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Spatial and temporal movement patterns of two snapper species at a multi-species spawning aggregation

Christopher R. Biggs[1,*], Richard S. Nemeth[2]

[1]Marine Science Institute, University of Texas at Austin, Port Aransas, Texas 78373, USA
[2]Center for Marine and Environmental Studies, University of the Virgin Islands, St. Thomas, United States Virgin Islands 00802, USA

ABSTRACT: Spawning aggregations of reef fish tend to be predictable in time and space. The extent of movement, residence time and seasonality of the aggregation can be difficult to determine, but are important for effective management. We utilized acoustic transmitters and a receiver array to track dog snapper *Lutjanus jocu* and Cubera snapper *Lutjanus cyanopterus* within a multi-species spawning aggregation site at the Grammanik Bank in the US Virgin Islands from June 2014 to September 2015. Acoustic detections showed that both species utilized spawning areas of 1.4 to 1.5 km^2, centered at the shelf promontory. The aggregation area of *L. cyanopterus* was situated along the shelf edge; the *L. jocu* aggregation may have been displaced by *L. cyanopterus* as it occupied some of the inner shelf as well. Receivers along the shelf edge recorded the longest residence times during the hours of spawning (16:45 to 20:00 h), suggesting this is likely a spawning site for both species. *L. cyanopterus* aggregated monthly from May through November, with residence time peaking in August. *L. jocu* aggregated monthly throughout the year and residence time did not vary significantly by month. Each month, detections increased in the week before and the first week after the full moon, but then decreased to zero by the third week after the full moon. This study outlines the spatial and temporal dimensions of the spawning aggregation, which can be applied to the management and development of protected areas.

KEY WORDS: Acoustic telemetry · Reproduction · US Virgin Islands · Dog snapper · Cubera snapper

INTRODUCTION

Many reef fish species reproduce in spawning aggregations, where conspecifics gather at a specific location in numbers significantly greater than during non-reproductive periods (Domeier & Colin 1997). Although many characteristics of spawning aggregations are similar among species, they also display spatial, temporal and geographic variability (Domeier & Colin 1997). Perhaps the most important common trait is that fish tend to aggregate at nearly the same site annually (Domeier & Colin 1997, Claydon 2004, Heyman et al. 2005), often for decades (Colin 1996). This site fidelity puts spawning aggregations at great risk from fishing pressure (Sadovy de Mitcheson et al. 2008). In fact, fishermen have often targeted these aggregations, which has led to declines in many populations (Beets & Friedlander 1992, Coleman et al. 1996, Claro & Lindeman 2003, Russell et al. 2014).

Dog snapper *Lutjanus jocu* and Cubera snapper *Lutjanus cyanopterus* are important food fish (Claro & Lindeman 2003, Gobert et al. 2005) and have been observed forming spawning aggregations throughout the wider Caribbean region and Florida (Carter & Perrine1994, Domeier et al. 1996, Lindeman et al. 2000,

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*Corresponding author: cbiggs@utexas.edu

Claro & Lindeman 2003, Whaylen et al. 2004, Heyman et al. 2005, Kadison et al. 2006). The earliest report of a *L. jocu* spawning aggregation was by Carter & Perrine (1994), who observed aggregations in Belize at a depth of 25 to 30 m approximately 1 wk after the full moon. Courtship began around sunset, and spawning behavior was observed on the seaward side of the shelf edge; the aggregation would repeatedly swim towards the bottom and then rise rapidly towards the surface. Whaylen et al. (2004) observed a similar event in the Cayman Islands. Lindeman et al. (2000) identified *L. cyanopterus* spawning sites in Florida, and Claro & Lindeman (2003) identified multiple spawning sites around Cuba. Heyman et al. (2005) described spawning behavior of *L. cyanopterus* in Belize that included the cyclical movement within the water column from deep to shallow, but also involved twitching and several fish rubbing the abdomen of presumed females.

In St. Thomas, United States Virgin Islands (USVI), aggregations of *L. cyanopterus* and *L. jocu* have been observed along the promontory of the Grammanik Bank (Kadison et al. 2006, Biggs & Nemeth 2015). Large groups of *L. cyanopterus* (up to 1000 fish) were observed in an aggregation ascending and descending in the water column. Some fish were twitching and had distended abdomens similar to that described by Heyman et al. (2005), and milt was observed being released on 4 occasions (Kadison et al. 2006). The aggregations of *L. jocu* displayed similar behavior, and spawning was observed once in February 2008 (R. S. Nemeth pers. obs.). The largest *L. cyanopterus* aggregations formed between May and August, which coincided with rising water temperature.

L. jocu and *L. cyanopterus* are 2 of the largest lutjanid species in the world (Allen 1985). For *L. cyanopterus*, total length (TL) of 90 cm is common (Smith 1997) and 160 cm is the largest recorded TL (Allen 1985). *L. jocu* are smaller, with an average TL of 60 cm and maximum of 76 cm (Allen 1985). Sexual maturity is achieved at ~65 cm in *L. cyanopterus* and 30 to 40 cm in *L. jocu* (Allen 1985, Martinez-Andrade 2003); there is little to no sexual dimorphism in either species (Domeier et al. 1996, Martinez-Andrade 2003). Lutjanids are gonochoristic; sex ratios of *L. jocu* and *L. cyanopterus* are not known within aggregations or for the species in general, although a 1:1 ratio is typical for yellowtail snapper *Ocyurus chrysurus* (Trejo-Martínez et al. 2011), black spot snapper *Lutjanus fulviflamma* (Kamukuru & Mgaya 2004) and mutton snapper *L. analis* (Kojis & Quinn 2011).

The protection of spawning sites is becoming a more widely used fisheries management tool (Grüss et al. 2014), and these small management investments can generate large conservation benefits (Erisman et al. 2015). Therefore, it is important to understand the spatial and temporal dynamics of species that form spawning aggregations. Specifically, to gain the greatest benefit of an aggregation site that is to be closed to fishing, the timing must coincide with the presence of the target species and the boundaries of the area must be placed to encompass an effective portion of movement and migration around the site. Most studies of Caribbean spawning aggregations have focused on groupers (Sadovy de Mitcheson & Colin 2012, Kobara et al. 2013). Studies that have focused on *L. jocu* and *L. cyanopterus* have used visual surveys to describe the number of fish and behavior within an aggregation (Carter & Perrine 1994, Lindeman et al. 2000, Claro & Lindeman 2003, Whaylen et al. 2004, Heyman et al. 2005, Kadison et al. 2006).

Passive acoustic telemetry provides an opportunity to increase both the temporal and spatial extent of habitat utilization information gathered at spawning sites while at the same time providing a way to document fine-scale movements (Colin et al. 2003, Heupel et al. 2004, Starr et al. 2007, Hitt et al. 2011). Tracking and analyzing movement patterns can also inform the planning of protected areas and stock assessment (Hooge & Taggart 1998). Acoustic telemetry works by implanting acoustic transmitters into fish, which are then detectable by acoustic receivers moored around the tagging location. Data are collected whenever the fish is within range of the receiver. Arrays of multiple receivers can be set up to identify horizontal movements, residence time, home ranges and migration paths (Heupel et al. 2006). Likewise, determining the range and frequency of fish movement in the area of a spawning site can provide important information that can be used in the management of lutjanids and other commercially important species.

This study utilized passive acoustic telemetry and an acoustic receiver array along the south shelf of St. Thomas, USVI to track the movements of *L. jocu* and *L. cyanopterus* at a multi-species spawning aggregation site. The purpose of this work was to gain a better understanding of the duration and spatial extent of fish at an aggregation, and the variability within monthly, weekly and hourly time scales. This information can be used to advance our knowledge of aggregating species and will enhance the effective design of protected areas for spawning aggregations of *L. jocu* and *L. cyanopterus* as well as other species throughout the Caribbean.

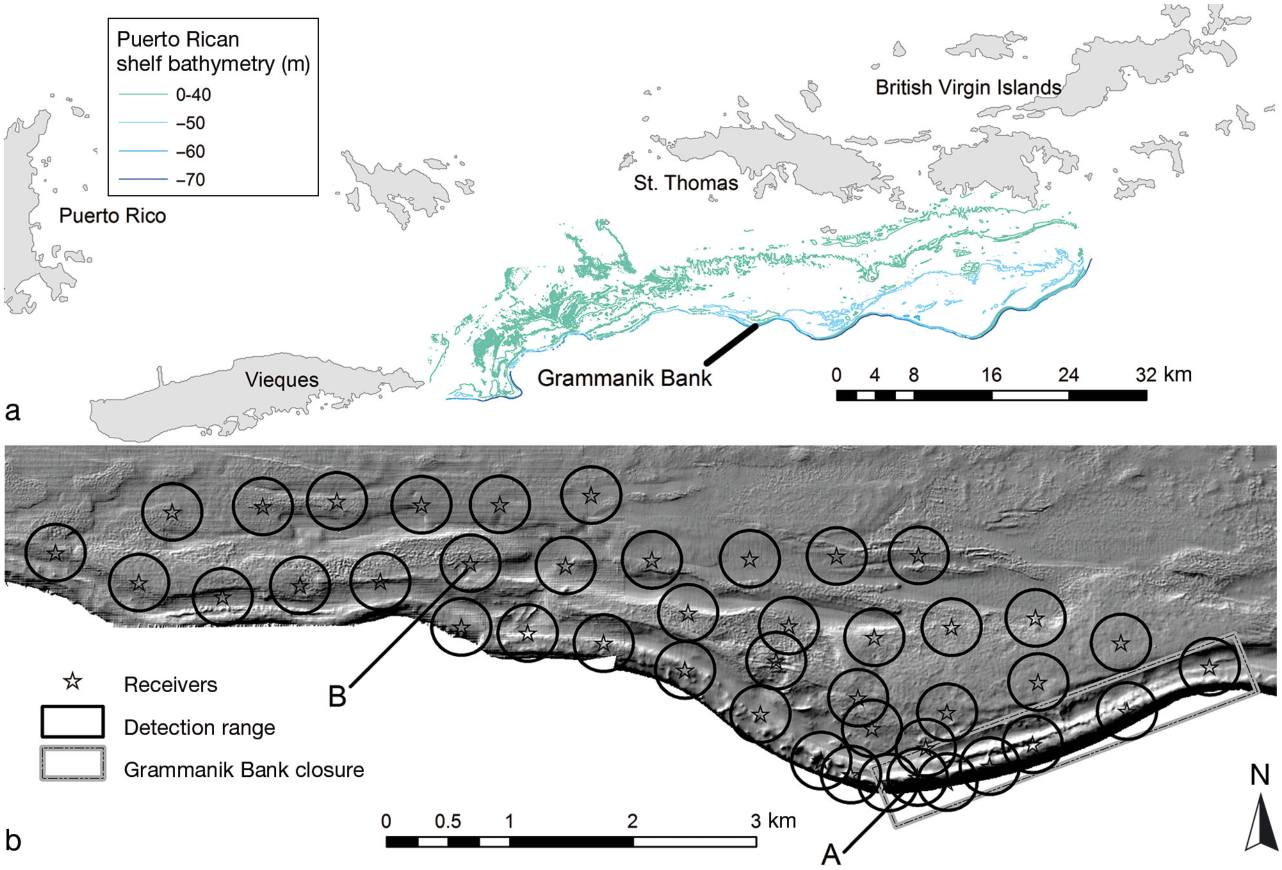

Fig. 1. (a) Bathymetry of the Puerto Rican shelf and the location of the Grammanik Bank, US Virgin Islands: a seasonal closed area and multi-species spawning aggregation site. (b) Acoustic receiver array surrounding the closure area and sites where snappers *Lutjanus jocu* and *L. cyanopterus* were captured, tagged and released (A: 48 fish; B: 3 fish). Circles: range of receiver detection (229 m)

MATERIALS AND METHODS

Study site

The Grammanik Bank is located on the edge of the Puerto Rican shelf, 15 km south of St. Thomas, USVI. It is a seasonal closure area (Feb 1 to Apr 30) designed to protect Nassau grouper *Epinephelus striatus* and yellowfin grouper *Mycteroperca venenosa* spawning aggregations (Fig. 1). The closure is 500 m wide and extends east/west for 3 km. The benthic habitat is primarily composed of a mesophotic coral reef at depths between 30 and 60 m, which includes a combination of *Montastrea/Orbicella* coral and hard bottom interspersed with gorgonians and sponges (Smith et al. 2008). Water temperature, current direction and speed at the aggregation site were recorded with an acoustic Doppler current profiler (Nortek) placed at a depth of 44 m on the shelf edge, and a HOBO temperature logger (Onset) at a depth of 30 m.

Telemetry

Acoustic data were collected with VEMCO receivers (VR2W, 69 kHz) and transmitters (V13, 147 to 153 dB, 13 × 36 mm) with a ping rate of 60 s and battery life of ~450 d. An array that included 42 VR2 receivers was placed along the shelf from the Grammanik Bank eastward ~6 km. Receivers were placed 500 m apart with a tighter cluster of receivers spaced 250 m apart around the suspected spawning site (Fig. 1). They were anchored on the bottom to a cement block with a polypropylene line at bottom depths between 30 and 45 m. The receivers were suspended ~15 m above the bottom pointing downward, supported from above by styrofoam floats. The entire array covered an area of 15.33 km^2.

To implant acoustic transmitters, fish were caught with hook and line baited with squid between 18:00 and 22:00 h (AST), 0 to10 d after the full moon in June, July, August and September 2014. All fish were caught and released at the Grammanik Bank aggregation site near the promontory (Fig. 1; Site A), except for 3 *L. jocu*, which were caught 4 km to the east (Fig. 1; Site B). The fish were placed in a seawater tank on board the boat. TL, weight and gender were recorded for each fish. Gender was determined by cannulation (Felip et al. 2009) or abdominal massage and squeezing (Nemeth et al. 2006). Fish were deemed male if milt was extracted, and female if eggs were successfully extracted. The presence of hydrated eggs indicated that spawning was imminent near the capture/tagging site and supported the classification as a spawning aggregation. The air bladder was deflated with a hypodermic needle (14 gauge, 38.1 mm). A 2 to 3 cm incision was made along the ventral side of the body cavity and the acoustic tag was inserted. The incision was closed using absorbable chromic gut sutures (0.35 mm) and a 24 mm reverse cutting needle. The acoustic transmitter and incision area was covered with antibiotic gel. The fish were placed back in the water and lowered to the bottom with the assistance of a barbless hook and weighted line attached to the lower jaw.

Successful detections recorded the date, time and identification code when a tagged fish was in range of a receiver. Range tests were conducted on 6 of the receivers within the array. The test tag was suspended at a depth of 15 m and pulled across the array by boat while drifting or slowly motoring. Two passes were made in a general east-to-west direction. Coordinates of the tag location and time were recorded every minute. Using ArcGIS (ESRI), the table of test tag locations was joined with the table of receiver detections based on time stamps in both records. Detections were then positioned based on the location of the test tag, and the distance from the corresponding receiver was calculated. The furthest detection recorded for each receiver was averaged over all receivers to obtain the average detection range. The range testing resulted in 75 detections of the test tag successfully joined to the boat location. The detection radius of the Grammanik Bank receivers varied from 150 to 286 m with an average radius of 229 ± 23 SE m. In addition, 5 sentinel tags were placed at various distances (75 to 590 m) around 6 receivers (Stns 153, 151, 150, 103, 102, 9; see Fig. 3 for station locations) within the Grammanik closure area from 15 November to 12 December 2014 (26 d). More than 80% of the 65 136 successful sentinel tag detections were from tags that were ≤229 m from a receiver, further supporting the use of the 229 m average detection radius. Stn 9 had the greatest detection radius and the most successful detections, while Stn 103 had the shortest detection radius and the fewest number of successful detections.

Data analysis

The detections were downloaded from each receiver and analyzed using the VTrack package (Campbell et al. 2012) created for the R environment (R Development Core Team 2008) to identify detection events. Detection events were identified based on the amount of time it would take a fish to swim outside the detection range of 1 receiver (229 ± 23 m) using each species' average swim speed (*L. jocu*: 0.38 ± 0.01 m s^{-1}; *L. cyanopterus*: 0.40 ± 0.02 m s^{-1}) (authors' unpubl. data). Based on these swim speeds and the average detection range, a detection event was created when one receiver recorded at least 2 detections within 19.9 min for *L. jocu* and 19.1 min for *L. cyanopterus*. In other words, to increase our confidence that a fish remained within the area of a designated receiver, detection events were constrained by the time it would take a fish to swim from the receiver to the edge of its detection range. The duration of the event was recorded along with the start time, end time and date. Total detection time was calculated for each fish and station.

Detection events were imported into ArcGIS and displayed according to the receiver location. The distribution of detection events among receivers was analyzed using Hot Spot Analysis in ArcGIS, with individual fish as the sampling unit (Getis & Ord 1992). Receivers that were significantly 'hot' (>90% confidence) were bounded with minimum convex polygons (MCPs) (Hooge et al. 2001) and the areas were calculated. The duration of the detection events was used to calculate the amount of time fish remained within each MCP. To be clear, detection time indicates occupancy within the entire receiver array, while residence time is limited to time spent within the MCP. Total residence time per month within the MCP was summed for each individual and compared for each species using a nonparametric Kruskal-Wallis test and Dunn's post hoc tests with Bonferroni correction (Rogers & White 2007). A kernel density raster was created based on residence time to illustrate spatial utilization within each MCP (Hooge et al. 2001). A Fisher's exact test was used to test for a 1:1 sex ratio for each species (Siegel & Castellan 1988), a Shapiro-Wilk test was used to test for normality of length data, and Mann-Whitney *U*-test analyzed differences in size by sex for each species.

RESULTS

A total of 22 *Lutjanus cyanopterus* were tagged in June (n =14), July (n = 5) and August (n = 3) 2014; 8 were female, 7 male and sex was indeterminate for 7 individuals (Table 1). Hydrated eggs were extracted from female fish, indicating spawning was imminent. The sex ratio for *L. cyanopterus* was 1:1.1 males to females and was not significantly different from a 1:1 ratio (Fisher's exact test, $p = 0.49$). Tagged *L. cyanopterus* ranged from 68.0 to 109.7 cm TL with an average of 92.8 ± 2.3 cm, and the data were normally distributed ($W = 0.95$, $p = 0.25$) (Fig. 2). TL was not significantly different between males and females ($U = 50$ $Z = -0.64$, $p = 0.51$). A total of 29 *L. jocu* were tagged in June (n = 20), July (n = 5), August (n = 3) and September (n = 1) 2014 (Table 1); 7 were female, 11 male and 11 were of indeterminate sex. Hydrated eggs were extracted from female fish, confirming the location as a spawning aggregation. The sex ratio, 1.6:1 males to females, was not significantly different from a 1:1 ratio (Fisher's exact test, $p = 0.45$). Tagged *L. jocu* averaged 65.2 ± 1.2 cm TL with a range of 50.1 to 76.5 cm and were also normally distributed ($W = 0.97$, $p = 0.44$). The TLs of male and female *L. jocu* were not significantly different ($U = 69$, $Z = 0.18$, $p = 0.86$).

A total of 342 905 detections across 36 receiver stations were recorded between 11 June 2014 and 17 September 2015 within the Grammanik Bank receiver array (Table 1). There were 139 608 successful detections of *L. cyanopterus*, which resulted in 33 931 detection events. The average duration of 1 detection event was 16.9 ± 0.4 min (95% CI). Tagged *L. jocu* were detected 203 297 times, resulting in 32 679 detection events. The average duration of 1 detection event was 13.2 ± 0.4 min (95% CI). Out of a possible 463 d, at least 1 *L. cyanopterus* was detected within the array on 181 d and at least 1 *L. jocu* was detected on 322 d. Sea water temperature at 30 to 40 m depth during that period ranged from 26.71 to 28.75°C. The coolest temperatures were recorded in March and the warmest temperatures occurred in September (see Fig. 4). Currents measured at a depth of 30 m over the course of the study varied in direction and speed throughout the day and year, but during the hours of expected spawning (16:45 to 20:00 h) currents were moving predominantly to the southwest at an average heading of 225.2 ± 4.4° (95% CI), at an average of rate of 13.1 ± 0.2 cm s^{-1} (95% CI).

Hot spot analysis identified clusters of stations where fish spent significant ($p < 0.1$) amounts of time based on the duration of detection events. Significantly 'hot' stations for *L. cyanopterus* were Stns 9, 56, 103, 109, 149, 150, 152, 153 and 158, and for *L. jocu* were Stns 9, 102, 103, 109, 110, 149, 150, 151, 152 and 153 (Table 2). A MCP was created around these stations for each species. The *L. cyanopterus* MCP accounted for 89.4% of the total detection time within the array and had an area of 1.4 km^2 (Fig. 3). The MCP for *L. jocu* had an area of 1.5 km^2 and accounted for 88.7% of the total detection time within the array (Fig. 3). The majority of receivers within the MCPs were located on the shelf edge, and the areas of both species overlapped at the tip of the shelf promontory (Fig. 3a). The spatial distribution within each MCP was illustrated with a kernel density raster showing that the highest density of residence time within the MCP for both species was recorded along the shelf edge, but *L. jocu* also showed high densities of residence time 700 m in from the shelf edge at Stn 110 (Fig. 3b).

Of the 29 tagged *L. jocu,* 25 recorded valid detection events at the Grammanik Bank and 4 individuals were removed from analysis (Table 1) due to suspicious detections that indicated either mortality or an ejected tag (nearly constant detections at 1 station). *L. jocu* were detected within the entire receiver array an average of 4.7 ± 1.1 d mo^{-1}, and 14 of 25 individuals were detected in more than 1 mo (5 males, 5 females and 4 of unknown sex). Four males, 2 females and 5 individuals of unknown sex did not return after the month they were tagged (44%).

Over the entire study, 74.8% of *L. jocu* monthly detection time occurred during the 2 wk after the full moon, with no fish present 7 to 9 d before the full moon in any month (Fig. 4). The number of fish within the MCP generally increased in the first week after the full moon and then declined during the next week. Monthly average residence time per fish within the MCP ranged from 18.0 ± 3.8 h in December to 59.3 ± 12.9 h in April, although there were no significant differences among months ($\chi^2 = 18.5$, df = 11, $p = 0.07$; Fig. 5).

Of the 22 tagged *L. cyanopterus*, 19 individuals recorded detection events for an average of 8.38 ± 2.2 d mo^{-1}. Three individuals did not record valid detection events and were excluded from analysis. The majority of detection time (75.6%) was recorded in the first 2 wk after the full moon, and no fish were detected within the array 6 to 9 d before a full moon in any month (Fig. 4). Ten fish were detected within the MCP in multiple months; 4 females, 3 males, and 3 of unknown sex. Two females, 3 males and 4 fish of unknown sex did not return to the MCP after being

Table 1. Detection summary, total length (TL) and sex (M: male; F: female; Unk: unknown) of tagged *Lutjanus cyanopterus* and *L. jocu*, sorted by TL from smallest to largest for each species

Transmitter	TL (cm)	Sex	Tag date	No. of detections	First detection	Last detection	Days between first/last detections	Total days detected
L. cyanopterus								
24955	68	Unk	09/Aug/14	44	09/Aug/14	13/Aug/14	5	4
24930	78.9	M	19/Jun/14	20794	19/Jun/14	06/Sep/15	445	95
24947	81.5	M	15/Jul/14	1298	15/Jul/14	22/Jul/14	8	8
24935	84	F	20/Jun/14	15708	20/Jun/14	06/Sep/15	444	71
24962	84	M	11/Jun/14	5243	11/Jun/14	19/Oct/14	131	53
24926	84.5	M	19/Jun/14	16	19/Jun/14	20/Jun/14	2	2
24928	85.4	F	19/Jun/14	40	19/Jun/14	22/Jun/14	4	4
24958	85.5	M	11/Jun/14	12978	11/Jun/14	15/Nov/14	158	59
24924	87	F	19/Jun/14	3761	19/Jun/14	17/Sep/15	456	46
24960	87	Unk	11/Jun/14	419	11/Jun/14	01/Jul/14	21	10
24952	95.5	M	09/Aug/14	11	09/Aug/14	09/Aug/14	1	1
24953	96.5	Unk	09/Aug/14	14286	09/Aug/14	07/Sep/15	395	110
24949	97.5	F	16/Jul/14	13585	16/Jul/14	17/Sep/15	429	73
24938	98	F	20/Jun/14	21250	20/Jun/14	23/Sep/15	461	120
24967	98	Unk	18/Jun/14	11921	19/Jun/14	05/Sep/15	444	87
24927	98.9	F	19/Jun/14	5693	19/Jun/14	10/Jun/15	357	52
24961	103	Unk	11/Jun/14	335	11/Jun/14	01/Jul/14	21	10
24945	104	F	15/Jul/14	5177	15/Jul/14	17/Oct/14	95	32
24946	104	Unk	15/Jul/14	18194	15/Jul/14	10/Sep/15	423	94
24959	104	Unk	11/Jun/14	645	11/Jun/14	26/Jun/14	16	15
24951	108	M	16/Jul/14	4	16/Jul/14	20/Jul/14	5	2
24929	109.7	F	19/Jun/14	57	20/Jun/14	22/Jun/14	3	3
L. jocu								
24932	50.1	Unk	20/Jun/14	22352	20/Jun/14	07/Feb/15	233	123
24944	50.2	Unk	15/Jul/14	430	15/Jul/14	18/Jul/14	4	4
24964	57	M	17/Jun/14	38	17/Jun/14	17/Jun/14	1	1
24954[a]	58	Unk	09/Aug/14	13682	10/Aug/14	9/Sep/14	31	31
24957	59.8	Unk	20/Aug/14	700	20/Aug/14	15/Apr/15	239	8
24963	61	M	12/Jun/14	47	12/Jun/14	14/Jun/14	3	3
24975	61	Unk	16/Sep/14	21	16/Sep/14	18/Sep/14	3	3
24933	61.2	F	20/Jun/14	2234	20/Jun/14	16/Jun/15	362	4
24939	61.3	F	20/Jun/14	13794	20/Jun/14	17/May/15	332	64
24969	61.5	M	19/Jun/14	3475	19/Jun/14	09/Sep/15	448	25
24972	61.5	F	19/Jun/14	2911	19/Jun/14	01/Sep/15	440	37
24948	62.8	Unk	15/Jul/14	18	15/Jul/14	16/Jul/14	2	2
24923	64	M	19/Jun/14	934	19/Jun/14	28/Nov/14	163	20
24971	64.2	F	19/Jun/14	7937	19/Jun/14	29/May/15	345	49
24931	66	F	20/Jun/14	10221	20/Jun/14	30/Aug/15	437	43
24934	66	Unk	20/Jun/14	28664	20/Jun/14	07/Sep/15	445	120
24965	67	M	17/Jun/14	464	17/Jun/14	20/Jun/14	4	4
24925	67.3	F	19/Jun/14	7	19/Jun/14	19/Jun/14	1	1
24956	67.6	Unk	20/Aug/14	51	20/Aug/14	10/Sep/14	22	4
24950[a]	68.5	Unk	16/Jul/14	49527	17/Jul/14	12/Dec/14	149	135
24942	69	M	14/Jul/14	111	14/Jul/14	17/Jul/14	4	4
24966[a]	69.8	M	17/Jun/14	84762	18/Jun/14	12/Dec/14	178	178
24940	69.9	M	26/Jun/14	401	26/Jun/14	01/Nov/14	129	44
24943	71.5	Unk	14/Jul/14	134	14/Jul/14	16/Jul/14	3	3
24936[a]	71.8	M	20/Jun/14	488	21/Jun/14	12/Nov/14	145	25
24970	72.5	M	19/Jun/14	47001	19/Jun/14	14/Sep/15	453	133
24937	74.2	M	20/Jun/14	7275	21/Jun/14	06/Sep/15	443	69
24941	74.5	Unk	26/Jun/14	121	26/Jun/14	14/Jul/14	19	6
24968	76.5	F	19/Jun/14	466	19/Jun/14	26/Jun/14	8	8

[a] Fish that were not included in analysis

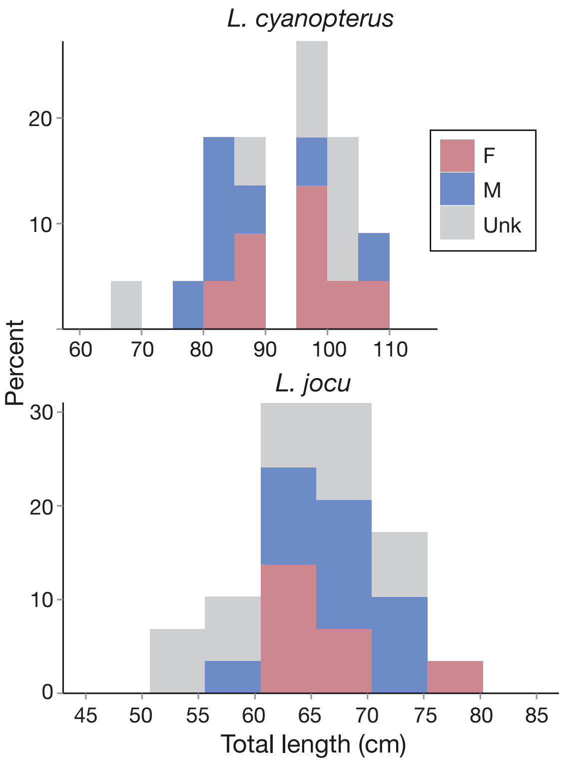

Fig. 2. Size frequency distribution of tagged male (M), female (F) and unknown sex (Unk) *Lutjanus cyanopterus* (n = 22) and *L. jocu* (n = 29). *L. cyanopterus* mean size: 92.8 ± 2.3 SE cm; *L. jocu* mean size: 65.2 ± 1.2 cm

Table 2. Receiver stations recording significant amounts of detection time (90% confidence, $p < 0.1$) for *Lutjanus cyanopterus* and *L. jocu* with *Z*-scores and p-values calculated from Hot Spot Analysis (ArcGIS)

Receiver station	Detection time (h)	*Z*-score	p-value
L. cyanopterus			
150	120.65	2.82	<0.01
158	35.27	2.70	0.01
153	142.73	2.57	0.01
103	1545.99	2.43	0.02
109	116.27	2.26	0.02
149	1414.08	2.26	0.02
152	21.26	2.01	0.04
9	417.73	1.85	0.06
56	1107.63	1.82	0.07
L. jocu			
153	440.85	4.68	<0.01
149	301.97	4.23	<0.01
103	710.52	4.03	<0.01
152	189.83	3.86	<0.01
150	621.97	3.60	<0.01
9	763.31	3.54	<0.01
102	26.68	3.07	<0.01
109	75.09	2.74	0.01
151	30.07	2.24	0.03
110	875.77	1.83	0.07

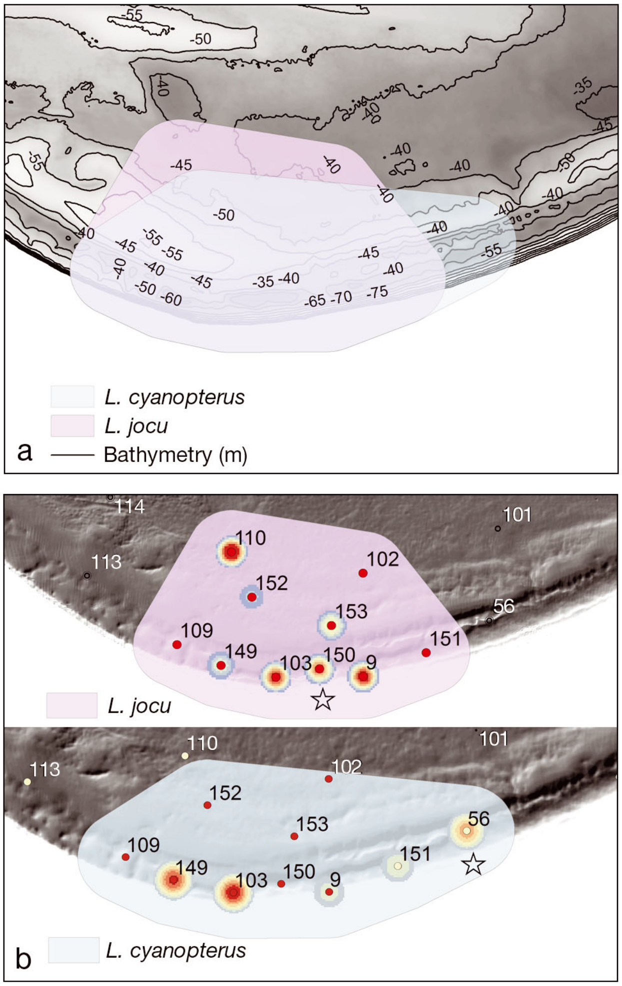

Fig. 3. Minimum convex polygons (MCPs) encapsulating the cluster of receivers identified as significant through hotspot analysis for *Lutjanus cyanopterus* (blue, 1.4 km^2) and *L. jocu* (red, 1.5 km^2). The MCPs account for 89.4% of *L. cyanopterus* detection time and 88.7% of *L. jocu* detection time at the Grammanik Bank spawning aggregation from 11 June 2014 to 17 September 2015. MCPs in relation to (a) the bathymetry (m) of the shelf edge and (b) the kernel density raster for *L. jocu* and *L. cyanopterus* illustrate the density of detection events, with high values in red and low values in blue. Numbers in (b): receiver stations; stars: site of previously observed spawning for *L. jocu* (R. S. Nemeth pers. obs.) and suspected spawning site of *L. cyanopterus*

tagged (40.9%). Average residence time within the MCP increased from May (14.2 ± 11.8 h) to July (73.2 ± 7.5 h) and peaked in August (80.8 ± 7.4 h) followed by declines in September (66.0 ± 9.6 h), October (41.5 ± 8.1 h) and November (24.2 ± 8.7 h) (Fig. 5). There were no detections of *L. cyanopterus* between December 2014 and April 2016. Average residence time per month was significantly different ($\chi^2 = 34.4$, df = 6, $p < 0.01$), and post hoc tests revealed significant dif-

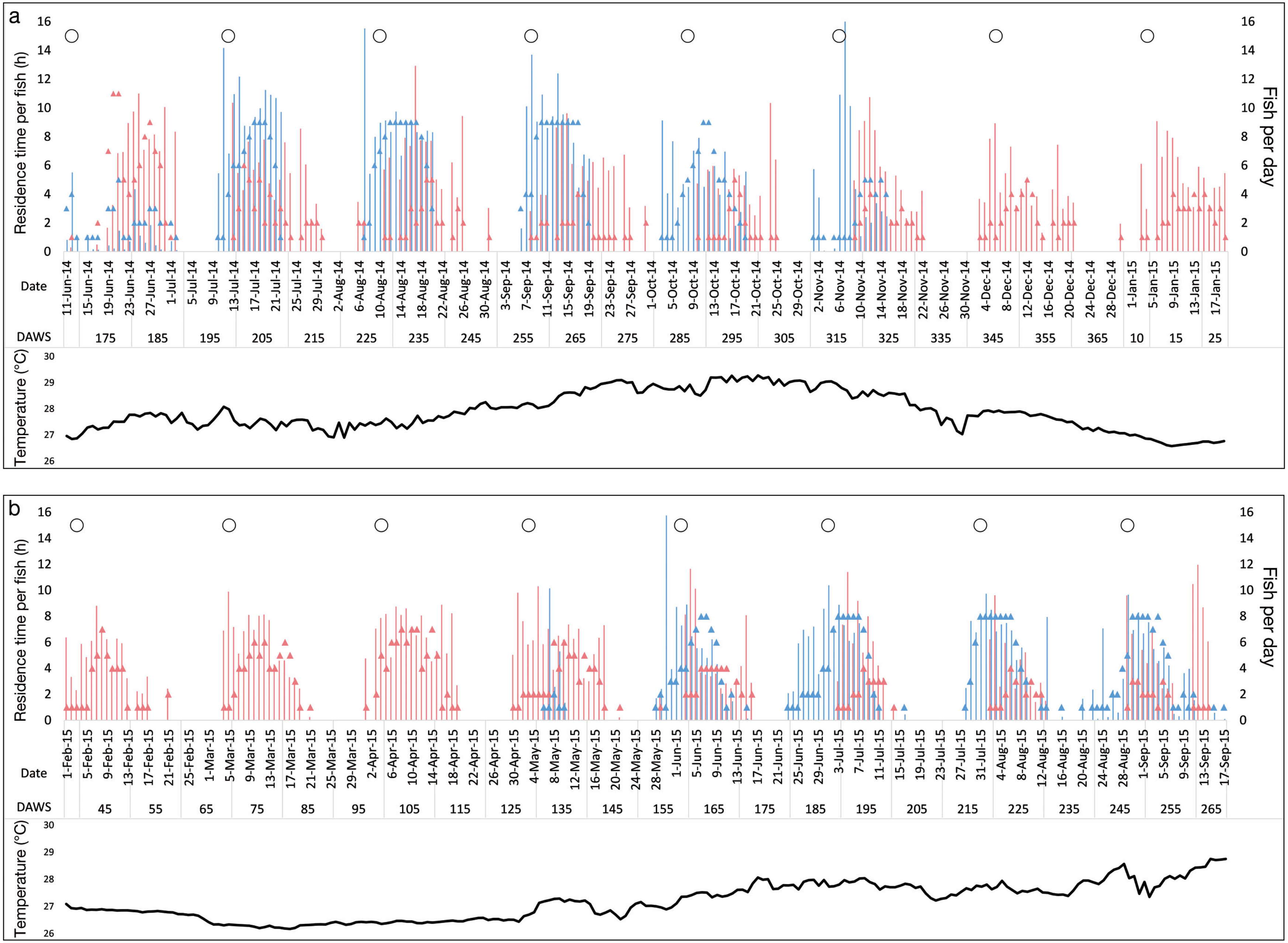

Fig. 4. Average residence time per fish within the minimum convex polygon (MCP) and water temperature by date and days after the winter solstice (DAWS) from (a) 11 June 2014 to 17 January 2015 and (b) 1 February to 17 September 2015 for *Lutjanus jocu* (red) and *L. cyanopterus* (blue). Triangles: number of fish detected during the corresponding day; white circles: date of the full moon. Water temperature was taken at 30 to 44 m depth

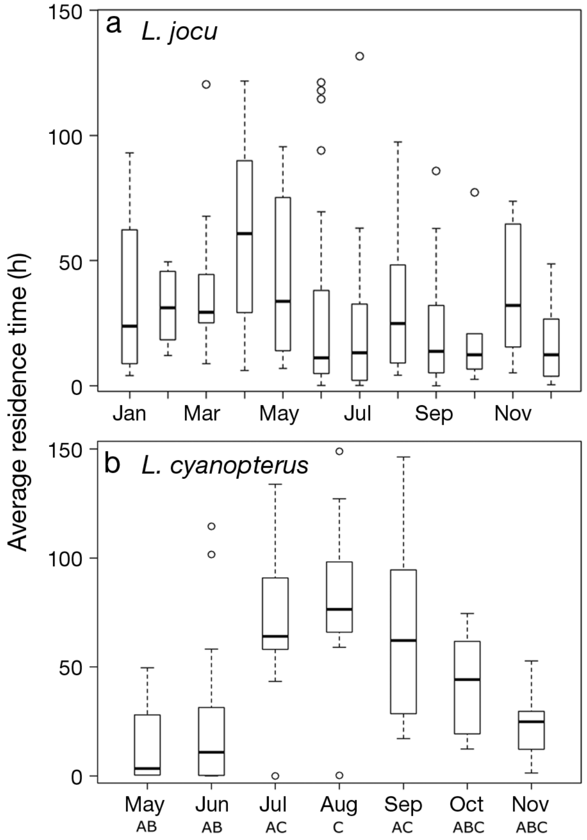

Fig. 5. Average residence time within each minimum convex polygon (MCP) per fish by month for (a) *Lutjanus jocu* and (b) *L. cyanopterus*. Horizontal line within the box represents the median value and the box outlines the interquartile range. Whiskers indicate the maximum and minimum values and circles are outliers. Residence time of *L. cyanopterus* was significantly different among months ($\chi^2 = 34.4$, df = 6, $p < 0.01$). Months with the same letter are not significantly different

ferences between May–August, June–July, June–August and June–September.

The time spent at each receiver station within the MCP varied by time of day for both species (Fig. 6). *L. jocu* spent the majority of the night (19:00 to 05:00 h) at Stns 9 and 150, the morning hours (06:00 to 12:00 h) at Stn 110 and afternoon hours (13:00 to 18:00 h) at Stn 103. Stn 103 recorded the greatest amount of residence time (118.5 h) at 15:00 h followed by Stn 9 (66.2 h). *L. cyanopterus* spent the most time at Stns 103 and 149 from 01:00 to 13:00 h, followed by Stn 56 from 14:00 to 00:00 h. The peaks at Stn 103 occurred at 06:00 h (121.0 h) and 10:00 h (131.1 h). The peaks in residence time at Stn 56 were recorded at 20:00 h (90.0 h) and at 16:00 h (78.5 h), but there was a sharp decrease at 18:00 h (51.0 h).

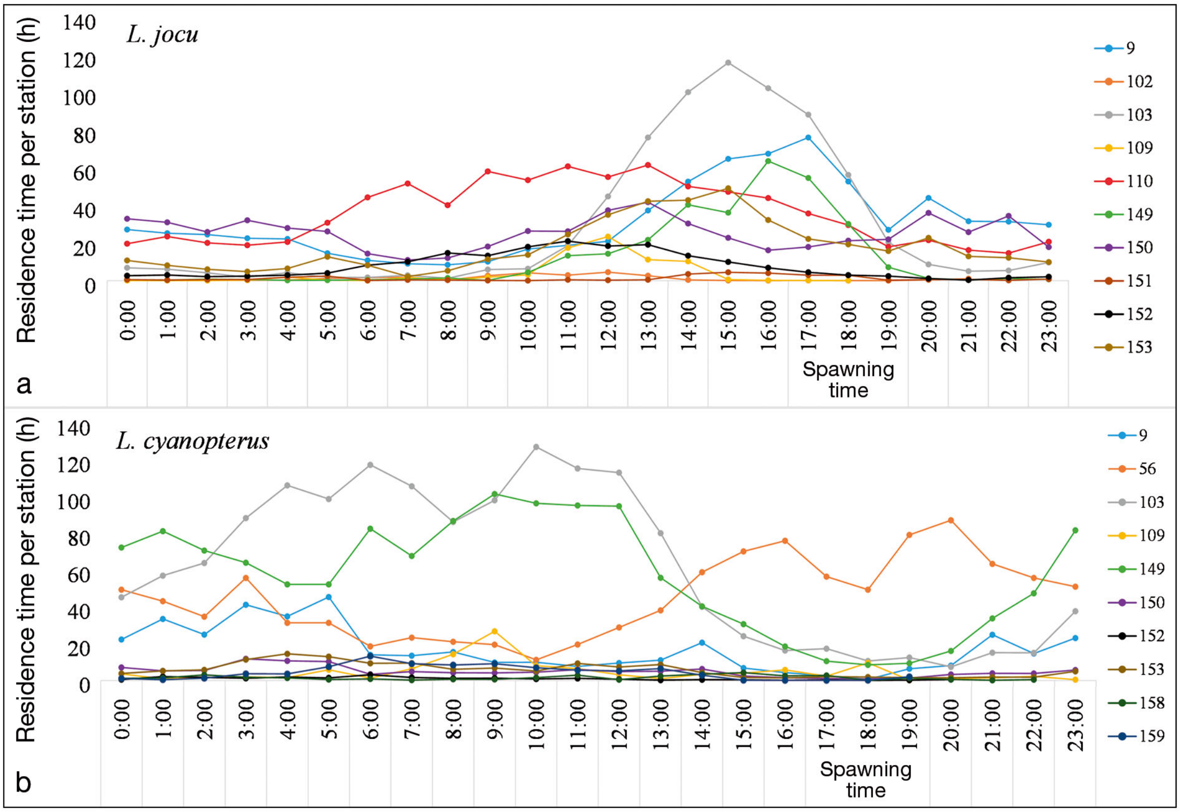

Fig. 6. Total residence time at each station (9, 56^2, 102^1, 103, 109, 110^1, 149, 150, 151^1, 152, 153, 158^2, 159^2) within the minimum convex polygon (MCP) by time of day for (a) *Lutjanus jocu* and (b) *L. cyanopterus*. ^{1}Stations only within the *L. jocu* MCP; ^{2}Stations only within the *L. cyanopterus* MCP. See Fig. 3b for station locations

DISCUSSION

Spatial distribution

Using acoustic telemetry, this study found that within the 15.3 km^2 receiver array, *Lutjanus jocu* and *L. cyanopterus* spent 88.7 and 89.4% of their time, respectively, within a small overlapping area of 1.4 to 1.5 km^2, illustrating tight site fidelity and displaying characteristics indicative of the courtship arena described by Nemeth (2012). The courtship arena is an area in which fish densities dramatically increase and spawning behavior and/or color changes can be observed. Limited studies have quantified this courtship arena, but it is generally <10 km^2 and has been estimated to be ~4.5 km^2 for *L. jocu* and *L. cyanopterus* (Heyman et al. 2005, Kadison et al. 2006). The courtship arenas defined here (as the MCPs) are smaller, but are supported by the detection data and the associated behaviors observed during visual surveys, which match well with other reports. Prior descriptions of courtship behavior found that groups of *L. cyanopterus* would swim slowly along the shelf edge at 30 to 40 m depths, 75 m on either side of the break (Heyman et al. 2005). Likewise, Carter & Perrine (1994) and Heyman & Kjerfve (2008) observed groups of *L. jocu* behaving similarly before spawning where they would swim along the edge of the reef near the bottom at depths of 27 to 50 m. Visual surveys conducted at the Grammanik Bank in association with this study also observed large groups of both species swimming slowly parallel to the shelf break at 20 to 30 m depths, but also ascending to mid water and descending to the bottom as a group at regular intervals.

Spatial distribution patterns were intimately linked to small-scale temporal patterns, where snappers showed distinct movements depending upon time of day. The majority of detections were on the shelf edge promontory, which is a typical location for species that form spawning aggregations (Carter & Perrine 1994, Whaylen et al. 2004, Heyman et al. 2005, Kadison et al. 2006, Kobara & Heyman 2010, Kobara et al. 2013). The *L. cyanopterus* MCP we defined here was situated entirely along the shelf edge. Within the MCP areas, both species showed overlap at Stn 103. The kernel density map showed the most intensely occupied areas for *L. jocu* were Stns 103 and 150, and for *L. cyanopterus* was Stn 103. All of these stations were located on the promontory, but the MCP for *L. jocu* also included Stn 110, which was ~700 m in from the shelf edge. The shelf edge seems to be the preferred habitat for both species, and *L. jocu* may be displaced by the larger *L. cyanopterus* when both species are present at the same time. In fact, the average residence time recorded at Stn 110 was reduced by half when *L. cyanopterus* was not present compared to when the 2 species coincided. *L. jocu* also appeared to occupy more of the eastern shelf edge within the MCP when *L. cyanopterus* was absent (i.e. Stns 113, 109 and 149). The habitat along the shelf edge is predominantly hard bottom, with gorgonians, sponges and sparse coral colonies. North of the drop-off, ~100 m from the shelf edge, is a large sand channel that is ~100 m wide, and separates Stn 103 from Stn 110, which is surrounded by an area of dense coral reef. The spatial distribution of these species relative to the shelf promontory closely matches their distribution patterns within a spawning aggregation site in Belize (Heyman & Kjerfve 2008). However, based on visual observations of *L. jocu* spawning and acoustic detections at time of sunset (when spawning occurs) (Fig. 4), the spatial distribution of these species relative to the shelf promontory shows *L. jocu* positioned more closely to the promontory (Stn 103) than *L. cyanopterus* (Stn 56).

The movement and location of fish within the MCP varied on an hourly time scale (Fig. 6). *L. jocu* spent more time on top of the shelf during the morning hours (06:00 to 12:00 h) and then moved towards the promontory in the afternoon. *L. cyanopterus* were detected most often at the shelf promontory (Stn 103) from 03:00 to 13:00 h, but then moved east to Stn 56 from 14:00 to 23:00 h. Based on reports throughout the Caribbean, spawning occurs in the hour before and after sunset (Carter & Perrine 1994, Heyman et al. 2005). In the USVI, the sun sets between 17:45 and 19:00 h. During that time, *L. jocu* appeared to be moving from Stns 103 and 149 to Stn 150. Spawning at this site has only been observed once for *L. jocu* in February 2008 at 17:49 h between Stns 9 and 103 (R. S. Nemeth pers. obs.) (Fig. 3b), and is consistent with the spatial data reported here. *L. cyanopterus* has never been observed spawning at the Grammanik Bank, but during spawning hours *L. cyanopterus* appeared to move from Stn 103 to Stn 56, which are situated around the shelf promontory (Fig. 3b). During the hours of spawning (16:45 to 20:00 h) residence time fell sharply, but was followed by a peak at 19:00 to 20:00 h. A possible explanation for this drop in detections is that the fish were swimming down the shelf edge, below the depth that the receiver was able to detect (>40 m) as they began the spawning sequence. This effect would be exacerbated if the fish descended below the thermocline, since there is a large reduction in detection range when the thermocline is between transmitter and receiver (authors' unpubl. data). A fish would have to be below the detection range for longer than 19.1 min to avoid recording a detection event, and each fish would have had to be undetected for only ~22 min d^{-1} to cause the observed decline. This behavior has been described for *L. cyanopterus* in Belize, where the aggregation starts deep and then move upwards in the water column in a spiral (Heyman et al. 2005). Testing this hypothesis would require pressure sensitive acoustic transmitters and receivers placed over the shelf edge so that depth ranges could be determined. The drop in detections during the time of spawning may also be the result of an increase in transmitter signal collisions, which could prevent successful detections. Signal collisions and failed detections have been shown to increase as the number of tagged fish within proximity of a receiver increases (Heupel et al. 2006, Simpfendorfer et al. 2008).

Seasonality

The seasonality of the *L. cyanopterus* aggregations is illustrated by the detections and average duration of detection events per month, which began in May, peaked in August and then declined in October and November. There were no detections of *L. cyanopterus* between December and April, suggesting that November is the end of the spawning season. Other reports have suggested that *L. cyanopterus* may begin aggregating again as early as February based on visual survey data (Kadison et al. 2006, Biggs & Nemeth 2015), but none of the fish tagged in this study were detected that early in the year. Our data does support the previous studies that found that *L. cyanopterus* aggregations began forming in accordance with rising water temperatures and ceased when water temperatures began to decline (Heyman et al. 2005). *L. jocu*, on the other hand, were detected each month, and monthly average duration of detection events did not change significantly over the course of the study. This indicates that *L. jocu* aggregate at the Grammanik Bank year-round, which is also in accordance with reports of *L. jocu* aggregations in Belize (Carter & Perrine 1994, Heyman & Kjerfve 2008) and Cuba (Claro & Lindeman 2003).

The ephemeral nature of spawning aggregations for *L. cyanopterus* and *L. jocu* is also evident in the monthly cycle of detections and residence times. All fish left the array by 19 d after the full moon and none were detected in the third week after the full moon in any month of the study. For both species, ~50 % of the tagged fish returned to the array for multiple months. Neither sex nor size affected the time spent at the aggregation or the number of visits per month that a fish was detected. The demographics of the fish that returned were evenly distributed among males, females and fish of unknown sex for both species. Twice as many female *L. cyanopterus* (n = 4) and *L. jocu* (n = 5) returned for multiple months than did not (n = 2 for each species). However, this finding is based on a small sample size and should be interpreted with caution. If these data are indeed representative of the entire population, it would indicate no difference in male and female residence times for these snappers, which contrasts with studies that have noted differences in residence times between male and female grouper at a spawning site. In Micronesia, male camouflage grouper *Epinephelus polyphekadion* and brown marbled grouper *E. fuscoguttatus* arrived at the spawning site several days earlier than females (Rhodes & Sadovy 2002, Rhodes et al. 2012), and Zeller (1998) found that male coral trout *Plectropomus leopardus* in Northern Australia made more trips to aggregation sites than females. However, our data does suggest that there is some degree of turnover of snapper at the Grammanik Bank spawning aggregation, and not all potential spawners are present every month that there is an aggregation.

Length and sex ratio

The TLs of all tagged fish were greater than or equal to the size at sexual maturity associated with each species (*L. cyanopterus*: 65 cm; *L. jocu*: 40 cm) (Allen 1985, Martinez-Andrade 2003). This was expected since the fish were caught at the aggregation site, and it further supports the classification as a spawning aggregation for *L. jocu* and *L. cyanopterus* (Kadison et al. 2006). The lengths of tagged *L. cyanopterus* (68.0 to 109.7 cm TL) were also within the range of lengths observed in Belize (40 to 120 cm TL) by Heyman et al. (2005). In contrast, the lengths of tagged *L. jocu* (50.1 to 76.5 cm) were larger than those observed by Carter & Perrine (1994) in Belize (25 to 35 cm SL). However, it should be noted that while tagged fish were measured, both reports from Belize were based on visual estimates of length. The disparity in lengths between *L. jocu* aggregations may also be attributable to fishing pressure, which can lead to shifts in the size structure (Munro 1996). *L. jocu* are targeted by fishers in Belize but not in the

USVI due to ciguatera fish poisoning. Previous work found that the average size of tagged *L. jocu* was larger than the average size of fish at the Grammanik Bank aggregation as measured with laser calipers mounted on a video camera during visual surveys (Biggs & Nemeth 2015). The difference in sizes between tagged fish and fish within the aggregation may be attributable to the hook size used to catch fish for tagging, which has been shown to affect the mean size of fish caught (Alós et al. 2008) and may effectively select for larger individuals (Nemeth 2005). We also acknowledge that differences in sizes may be attributable to other exogenous characteristics of the particular locations.

The sex ratios of the tagged *L. jocu* (n = 29) and *L. cyanopterus* (n = 22) were not significantly different from a 1:1 ratio. This finding is stated with the caveat of small sample size. Nonetheless, this represents the first report of sex ratio for *L. jocu* or *L. cyanopterus* at an aggregation site. A 1:1 ratio was expected based on information for other snapper species (Kamukuru & Mgaya 2004, Kojis & Quinn 2011, Trejo-Martínez et al. 2011). Despite the fact that lutjanids are gonochoristic, females may live longer and be more abundant at larger sizes (Grimes & Huntsman 1980, Garcia-Cagide 1985, Claro et al. 2001). Indeed, the largest *L. jocu* tagged in our study (76.5 cm) was female. Furthermore, Kojis & Quinn (2011) found that a heavily fished mutton snapper *Lutjanus analis* population in St. Croix, USVI was skewed in favor of males. *L. jocu* and *L. cyanopterus* are not targeted by fishers in St. Thomas, but are actively fished in Puerto Rico (Ault et al. 2008). Connectivity and spawning migrations from eastern Puerto Rico to the Grammanik Bank have been observed in both species (authors' unpubl. data), but it has not appeared to impact the sex ratio of fish visiting the aggregation.

Management implications

Marine Protected Areas (MPAs) have been successful in protecting spawning aggregations from fishing and preserving the viability of the fishery (Alcala 1988, Roberts et al. 2001, Nemeth 2005, Grüss et al. 2014, Erisman et al. 2015). The efficacy of these MPAs is dependent on several factors, including the placement of the MPA boundaries relative to the extent of movement of the fish. Grouper at the Grammanik Bank, which were the targets of the current closures, were found to be within the 3 km^2 closure area only 44 to 75% of the time (R. S. Nemeth unpubl. data). Our data indicate that a closure area of 1.5 to 2 km^2, properly situated, is the minimum size that could protect spawning aggregations of *L. jocu* and *L. cyanopterus* for up to 88.7 to 89.4% of the time. The estimate for this area is based on a MCP and therefore represents the minimum area required by the species in this study. The size of this area would likely need to increase to encompass a greater percent of the individual movements or to accommodate a larger aggregation. However, our observations also show that these fish tend to move as a group within the MCP area, which suggests that the few tagged fish may represent the movements of the larger aggregation fairly well. The tight site fidelity of these snapper offers a distinct opportunity for effective management of their spawning aggregations that may be applicable throughout the Caribbean region.

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Editorial responsibility: Charles Birkeland,
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