Monument on receiver arrays deployed for separate studies (Fig. 1C) (Selby et al. 2016, Bryan et al. 2019).

Poaching was prevalent during the spawning season. During 15 of 16 fishing trips (94%) when the MSSCA was closed (3 trips were in July 2014 when MSSCA was open), 1–5 vessels were observed within the MSSCA, with more vessels present when weather and sea conditions were calm. Poachers arrived at the site just after sunset, which occurred from 18:30 to 19:00 h between March and June, and they remained on site after 22:30 h (R. S. Nemeth pers. obs.). All vessels had small lights and were anchored on site, and one vessel had a permanent mooring with surface float. No enforcement vessels were ever seen within the MSSCA.

3.3. Visual observations

Efforts to observe the aggregation and document spawning occurred during 4 spawning seasons at MSSCA and 3 at Tampo. A total of 36 surveys were conducted on St. Croix in 2014 (n = 11), 2015 (n = 2), 2016 (n = 9), and 2017 (n = 14) and 20 surveys at Tampo on St. John in 2015 (n = 8), 2016 (n = 7), and 2017 (n = 5). Diver surveys in St. Croix started within the MSSCA in 2014 (May, June, July) during late afternoon hours near sunset but no more than 5 *L. analis* were seen on any one dive. In 2015 (April, May) and 2016 (April), drift dives from east to west were initiated inside and outside the MSSCA boundary with a maximum of 12 *L. analis* seen on any single dive.

At Tampo, however, surveys in 2015 (May, June), 2016 (May), and 2017 (July) found aggregations of 500 to over 1000 *L. analis* during early to mid-afternoon at 35–60 m depth. On these occasions, *L. analis* were first encountered in large schools swimming into the current and westward along the bottom at 36 m depth. Shortly afterward, the school moved off the shelf edge into about 61 m depth and then alternated ascending to 36 m and descending to about 60 m at regular intervals while drifting east with the prevailing current. At some point, the aggregation swam into the current again, followed by a drift with the current. The first spawning rush at Tampo was observed on 4 June 2015 (2 DAFM) at 12:30 h. Over the next 30 min, we observed several more spawning rushes that were characterized by 10–20 males slowly following a presumed female up into the water column from about 46 to 36 m depth. During all spawning events, *L. analis* in the spawning group developed darkened or black caudal fins and white lips. Similar large aggregations of *L. analis* were seen at Tampo in 2016 and spawning was observed on 26 and 27 May (5 and 6 DAFM) at 14:00–15:00 and 12:15–12:45 h, respectively.

Based on these spawning observations and 2016 acoustic telemetry data at MSSCA, dive surveys on St. Croix in 2017 focused along the far western shelf edge near receivers where numbers of detections were greatest during afternoon hours. During diver surveys from 11 to 15 May 2017 (1–5 DAFM), between 10:30 and 12:30 h, divers on CCR documented 200–500 *L. analis* descending from midwater to just above the reef and ascending from deep water around Stn 540 (Fig. 5). These swimming behaviors were similar to those seen at Tampo. Although no spawning coloration or gamete release was observed, these observations were very encouraging and supported the results of the acoustic study.

3.4. Oceanographic influence on adult movements

The *L. analis* breeding population showed a highly cyclical and synchronized pattern of movement along the shelf-edge into and out of the MSSCA during the spawning season that related to oceanographic current patterns at the site. Typical movements showed *L. analis* swimming west out of the MSSCA in the early morning hours, reaching their western-most extent between 12:00 and 15:00 h, returning east during late afternoon and evening, and being resident within the MSSCA between 20:00 and 23:00 h (Figs. 6 & 7). There was a significant correlation between the longitude of tagged fish and time of day (relative to 13:00 h for linearity; rho = 0.69, $p < 0.001$) that was consistent among years (Fig. 7). These movements corresponded with the direction of bottom currents in the MSSCA that typically alternated between west-northwest and east-southeast. Current direction during days of greatest fish presence (4–6 DAFM) for June, July, and August 2015 tended towards the west in the morning and east in the afternoon (Fig. 8A,C,E) and showed corresponding *L. analis* migration patterns (Fig. 8B,D,F). Mean (±SD) current speed 4–6 DAFM averaged 0.18 ± 0.11 m s^{-1} (range: 0.02–0.63 m s^{-1}) and seawater temperature increased from June (28.3 ± 0.24°C) to August (28.9 ± 0.24°C). Slack low tide on these days averaged 0.06 ± 0.02 m s^{-1} (range: 0.03–0.09 m s^{-1}) and occurred from 15:00–16:00 h in June, 13:00–14:00 h in July, and 11:00–15:00 h in August, when a high proportion of tagged fish were aggregating at the presumed spawning site. Tagged *L. analis* were at the presumed spawning site before slack tide and typically began migrating eastward toward MSSCA after slack tide when the current turned easterly.

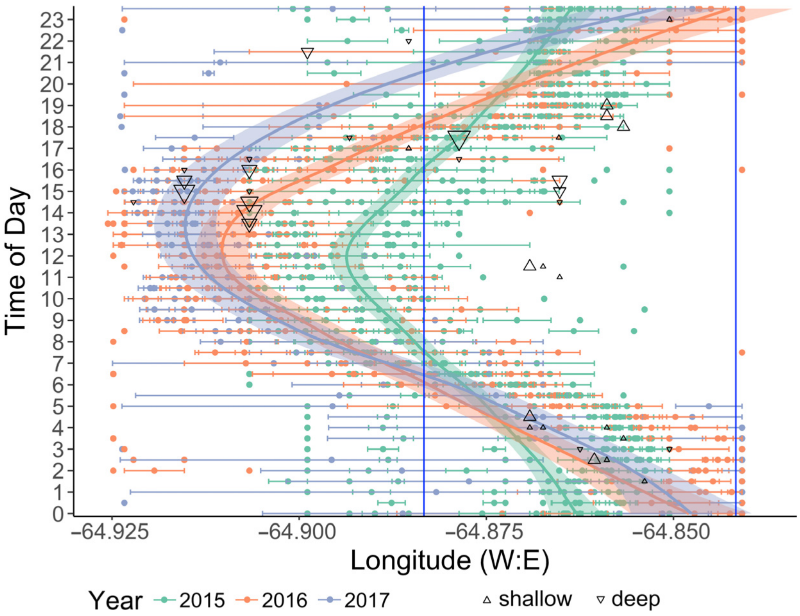

Fig. 7. Relationship of diel movements of tagged *Lutjanus analis* relative to longitude for 3 spawning seasons in 2015, 2016, and 2017. Each point represents the mean longitude (±SE) of all detections of a fish within each hour of the day, with locations organized west to east from left to right. Blue solid vertical lines: longitudinal boundaries of the Mutton Snapper Seasonal Closed Area. Up and down pointing triangles indicate when the 2 fish with depth transmitters were shallow (<10 m) and deep (>30 m), respectively. Size of triangles signifies increasing frequency of hourly detections (range = 1− 8) at each station during spawning season

4. DISCUSSION

4.1. Documenting the spatial components of the St. Croix *Lutjanus analis* FSA site

This study found that *Lutjanus analis* exhibited consistent and daily use of a migration corridor along the southwestern shelf-edge that followed the tide-driven prevailing current during lunar periods of the spawning season (Figs. 4, 6, 7 & 8). Tagged fish moved out of the MSSCA in the morning when the current flowed west towards the western curve of the shelf, remained there through the early afternoon during slack low tide, and then returned east to the MSSCA in the early evening when the current flowed east. Selective tidal stream transport is a common strategy that allows fish in estuaries and offshore coastal waters to cover a greater distance with reduced energy expenditure (Almeida 1996, Gibson 2003).

Evidence for the location of the spawning site relied on several sources of acoustic and visual data. Observations at Tampo, St. John, showed that *L. analis* spawns in the early afternoon in the USVI. Observations of *L. analis* spawning elsewhere are limited but reported at Gladden Spit, Belize (Heyman & Kjerfve 2008), Mexico (Heyman et al. 2014), and the Dry Tortugas, Florida (Feeley et al. 2018), with gamete release occurring 13:00−16:30 h, 16:10 h, and 16:45 h, respectively. If the timing of spawning on St. Croix was similar to Tampo, then the spawning site would be located several km west of the MSSCA. We also found that mean depth of fish with pressure transmitters was 20 m and the largest number of detections at depths of >30 m usually occurred during the afternoon, near Stn 540, which was located 3 km west of the MSSCA. Mutton snapper occur in depths of 25−95 m (Allen 1985), but the deep dives of >30 m were most likely related to spawning behaviors since divers observed groups of 200−500 *L. analis* only at this receiver station. Although gamete release was not observed, courtship and vertical movement behaviors were similar to those seen at Tampo, St. John, and were consistent with the acoustic telemetry data. Telemetry data showed relatively quick depth changes (<10 min) at receiver station 540, indicating that the fish swam straight down the shelf edge and back up. The rapid upward ascent, or spawning rush, causes an expansion of the swim bladder and may facilitate expulsion of gametes during spawning (Randall & Randall 1963). We also observed these deeper descents and rapid ascents at Tampo, where spawning was confirmed, and Heyman & Kjerfve (2008) reported similar observations of *L. analis* that spawned at >30 m depth in Belize.

4.2. Conservation capacity of the MSSCA

Using acoustic telemetry and visual observations, this study evaluated the conservation capacity of the St. Croix MSSCA, established in 1993 to provide spatial protection to *L. analis* during the spawning season. We found that the timing of the MSSCA was mostly appropriate, since April, May, and June were the primary spawning months for *L. analis* on St. Croix, and this has remained consistent for at least 10 yr of observations (Kojis & Quinn 2010). We also found the month of July had similar detection frequencies as March, and therefore should be considered for inclusion in the MSSCA seasonal closed period to improve its protection efficacy.

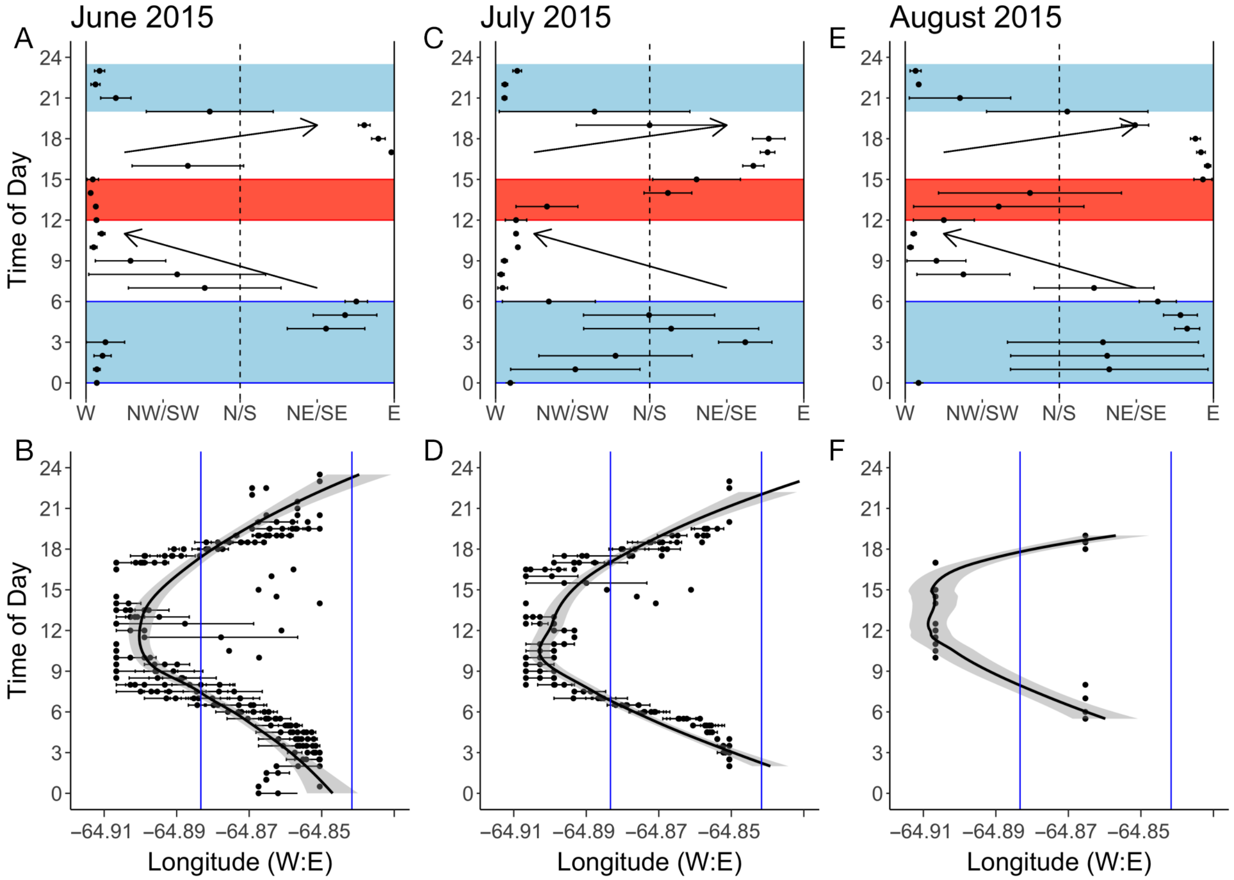

Fig. 8. (A,C,E) Ocean current direction as measured by an acoustic Doppler current profiler and (B,D,F) longitude of tagged *Lutjanus analis* for each hour of the day during peak spawning aggregation periods in 2015 for 6–8 June, 5–7 July, and 4–6 August (i.e. 4–6 d after full moon each month). (A,C,E) Hourly averages (±SE) of current direction; dashed vertical lines represent either N or S. Movement periods of *L. analis* are unshaded regions with arrows showing direction of fish movements. Blue-shaded region: approximate time when *L. analis* fish were within the Mutton Snapper Seasonal Closed Area (MSSCA); red-shaded region: time spawning is thought to occur. (B,D,F) Mean longitude (±SE) of all detections of tagged fish within each hour of the day, with locations organized west to east from left to right. Blue solid vertical lines: longitudinal boundaries of the MSSCA. Note that May 2015 was not included in this analysis since the acoustic Doppler current profiler was deployed in the middle of the May spawning period

Spatial analysis of our acoustic data also discovered a mismatch between MSSCA boundaries and the movement patterns and space use of aggregating *L. analis*. Specifically, we found that *L. analis* used the MSSCA only 49% of the time, primarily as a staging area at night and after spawning, and the current MSSCA boundaries do not include the presumed spawning site, nor do they encompass the primary migration corridor from staging area (i.e. MSSCA) to spawning site. Identifying space use of aggregating species is challenging, since FSAs may occupy distinctly different areas over a diel cycle as fish migrate from staging areas to sites used for courtship and spawning (Nemeth 2012). Therefore, relying only on visual observations or traditional ecological knowledge may increase the likelihood of a mismatch between protected area boundaries and space use during spawning periods (Eklund et al. 2000, Nemeth et al. 2023). When the MSSCA was established, managers used the best available information, which included limited data on *L. analis* and conspecific spawning behaviors and local ecological knowledge from fishers (Kojis & Quinn 2010). The MSSCA boundaries enclosed the traditional nighttime fishing grounds, where fishers targeted *L. analis* during the spawning season, but excluded critical components of this FSA site such as the migration pathway, courtship arena, and spawning site (Nemeth 2009, 2012, Kobara et al. 2013). Recent studies have begun to provide valuable spatio-temporal information for a variety of commercial species, including snappers, groupers, and triggerfish (Biggs & Nemeth 2016, Feeley et al. 2018, Bryan et al. 2019, Nemeth et al. 2023). Feeley et al. (2018) used acoustic telemetry to track

L. analis to their spawning site in the Dry Tortugas, Florida, USA, and estimated an average staging area of 4.51 km^2, which provides a template for spatial management of this species. For example, extending the MSSCA boundaries along the shelf edge 5 km to the west to include the staging area, primary migration pathway, and presumed spawning site of this *L. analis* FSA may increase the conservation capacity of the MSSCA.

4.3. Sustainability and management of the *L. analis* population in St. Croix

The MSSCA boundaries are based on the traditional fishing grounds where St. Croix fishers targeted *L. analis* at night on their staging areas during the spawning season (Kojis & Quinn 2010). Heyman et al. (2014) reported a similar scenario where fishers in Banco Chinchorro, Mexico, caught large numbers of *L. analis* at night on sand flats about 3 km from the actual spawning site. The acoustic data showed that the current MSSCA boundaries enclose the nighttime staging area of fish after spawning has occurred but provide no protection for high-use migration corridors along the shelf edge or the suspected *L. analis* spawning site. Despite this spatial mismatch, the timing of the MSSCA (1 March to 30 June) and the market closure (1 April to 30 June) for *L. analis* in the USVI should be sufficient to protect reproductively active *L. analis* during the spawning season. However, extensive poaching during the closed season and within the MSSCA and an absence of enforcement threaten the *L. analis* spawning stock.

With sufficient spatial and temporal protections, species that spawn in FSAs often show increases in fish length (Nemeth 2005, Stock et al. 2021). Therefore, we would expect the size frequency of *L. analis* at the MSSCA FSA to be significantly better than at unprotected spawning sites. In a fishery-independent study, Olive (2022) compared *L. analis* size frequency distributions among MSSCA and Tampo (unprotected FSA) populations and found no significant difference in mean FL (52.5 vs. 51.8 cm FL, respectively) although the maximum size of *L. analis* at the MSSCA was 17 cm larger (79.7 vs. 62.8 cm FL, respectively). This similarity in mean fish size between the 2 FSA sites could simply be the result of the 2005 seasonal market closure, making *L. analis* illegal to catch in the USVI, thus equally protecting all FSAs during the spawning season. *L. analis* at the Tampo FSA site also appear to cause a higher incidence of ciguatera fish poisoning (D. Greoux pers. comm.), which may reduce or eliminate the incentive for poaching at the Tampo FSA during the closed season. In addition, using fishery independent data (Olive 2022) found no difference in mean FL between *L. analis* caught in the MSSCA in 2009 (51.1 cm; Kojis & Quinn 2010) and this study (52.5 cm; 2014–2016) but found that the maximum FL had increased 13.7 cm (66.0 vs. 79.7 cm) over the 5 to 7 year period. The mean FL of *L. analis* caught within the MSSCA is similar to the mean FL of male (52.3 cm) and female (55.4 cm) *L. analis* (n = 7419 fish) caught by the commercial fishery near the Gladden Spit FSA in Belize from 2002 to 2006 (Graham et al. 2008). This suggests that the extensive poaching that has been witnessed for decades within the MSSCA (Kojis & Quinn 2010, this study) may be having a negative effect on fish length similar to commercial fishing at the Gladden Spit FSA.

In these Caribbean locations, the mean length of *L. analis* represents fish of about 5 yr of age, with the largest fish being 10–15 yr old (O'Hop et al. 2015). Chronic poaching within the MSSCA and extraction of breeding adults can drive population changes in life history characteristics, including declining numbers of spawning adults and changes in sex ratios and size frequency distributions (Beets & Friedlander 1999, Nemeth et al. 2006). Decreasing average length and minimum size at maturity is a known consequence of size-selective fishing pressure (Hsieh et al. 2010). An ecosystem model by Audzijonyte et al. (2013) showed how a 0.1% annual decrease in fish length from size-selective commercial harvesting could drive changes in natural mortality rates, size at reproduction, and fishing yields. Smaller length at maturity estimates were also documented from a long-term study of commercial landings (Stevens et al. 2019), showing that site-specific information is required for management to adapt regulations to changing population characteristics.

Two additional management concerns in St. Croix include the possibility that the *L. analis* population is supported by only one FSA site and that replenishment is largely from self-recruitment. It is likely that the MSSCA is the only FSA site on St. Croix since no other *L. analis* FSA site is known to fishers. Moreover, we found that one *L. analis* tagged in the MSSCA in our study migrated across the entire St. Croix shelf from the southwest to the northeast end of the island, suggesting that the St. Croix population may be composed of a single stock. While some studies have suggested the importance of source–sink dynamics of larval dispersal in replenishing more distant reefs (Roberts 1997, Domeier 2004), others have demonstrated that larval retention can make a significant contribution to local populations (Jones et al. 1999, Swearer et al. 1999). For FSA sites, however, the degree of larval retention or export may be based on species and site-specific conditions (Paris et al. 2005). In Cuba, for example, *L. analis* FSA sites on the west end of the island had greater larval dispersal to neighboring islands while FSA sites along the southeastern and north-central coasts of Cuba had higher larval retention rates (Paris et al. 2005, Kough et al. 2016, Claro et al. 2019).

Potential self-recruitment is most likely during periods when the tide and prevailing currents would bring gametes back onto the natal shelf, maximizing retention (Nemeth et al. 2008, Heppell et al. 2009, Chérubin et al. 2011, Karnauskas et al. 2011, Méndez-Jiménez et al. 2015, Stock et al. 2023). We believe that St. Croix *L. analis* use these consistent daily migrations to move between the staging area within the MSSCA and the presumed spawning site, where fertilized eggs broadcast into the prevailing current may then be carried eastward and onto the southern St. Croix shelf. The St. Croix *L. analis* population might also rely on larval retention and self-recruitment to maintain its population, as described above for several *L. analis* FSA sites in Cuba (Paris et al. 2005, Kough et al. 2016, Claro et a. 2019). If the St. Croix *L. analis* population is partly replenished via larval retention from the FSA site near the MSSCA, then the vulnerability of this population to collapse is greatly increased. Future studies should use genetic parentage analyses to examine recruitment rates of *L. analis* around St. Croix to determine if settlement patterns match the timing of peak spawning or if larvae from elsewhere are replenishing the population. Moreover, virtual particle simulation models would be a valuable contribution to better understand recruitment dynamics and compare this species to previous recruitment studies conducted on St. Croix (Caselle & Warner 1996, Swearer et al. 1999).

Periodic evaluations of marine protected areas are necessary to determine if the target species or harvested populations are responding positively, and if not, to identify when and how management adjustments might be implemented to achieve predicted goals (Nickols et al. 2019). Our study evaluated the efficacy of the MSSCA in protecting an *L. analis* FSA site and found that improvements could be made by modifying existing regulations, improving enforcement, and engaging fishers in co-management actions. Specific adjustments that would align behavioral data of *L. analis* from the acoustic study with MSSCA regulations would include adding the month of July to the closed period and adjusting the MSSCA boundaries to incorporate *L. analis* movements during lunar spawning periods. However, relying only on spatial and temporal closures may not be effective, since the likelihood that poaching will continue is largely based on the distinct attitudes and behaviors associated with different groups of fishers in St. Croix (Carr & Heyman 2012). Improving enforcement by increasing the presence of officers at the MSSCA during spawning periods may discourage poaching but relies on funding and political will. Alternatively, implementing co-management approaches with existing regulations and ensuring that capacity-building and dissemination activities are regularly implemented may produce more meaningful results (Nielsen & Vedsmand 1997, Acheson 2013, Adams et al. 2019, Pelletier 2020). Examples of increased fisher and community engagement activities may include (1) fisher-based enforcement and participation in monitoring and research; (2) frequent updates to user groups of resource status from research and monitoring activities; (3) increased multi-media coverage to inform the broader community and end-users, such as restaurants, of market closures and other regulations; and (4) increased effort on mitigating environmental impacts on adult and juvenile *L. analis* habitats (Lindeman et al. 2000). These community-based actions may strengthen fishers' sense of resource ownership, encourage fisher participation in co-management, and increase compliance with existing regulations (Carr & Heyman 2012).

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