



Spawning migration movements of Mutton Snapper in Tortugas, Florida: Spatial dynamics within a marine reserve network

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ARTICLE INFO

Handled by B Arara

Keywords:

Marine reserves

Fish spawning aggregation (FSA)

Fish migration

Lutjanus analis

Acoustic telemetry

Florida keys

ABSTRACT

A marine reserve's effectiveness for sustaining transient spawning reef fish populations is dependent on inclusion of fish spawning aggregations and consideration of the natural spatial boundaries of the populations themselves. Seasonal migrations of Mutton Snapper *Lutjanus analis* between protected nearshore areas and spawning grounds on Riley's Hump in Dry Tortugas, Florida, were assessed from 2008 to 2012 by acoustic telemetry. Individual fish showed synchronized reproductive migrations (up to 5 trips fish⁻¹ yr⁻¹) from resident habitats to spawning grounds swimming at an estimated $63 \pm 18 \text{ cm s}^{-1}$ (mean \pm SD) over minimum linear distances up to 35.2 km. Migrations occurred from April to August, corresponding with the lunar cycle and an increase in water temperature from 25 to 30 °C. Fish arrived on spawning grounds on the full moon and stayed for $7 \pm 2 \text{ d}$ (mean \pm SD). Observations of multiple spawning events made one to five days after the full moon in the late afternoon confirm these movements as spawning migrations. Functional migration areas ($109.59 \pm 61.01 \text{ km}^2$; mean \pm SD), which included estimates of staging/courtship/spawning area ($4.51 \pm 1.84 \text{ km}^2$ [mean \pm SD]) and home site area ($2.50 \pm 1.31 \text{ km}^2$ [mean \pm SD]), were combined to estimate the minimum catchment area of the population studied (291.3 km^2). Although this study focuses on movements and habitat use of a single fish species in the Tortugas, the results are relevant to the design of marine reserve networks intended to protect and manage fishes that undergo transient spawning migrations in other locations as well.

1. Introduction

Lutjanidae and Serranidae include the most commonly listed fishes in the Science and Conservation of Reef Fish Aggregations global database on spawning aggregations (Sadovy de Mitcheson et al., 2008; SCRFA, 2017). These families are not only economically important but include critical primary predators that maintain the balance and diversity of fishes in coral reef ecosystems (Stallings, 2008; Nemeth, 2012). The larger species of the snapper-grouper complex tend to be transient aggregating species that undertake seasonal migrations to discrete sites for reproductive purposes (Thresher, 1984; Sadovy, 1996; Nemeth, 2009). Although the location of numerous spawning aggregations are known, little information is often available on the environmental factors and ecological processes that make these sites unique (Nemeth, 2009; Kobara et al., 2013). The functional migration area is defined by the biological processes and interactions that occur when fish swim between home sites and spawning grounds; collectively

these areas represent the catchment area for the population that uses a particular spawning site (Nemeth, 2012). Understanding the processes that occur within these areas is vital to the successful management and development of protected areas for these aggregating species.

Mutton Snapper *Lutjanus analis* is a transient aggregating species within the family Lutjanidae that migrates to specific sites to create spawning aggregations during specific times of the year (Claro, 1981; Graham et al., 2008; Heyman and Kjerfve, 2008; Claro et al., 2009). Mutton Snapper usually aggregate around the time of the full moon in late spring to early summer and is of significant value to the recreational and commercial fishing industries with 386 mt landed in the Southeast United States in 2013 (Domeier, 2004; O'Hop et al., 2015). The Mutton Snapper population in the Tortugas once aggregated by the tens of thousands to spawn at Riley's Hump (Domeier, 2004; Burton et al., 2005). Riley's Hump is currently located within a marine reserve and is considered the most valuable known lutjanid spawning habitat in south Florida (Lindeman et al., 2000). Nonetheless, little was known

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<https://doi.org/10.1016/j.fishres.2018.02.020>

Received 31 March 2017; Received in revised form 19 January 2018; Accepted 21 February 2018

0165-7836/ Published by Elsevier B.V.

about the movements of adult Mutton Snapper in the Tortugas or the spatial extent of the catchment area of this species prior to the protection of this site. Additionally, the functional migration area and the actual spawning site were not well defined.

Functional migration areas include a wide breadth of biological processes and habitats used by aggregating species, and thus may be appropriate for setting the geographic boundaries to meet ecosystem-based management objectives (Nemeth, 2012). Quantifying movements by acoustic telemetry can provide detailed spatial and temporal information such as directional movement, spawning behavior and residence times (Starr et al., 2007; Nemeth, 2009; Mann et al., 2009; Danylchuk et al., 2011; Farmer and Ault, 2011). In this study, field work was undertaken to monitor the spatial and temporal movements of Mutton Snapper in the greater Tortugas region. The seasonal, annual timing, location, speed and movements of Mutton Snapper between home and spawning grounds were evaluated using telemetry. Established no-take marine reserves provided an excellent system for examining movements across reserve boundaries and to determine if the size and location of these marine reserves are biologically-relevant. This study assesses the effectiveness of a marine reserve network in the Tortugas and is relevant to the design of marine reserve networks intended to protect and manage fishes that undergo transient spawning migrations in other locations. This empirical information can then be applied to influence management and policy (Crossin et al., 2017).

2. Materials and methods

2.1. Study area

The Tortugas region has some of the most diverse marine fauna and complex coral reef habitats in the tropical Atlantic (Davis, 1977; Miller et al., 2001; Franklin et al., 2003; Ault et al., 2006a; Waara et al., 2011). Located near the edge of the Loop Current in southeastern Gulf of Mexico and the Straits of Florida, 225 km from mainland Florida, the region comprises approximately 1243 km² of ocean. The Tortugas includes seven small islands and three carbonate banks (U.S. Department of Commerce, 2000) that make-up the western extension of the Florida Keys archipelago. The banks are individually known as the Dry Tortugas, Riley's Hump and Tortugas Bank (Fig. 1). The geomorphology of the Dry Tortugas is described as a circular, shallow-water atoll (Vaughan, 1914) and numerous high-relief banks, sandy channels, and reef margins to approximately 24 m in depth. Tortugas Bank, located west of the Dry Tortugas contains complex high-relief patch reefs and deep reef terrace habitat (Miller et al., 2001) at depths of 20–40 m. Riley's Hump, approximately 20 km southwest of the Dry Tortugas, is a low-relief, predominately hardbottom bank, that rises from surrounding deep waters to approximately 30 m.

Dry Tortugas National Park (Dry Tortugas NP) was established in 1992, closing the park to all forms of fishing except recreational hook and line fishing (i.e. no commercial fishing, no lobstering and no spearfishing). The Research Natural Area (RNA) and the Natural Cultural Zone/Historical Adaptive Use Zones (NCZ/HAU) were added within Dry Tortugas NP in 2007 (Brock and Culhane, 2004). Recreational fishing is still allowed in the eastern half and southern part of the park (NCZ; 125 km²) and the area immediately around Garden Key (HAU) (Fig. 1). The RNA is a no-take marine reserve that closed the western half of the Dry Tortugas NP to fishing (119 km²). In 2001, two large non-contiguous no-take marine reserves were also established (355 km²); the Tortugas North Ecological Reserve covering the northern half of the Tortugas Bank and the Tortugas South Ecological Reserve (TSER) that shelters the spawning grounds on Riley's Hump and deep water habitat to the south.

2.2. Telemetry array

An array of 84 Vemco acoustic receivers (Vemco, Bedford, NS)

covering approximately 800 km² of the greater Tortugas region was deployed in three phases from May through July 2008. The array was shared with two collaborative acoustic telemetry projects managed by Mote Marine Laboratory and the U.S. Geological Survey (USGS) (Whitney et al., 2010; Hart et al., 2012). Receiver sites were selected based on reef fish population density estimates from visual population surveys, 200 m × 200 m gridded benthic habitat maps, bathymetry maps, reserve/park boundaries, and established monitoring sites (Ault et al., 2006b; Burton et al., 2005). Receivers were broadly placed between 650 and 4000 m apart to maximize spatial coverage but recognizing 100% detection probability was not possible. The complete multiagency array was designed to capture small-scale movement and long-range migrations of fishes, sharks and turtles in water 12–50 m deep.

The acoustic receivers were positioned one meter above the seafloor in a PVC cup (63.5 or 76.2 mm dia.) similar to the arrangement described by Bertelsen and Hornbeck (2009). The PVC cup was attached with PVC cement to the top of a 60-cm-long PVC pipe (25.4 or 50.8 mm dia.) anchored in a concrete base (~36 kg) that provided ballast and stability. The exposed hydrophone tip of the receiver coated with antifouling paint was oriented toward the sea surface. Acoustic receivers were serviced and downloaded every six months using VUE software (Vemco, Bedford, NS) until September 2012.

Temperature data were collected by Hobo® waterproof data loggers (Onset Computer Corp; Bourne, MA) deployed at two locations in the study area. Loggers were positioned on the seafloor on Long Key Reef (14 m) and at two stations on Riley's Hump (33 m). Loggers collected temperature readings hourly, and data were downloaded annually. Mean daily temperatures were calculated for each site.

2.3. Acoustic tagging

Mutton Snapper were caught by hook and line or fish traps (5.1-cm × 2.5-cm, vinyl-coated 14-ga wire) within Dry Tortugas NP and at Riley's Hump. Traps were baited with Atlantic Thread Herring *Opisthonema ogliman* and Spanish sardines *Sardinella aurita* and deployed for 3–12 h. Fish caught in shallow water (< 15 m) were first brought to the surface, and if necessary, had their air bladder deflated with a hypodermic needle. Fish caught in deeper water (30–40 m) were all tagged underwater to avoid complications and mortalities associated with barotrauma (Starr et al., 2000; Lindholm et al., 2005). Trapped fish were transferred from traps using a catch bag by divers at depth.

All fish (both surface tagged and underwater tagged) were placed ventral side up in a V-cradle surgery station and their length recorded. Each fishes' eyes were covered with a towel or neoprene hood, and for surface tagging raw, seawater was flushed across the gills. In this position, fish remained still (catatonic), which is considered an ethical alternative to using a sedative (Lowerre-Barbieri et al., 2014). An incision approximately 2.5 cm long was made along the midline, posterior to the pelvic girdle. Scales were removed on either side of the incision to expose the skin. Coded transmitters (Vemco V16 (P)-4H-R04K or R64K; frequency 69 kHz; 16 mm diameter × 68 or 71 mm length) were implanted in the abdominal cavity via a 2.5 cm incision. The open incision was closed with a size 0 cutting needle and sterile synthetic absorbable braided suture (VICRYL Plus; Ethicon Inc., Somerville, NJ). Surgery times took 3–6 min. Fish tagged at the surface were placed in a holding tank with an aerator until it was confirmed they were neutrally buoyant and active (< 15 min). Surface tagged fish were then transported in a clear polyethylene bag from the surface to the bottom by a diver and released. All fish tagged in-situ were released immediately after surgery was completed. Initially in Dry Tortugas NP (May and October 2008), transmitter interval varied from 20 to 69.2 s or 30–90 s with an estimated tag life of 470 or 820 days. All tags used at Riley's Hump and throughout the remainder of the study were configured with a transmitter interval of 50–130 s with an estimated tag life of 1122–1160 days (Table 1). During suspected spawning times, divers

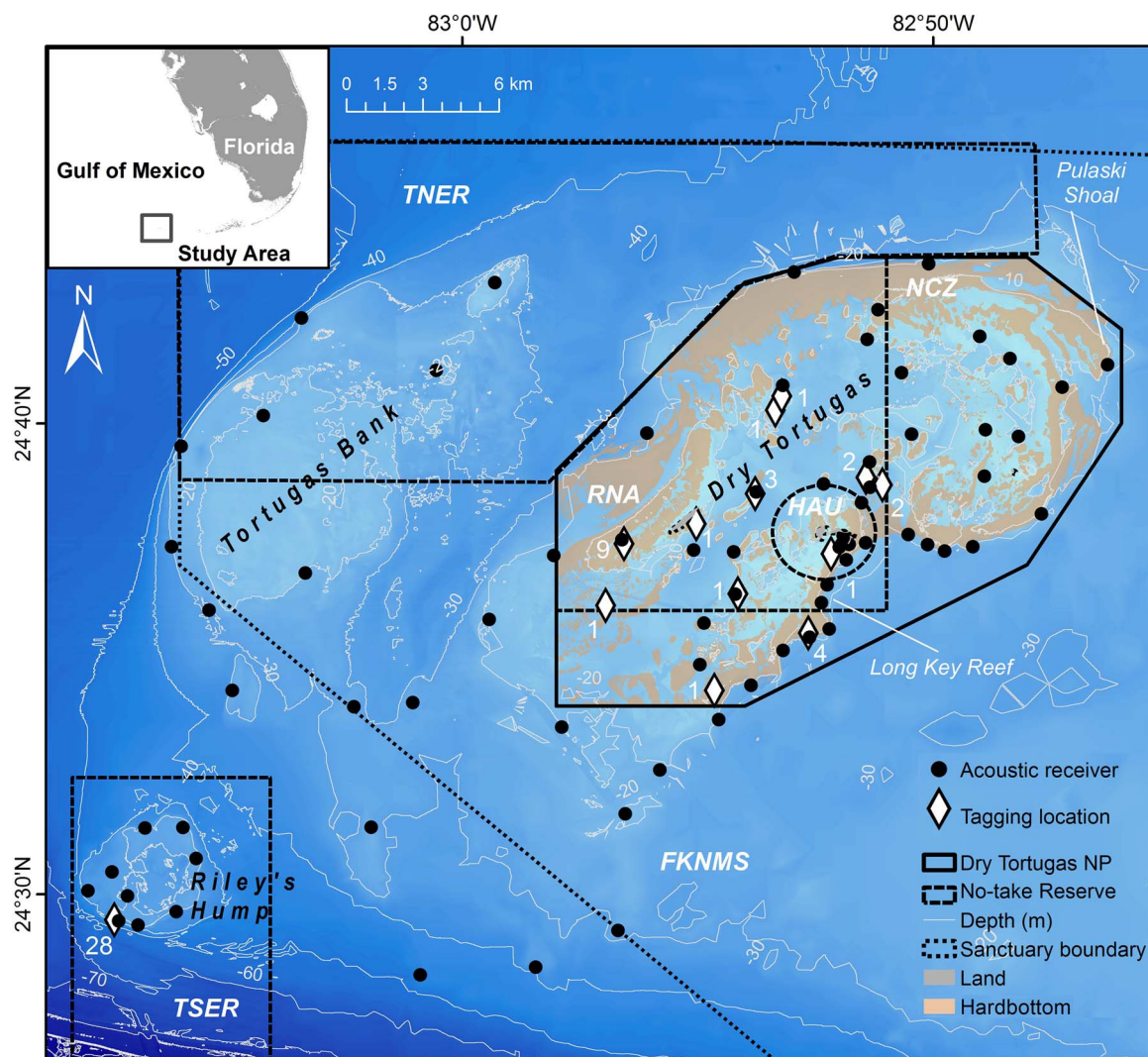


Fig. 1. The Tortugas Florida study area showing fish tagging and acoustic receiver locations (number of fish tagged is indicated) relative to management zones including the recreational fishing only Natural Cultural (NCZ) and Historic Adaptive Use Zones (HAU); the no-take Research Natural Area (RNA) of Dry Tortugas National Park; the no-take Tortugas South Ecological Reserve (TSER); the no-take Tortugas North Ecological Reserve (TNER); the open-use Florida Keys National Marine Sanctuary (FKNMS) and open-use waters of the Gulf of Mexico and Straits of Florida (OPEN). Long Key Reef is indicated by the 20 m edge and line of receivers that run south from the HAU. Bathymetry layer (meters [m]) courtesy J. Luo, Rosenstiel School of Marine and Atmospheric Science, University of Miami. Reef hardbottom layer (Waara et al., 2011).

using scooters searched for subgroups and documented spawning events with video and still imagery.

2.4. Analyses

Prior to analysis, detections within 24 h of release were removed to reduce the potential effects of tagging (Farmer and Ault, 2011). Detections that occurred within the same 25 h period, but at different stations, were evaluated by the Haversine formula to check if the distance was greater than the fish could have been expected to move (Pincov, 2011). This criteria was applied to minimize the probability of acceptance of false detections. To simplify analysis of zoning effects, detections within the recreationally fished areas of the Dry Tortugas NP were collectively referred to as HAU/NCZ.

2.4.1. Habitat use

Functional migration areas were estimated by minimum convex polygon (MCP) based on all detections of each individual fish. Polygons were constructed from a minimum of three peripheral stations at which a fish transmitter was detected and indicated the outer bounds of habitat use. Other position estimate methods were not used for functional

migration area estimation because of time gaps created by movements to habitat without acoustic coverage. Individual MCP asymptote values were determined on fish with detections on five or more stations using *adehabitatH*, a R software tool designed for analysis of space and habitat use (Calenge, 2006). Area curves based on location data must level off and reach an asymptotic value over time to standardize and validate the estimation of habitat use (Odum and Kuenzler, 1955). An asymptote (d) was reached when the cumulative value of area was within 5% of the total area for three consecutive detection locations (Laver and Kelly, 2008). Functional migration areas were estimated only on resident fish with defined home sites. An individual fish's home site was determined by the consistency and number of detections recorded by receivers (Davis et al., 2017). Home sites were characterized by a year round detection record in an area relative to other locations. The transmitter detection record combined with spatial plots of habitat use established whether a fish was a resident or transient within the array.

Sub areas within the functional migration area were assessed for migration movements, feeding and shelter areas (home site), and spawning grounds on Riley's Hump. A kernel density estimate (KDE) quantified spatial activity (95%, 50%) for individual fish at home sites and spawning grounds within the functional migration area, but was

Table 1

Acoustic tagging and detection summary including: fish tag transmitter code number (ID); date tagged; total length (TL); tag life; percentage of days detected; number of total days detected; number of total detections; number of stations on which fish was detected; last date of detection; and spatial area estimates (minimum convex polygon [MCP]) for 55 Mutton Snapper tagged inshore in Dry Tortugas National Park, within the Research Natural Area (RNA) and Historic Adaptive Use Zone/Natural Culture Zone (HAU/NCZ), and offshore in the Tortugas South Ecological Reserve (TSER). Percentage of days detected was determined by the proportion of days with a detection between date tagged and life of the tag.

ID	Date tagged	TL (cm)	Tag life (d)	Days detect (%)	Days detected	Total detects	Stations visited	Date last detect	MCP (km ²)
2167 ^r	30-May-08	69.2	470	64.89	305	127,076	19	15-Jul-09	115.11
2168 ^r	26-May-08	56.6	470	79.57	374	443,750	2	23-Aug-09	linear
2170 ^h	16-May-08	64.8	470	38.94	183	10,754	27	13-Sep-09	190.57
2174 ^h	22-May-08	46.8	470	–	–	–	–	–	–
2175 ^h	17-May-08	61.0	470	5.11	24	632	19	15-Jul-09	123.38
2176 ^h	17-May-08	55.1	470	11.91	56	2238	16	15-Jul-09	76.29
2177 ^r	30-May-08	64.5	470	62.13	292	7482	19	15-Jul-09	129.29
2185 ^r	24-May-08	61.0	470	1.49	7	988	4	28-Feb-09	11.61
2198 ^r	13-Oct-08	60.3	820	20.85	171	4371	10	02-Aug-10	32.08
2200 ^r	13-Oct-08	59.1	820	0.37	3	213	1	21-Oct-08	–
2201 ^r	13-Oct-08	57.2	820	27.44	225	2768	1	31-Mar-11	–
13674 ^t	05-Jul-08	45.7	1160	1.72	20	405	4	25-Jul-08	1.10
13675 ^t	02-Jul-08	47.0	1160	0.26	3	31	1	05-Jul-08	–
13676 ^t	09-Jun-09	63.5	1160	1.21	14	259	9	28-Jun-09	84.01
13677 ^t	05-Jul-08	48.3	1160	23.88	277	2663	2	07-Sep-11	linear
13678 ^t	05-Jul-08	48.3	1160	6.03	70	1537	12	19-Jun-11	130.75
13679 ^t	05-Jul-08	57.8	1160	1.90	22	667	3	26-Jul-08	0.32
13680 ^t	09-Jun-09	63.5	1160	0.60	7	371	6	18-Jun-09	3.91
13681 ^t	11-Jun-09	67.3	1160	0.09	1	1	1	15-Jun-09	–
13682 ^t	09-Jun-09	71.1	1160	1.64	19	455	7	02-Jul-09	29.90
13683 ^t	09-Jun-09	61.0	1160	1.72	20	90	5	13-Jul-09	4.23
14802 ^r	28-Sep-09	56.5	1122	0.29	3	29	1	05-Oct-09	–
14803 ^r	29-Sep-09	73.7	1122	–	–	–	–	–	–
14804 ^r	30-Sep-09	62.2	1122	21.97	230	1453	8	10-Jul-12	146.02
14805 ^t	09-Jun-09	61.0	1122	0.17	2	28	2	27-Feb-11	linear
14806 ^r	27-Sep-09	76.2	1122	–	–	–	–	–	–
49587 ^r	13-Oct-08	59.1	1160	0.17	2	8	3	15-Oct-08	1.55
49588 ^r	13-Oct-08	71.8	1160	4.31	50	1179	6	14-Jul-09	23.09
49589 ^t	01-Jul-08	50.8	1160	2.67	31	958	10	13-Aug-08	237.51
49590 ^t	01-Jul-08	63.5	1160	3.79	44	1099	6	22-Aug-08	5.15
49591 ^t	01-Jul-08	61.0	1160	2.67	31	1933	12	05-Sep-08	66.06
52502 ^h	14-Oct-08	61.6	1157	78.48	908	82,578	19	27-Jun-11	112.29
52503 ^r	15-Oct-08	74.3	1157	0.35	4	35	12	20-Oct-08	47.14
52504 ^r	15-Oct-08	70.5	1157	37.60	435	120,562	7	02-Jan-10	36.85
52505 ^r	15-Oct-08	53.3	1157	86.26	998	591,022	14	24-Dec-11	153.03
52507 ^r	12-May-09	61.0	1157	43.30	501	10,511	13	10-Jul-12	139.93
52508 ^r	12-May-09	58.4	1157	26.62	308	3140	10	11-Jul-12	78.24
52509 ^r	13-May-09	64.8	1157	4.41	51	651	1	19-Jul-12	–
52511 ^t	11-Jun-09	47.0	1157	6.31	73	5035	8	14-Oct-09	267.37
52512 ^t	11-Jun-09	66.0	1157	0.26	3	29	5	13-Jun-09	4.67
52513 ^t	11-Jun-09	62.2	1157	0.09	1	19	3	18-Jun-09	0.92
52514 ^t	11-Jun-09	73.7	1157	27.40	317	10,533	10	05-Aug-11	69.43
52515 ^t	10-Jun-09	61.0	1157	1.38	16	461	7	12-Jul-09	48.84
52516 ^t	11-Jun-09	58.4	1157	8.99	104	2695	3	28-Dec-10	0.37
56742 ^r	09-May-09	52.1	1157	14.09	163	9760	2	17-Jul-12	linear
56744 ^r	25-Sep-09	76.2	1157	26.24	276	11,925	16	03-Jun-12	240.75
56746 ^t	12-Jun-09	67.3	1157	0.26	3	35	4	19-Jun-09	1.35
56747 ^t	12-Jun-09	72.4	1157	0.69	8	60	5	19-Jun-09	3.94
56748 ^t	12-Jun-09	71.1	1157	2.33	27	809	10	15-Jul-09	103.02
61848 ^h	29-Mar-11	77.5	1157	30.28	152	3814	20	28-Jul-12	122.35
61849 ^t	31-May-10	71.1	1157	0.87	7	52	4	11-Jun-10	2.46
61851 ^t	30-May-10	71.1	1157	97.89	788	162,412	12	31-Jul-12	148.57
61852 ^t	31-May-10	68.6	1157	0.01	8	305	5	08-Jun-10	3.92
61853 ^t	31-May-10	74.9	1157	7.96	64	954	18	03-Aug-11	127.67
62115 ^t	01-Jun-10	89.7	1157	12.33	99	1925	12	11-Jul-12	107.22

^r Tagged in the RNA (on vessel).

^t Tagged in the TSER (in-situ).

^h Tagged in the HAU/NCZ (on vessel).

not an absolute value of space use in time (Rodgers and Kie, 2007). The 95% KDE polygon defined the area of habitat use; while the 50% polygon defined the core use within that area. Temporal use of habitat on the spawning grounds was estimated on the pooled data of all fish ($n = 43$) with detections on Riley's Hump. Data was binned into 4 h increments (Eastern Standard Time) to create six spatial use estimates. Interpretation of the 10% kernel was limited to inferring temporal-spatial movements on the spawning grounds.

Minimum convex polygon and kernel density estimate analyses

were performed in the Geospatial Modelling Environment (GME) software (Beyer, 2012) supported by R 2.15.2 (The R Foundation for Statistical Computing) and ArcGIS 10.1 using a North American Datum 1983 (NAD83) Universe Trans Mercator (UTM) Zone 17N projected coordinate system. Data was analyzed with the GME tools *genmcp* and *kde* (R Development Core Team, 2012). The GME command *isopleth* created 0.95 and 0.50 isopleths and created polygons from the KDE raster data set (R Development Core Team, 2012). A constant bandwidth (h_{ref}) for KDE was selected by the ad hoc method (Berger and

Table 2

Spatial information for migratory fish including: fish tag transmitter code number (ID); the total number of migration roundtrips; minimum linear distance between home site and spawning site; functional migration area asymptote; array residency index; functional migration area and 95% and 50% kernel density estimates (KDE) of habitat utilization at home site and on spawning grounds on Riley's Hump. The array index indicates the ratio of days detected in the array to the detection period (date tagged to date last detected; March et al., 2010). Functional migration area is reported for Dry Tortugas National Park (DTNP) resident fish only.

ID	Migration roundtrips	Minimum Linear Distance (km)	Asymptote (d)	Array Index	Functional Migration Area (km ²)	Home site (km ²)		Spawning grounds (km ²)	
						95% KDE	50% KDE	95% KDE	50% KDE
2167 [*]	3	32.4	368	0.74	115.11	2.03	0.63	2.34	0.67
2170	4		379	0.38				3.61	0.90
2175	2		393	0.06				3.12	0.71
2176	2		392	0.13				2.93	0.70
2177 [*]	3	32.4	377	0.71	129.29	6.63	0.76	2.84	0.70
2198 [*]	5	23.4	596	0.26	32.08	2.02	0.64	6.10	1.32
13678	3		1057	0.06				8.60	1.10
14804 [*]	3	23.4	982	0.23	146.02	2.06	0.66	3.70	0.70
49588 [*]	2	23.4	240	0.18	23.09	1.97	0.63	4.25	0.90
52502 [*]	2	29.7	940	0.92	112.29	2.01	0.65	5.16	0.79
52504 [*]	3	28.4	242	0.98	36.85	2.02	0.61	2.40	0.68
52505 [*]	2	28.4	976	0.86	153.03	2.05	0.66	3.00	0.78
52507 [*]	6	23.4	713	0.43	139.93	2.05	0.62	4.17	0.81
52508 [*]	4	23.4	NA	0.27	78.24	2.04	0.62	5.14	0.77
52514 [*]	5	25.2	662	0.40	69.43	1.97	0.65	5.62	1.01
56744 [*]	6	31.8	NA	0.28	240.75	3.46	0.72	2.83	0.76
56748	1		25	0.82				6.50	1.41
61848	4		92	0.31				8.66	1.21
61851 [*]	4	35.2	733	0.99	148.57	2.06	0.66	5.18	1.06
61853	4		61	0.15				5.17	0.94
62115	11		703	0.13				3.37	0.70

^{*} DTNP resident.

Gese, 2007; Jacques et al., 2009; Kie et al., 2010) using a quartic kernel. The quartic bandwidth relates to the distance beyond which locations do not contribute to the kernel estimate (Waller and Gotway, 2004). An h_{ref} of 1000 was selected based on the maximum range of detection in the shallow (< 35m) Tortugas coral reef environment reported in Farmer et al. (2013). A range test conducted by Florida Fish and Wildlife determined a similar maximum range of detection in the deeper waters of Riley's Hump (J. Renchen, unpublished data). We also used a binomial logistic regression model to examine the influence of distance and time period (day or night) on detection rate.

If any of the small islands of the Dry Tortugas were included within an MCP or KDE polygon, that area was subtracted from total area of the polygon. If a fish was recorded on only one or two receivers (linear), no determination of area was measured by MCP. The minimum catchment area was estimated by the polygon that defined the total unique area of individual functional migration areas.

2.4.2. Spatial and temporal patterns of movement

Twenty one fish were evaluated for migration movements. These fish demonstrated distinct repeated migrations to and from the spawning grounds. If a fish was originally tagged at Riley's Hump, information from that trip was excluded from analyses since the arrival date was not known. Day of arrival, day of departure, and time on the spawning ground were defined by the first and last detection recorded on Riley's Hump. One-way ANOVAs were used to compare length of time on the spawning grounds and tested for difference in day of arrival and day of departure on the spawning grounds relative to the full moon each month. Additionally, a one-way ANOVA tested for significance differences in mean size of fish by month of arrival at Riley's Hump. Separate linear regressions tested for the functional relationship between number of migration trips per season, swimming speed (cm s⁻¹) (described below) and habitat use (km²) on fish size (TL; cm). A square-root transformation was applied to the area of habitat use at home sites and on the spawning grounds to meet the assumption of normality. Finally, a Pearson correlation coefficient (ρ) estimated the association between mean daily temperatures at Riley's Hump and Long Key Reef to characterize temperature during the reproductive season.

2.4.3. Swimming speeds

A subset of nine fish was selected to determine swimming speeds. All these fish demonstrated directional swimming along reef edge habitat from one sequential receiver to the next along Long Key Reef. The only prerequisite was that a fish's movement was direct and defined by the sequence of detections. Swimming speeds from multiple trips were measured based on the time of departure to time of arrival on four or more sequential acoustic receivers. Multiple detections on a receiver were disregarded. Migrations moving towards or returning from the spawning grounds on Riley's Hump were included. Swimming speeds, assuming linear movement, were standardized to size (TL). Total distance traveled for timed movement varied from 3.5 to 16.2 km. The cumulative segment distances between receivers were divided by the time that elapsed between the first and last detections. Minimum linear distances between receivers were calculated using ArcMap 10.1 (Esri, Redlands, CA).

Travel time and distance between home sites and the spawning area was determined from the movements of nine resident fish from six different home receivers within Dry Tortugas NP. Calculation of travel speeds to and from residence grounds were limited to resident fish with succinct departure and arrival position fixes between a home site and the spawning area. Travel time from the Dry Tortugas NP to the TSER (i.e., across the open-use area) was also estimated for fish using Long Key Reef. These fish all provided a well-defined record of time it took to migrate across open fished waters from the south Dry Tortugas NP boundary receiver (535 m south of the boundary) to a TSER receiver.

3. Results

3.1. Acoustic tagging

Fifty-five Mutton Snapper (45.7–89.7 cm TL) were acoustically tagged in-situ at Riley's Hump ($n = 28$) and onboard a vessel within Dry Tortugas NP ($n = 27$) (Table 1, Fig. 1). Approximately 1.63×10^6 tag detections were recorded by the array from May 2008 through September 2012. Mean time-at-liberty (number of days between initial tagging and last detection) for individual Mutton Snapper was

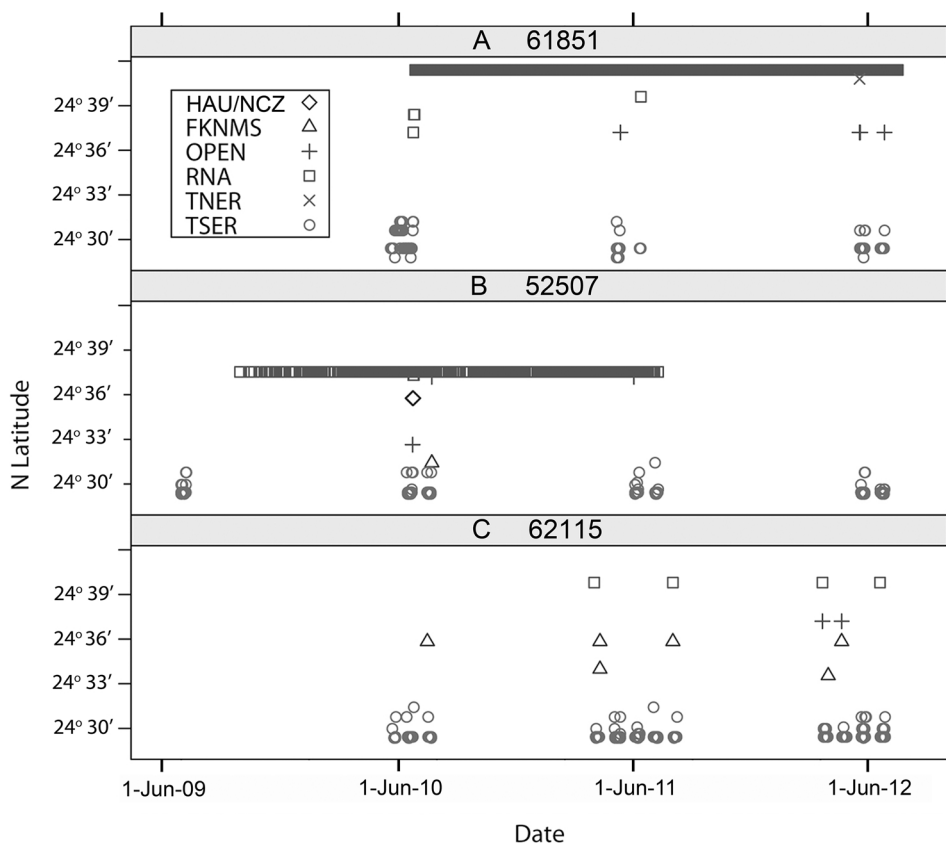


Fig. 2. Record of individual detections indicating latitude north position of select acoustically tagged Mutton Snapper: A) 61851 (71.1 cm *TL*), B) 52507 (61.0 cm *TL*), and C) 62115 (89.7 cm *TL*) recorded by receivers illustrating repeated annual seasonal migrations to spawning grounds on Riley's Hump in the Tortugas South Ecological Reserve (TSER). (See Table 1 for summary details.) During migrations to and from the spawning grounds fish change position quickly relative to time on the x axis. Symbols represent the management zone in which a detection occurred: Research Natural Area (RNA); Historic Adaptive Use Zone/Natural Culture Zone (HAU/NCZ); Tortugas North Ecological Reserve (TNER); Florida Keys National Marine Sanctuary (FKNMS) and Gulf of Mexico and Straits of Florida (OPEN).

408 ± 427 d (mean \pm SD) with a range of 2–1165 d. The mean number of days detected per individual fish was 151 ± 227 d (mean \pm SD) within time-at-liberty and ranged from 1 to 998 d.

3.2. Reproductive migrations

Twenty-one Mutton Snapper showed repeated migratory round trips (up to 5 trips fish⁻¹ season⁻¹) to Riley's Hump over one to three seasons (Table 2). The number of trips per year per individual was 2.3 ± 0.88 (mean \pm SD), with 88% of these fish migrating at least two times per year. Fish made northeast to southwest migration movements with thirteen fish showing distinct home ranges as part of the detection record. The one-way minimum linear distance traveled by resident fish ranged between to 23.4–35.2 km. Fish 61851 showed steady home site location fixes in the RNA north of 24°39' north latitude (N) from July 2010 to July 2012 and six seasonal migrations (two per year) to Riley's Hump south of 24°30'N (Fig. 2A). Fish 52507 also showed repetitive migrations from a home site with seasonal detections recorded on the spawning grounds in 2009–2012 (home receiver malfunctioned in the summer of 2011; Fig. 2B). Fish 62115 is an example of a migratory fish without a home site identified (Fig. 2C). This fish was tagged on the spawning grounds and showed 11 migrations to Riley's Hump over three spawning seasons from 2010 through 2012. Although movements for fish 62115 were recorded north of 24°39'N in the RNA, no home site area within the array was detected. Overall, limited movements of fish were detected to the northeast corner of Dry Tortugas NP or directly north to Tortugas Bank. However one Riley's Hump tagged fish (49589) was detected on Tortugas Bank and the Tortugas North Ecological Reserve and two days later at Pulaski Shoals, a minimum linear distance of 40 km. Additionally, one recapture (05-Dec-09; 56748) was reported by a fisherman approximately 50 km east of Riley's Hump from a depth of 27 m (Ada Afaro, pers comm).

Nine Mutton Snapper showed directional movement from one receiver to the next in a migration corridor along the reef edge south of

Long Key. The longest continuous reef-edge movement recorded was 16.2 km, including waters south of the RNA and east of Long Key on the eastern bank of Dry Tortugas NP. The swimming speed of migrating fish in the corridor was 63 ± 18 cm s⁻¹ (mean \pm SD; $n = 46$; 55.3–65.8 cm *TL*). There was no significant difference in swimming speeds to the spawning site or returning from the spawning site ($P > 0.05$). Migration swimming speed (cm s⁻¹) was not significantly dependent on size (*TL*; $P > 0.05$).

Fish migrating along the reef margin south of Long Key Reef also provided an estimate of the time required to navigate unprotected offshore waters between Dry Tortugas NP and the TSER, a minimum linear distance of approximately 17 km. The average time for these fish to migrate between the no-take reserves was 25.6 ± 15.3 h (mean \pm SD). The time to migrate between a home site and the spawning grounds was 52.3 ± 34.3 h (mean \pm SD) or approximately 2 days.

Over a four year period a seasonal pattern with three to five distinct peaks in daily transmitter detections occurred at Riley's Hump following the full moon during the April to August spawning season (Fig. 3). The majority of detections (94.8%) on Riley's Hump occurred as Long Key water temperature increased from 25 to 30 °C. Daily mean water temperature during the study period ranged from 18.6 to 31.3 °C at Long Key Reef and 18.6–30.2 °C at Riley's Hump (Fig. 3). The seasonal warming trend at Riley's Hump was interrupted by periodic cool water intrusions. Water temperature varied between inshore habitat and the spawning grounds, but mean daily temperatures were correlated ($\rho = 0.839$).

The number of migratory trips to Riley's Hump during a spawning season significantly increased with fish size (*TL*) at-capture, although the variation was not well explained ($Y = 0.0385 \cdot TL - 0.284$; $R^2 = 0.215$; $P = 0.006$). There was no significant difference in the mean size of fish at-capture returning to spawn each month of the season (ANOVA: $F = 2.495$; $df = 4$; $P = 0.186$). Size ranged from 69.1 ± 11.8 cm to 72.3 ± 15.1 cm *TL* (mean \pm SD) from May

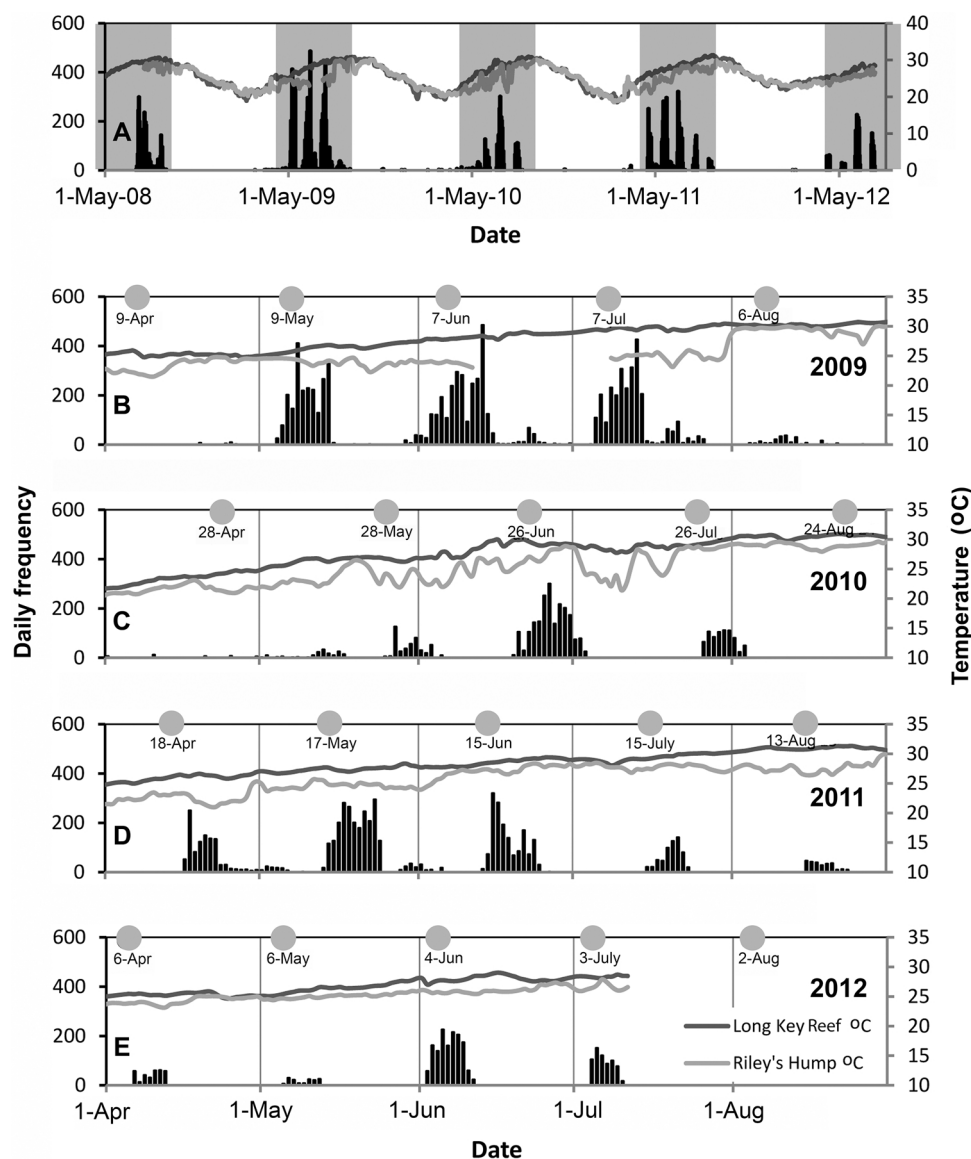


Fig. 3. Daily frequency of detections of Mutton Snapper from the upper south slope (station #2) on Riley's Hump and the mean daily water temperature (°C) on Riley's Hump (33 m depth) and Long Key Reef (14 m depth), Dry Tortugas National Park. A) All years, with gray shading indicating the spawning period from April to August and annual detailed panels with occurrence of the full moon indicated for B) 2009, C) 2010, D) 2011 and E) 2012. See Fig. 5 for location of station #2.

through August, while the mean *TL* in April (2009, 2010) was 84.4 ± 9.2 cm. The minimum size of a fish at-capture that returned to the spawning grounds was 48.7 cm *TL*.

3.3. Spawning grounds use

Resident times and habitat use on Riley's Hump were estimated for 21 individual Mutton Snapper that made migrations to the spawning grounds (Table 2). The day of arrival (0 ± 2 d [mean \pm SD]) and departure ($+7 \pm 2$ d) relative to the full moon varied significantly during 16 distinct spawning periods from 2009 to 2012 (ANOVA: $F = 4.07$; $df = 15$; $P < 0.001$ [arrival] and $F = 2.39$; $df = 15$; $P = 0.01$ [departure]; Fig. 4). Most interesting was that time of arrival and departure of fish shifted 1–2 days each successive month during the spawning season (see Fig. 4 2009 and 2011). Time spent on the spawning grounds was 7 ± 2 d (mean \pm SD; $n = 79$ trips) and did not vary significantly between months (ANOVA: $F = 1.70$; $df = 15$; $P = 0.073$). The mean 95% use area on the spawning grounds was 4.51 ± 1.84 km² (mean \pm SD). The majority of habitat use was centered near the central receiver on the south slope of Riley's Hump

(station #2), towards the central up-slope area (station #3), and near the eastern receivers (station #49) (Fig. 5). Total area of activity occupied on the spawning grounds was not significantly dependent on fish size (*TL*; $n = 21$; $P = 0.77$).

Temporal use of habitat by all fish on the spawning grounds pooled over all spawning cycles indicated a diel pattern with affinity towards the upper southern slope area (location of station #2) of Riley's Hump (Fig. 5). Frequency of hourly detections for all fish on the spawning grounds also indicated a peak of activity on the upper slope (station #2) between 1300 and 1700 h (Fig. 6). The core use of habitat (50% kernel) was centered on the south slope between 1200 and 2000 h (Fig. 5D, E). The central area utilized on the upper south slope during these hours was 0.97 km² between 1200 and 1600 h and 1.11 km² between 1600 and 2000 h. There was a transition of primary use area to include the more central upslope area after 0000 h; with a shift of the 10% kernel to the #3 receiver between 0400 and 0800 h (Fig. 5A, B). The aggregation begins a transition back towards the upper south slope again by 0800–1200 h (Fig. 5C). A binomial regression model on detection probability showed the time period and its interaction were not significant and did not improve model fit ($P = 0.797$ [day];

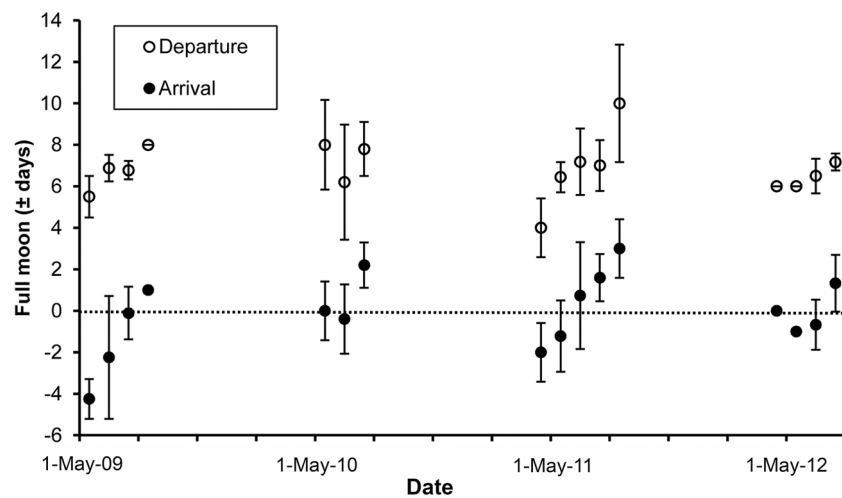


Fig. 4. Residence times of Mutton Snapper at the Riley's Hump spawning aggregation site indicated by mean day of arrival and departure relative to the full moon of 21 migrating individuals (monthly $n = 1-11$). Vertical bars indicate the standard deviation.

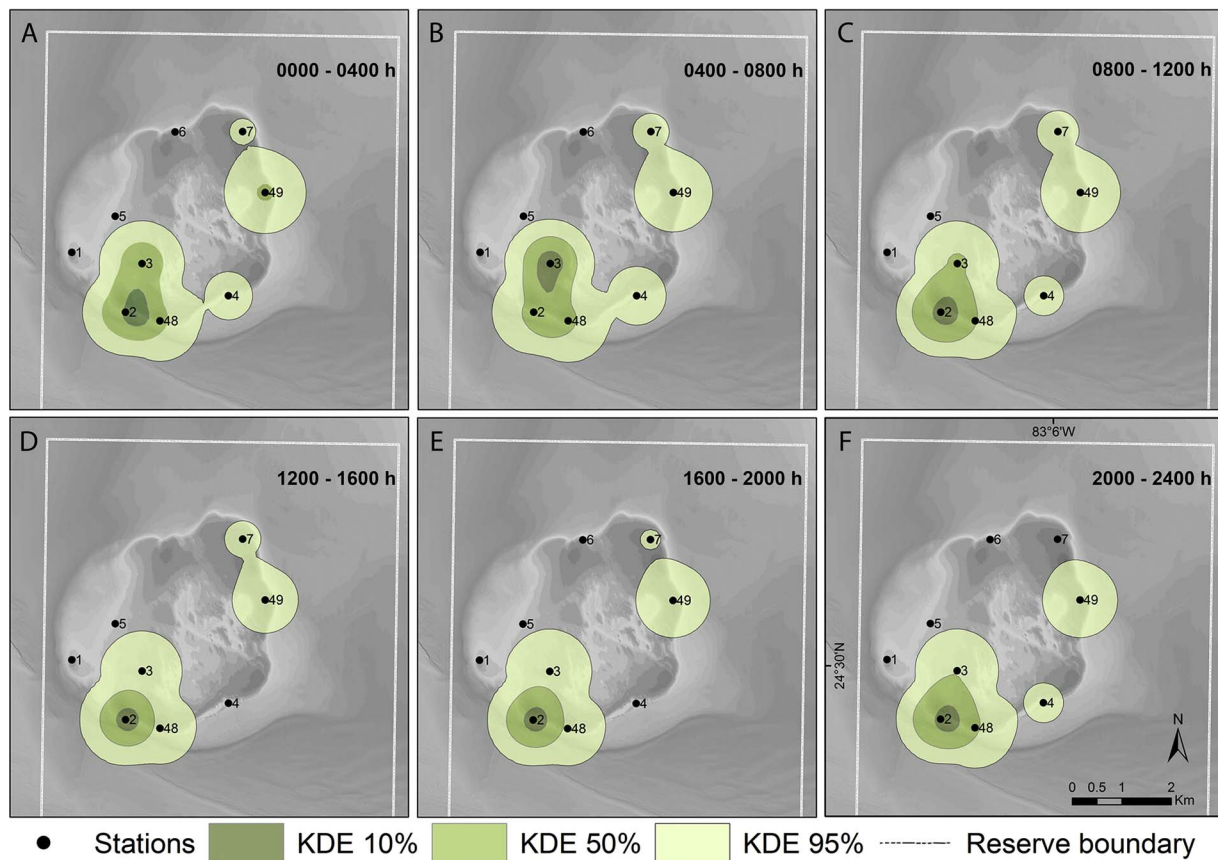


Fig. 5. Location of receivers (stations) and temporal dynamics of habitat utilization on the Riley's Hump spawning grounds indicated by 95%, 50% and 10% kernel estimates for pooled Mutton Snapper over all reproductive cycles from years 2009–2012. Core use of habitat (50% kernel) in A) 0000–0400 h, B) 0400–0800 h and C) 0800–1200 h, becomes more centered and compact near the spawning site on the upper slope (station #2) in D) 1200–1600 h and E) 1600–2000 h; then begins to expand back to the upper central area (station #3) in F) 2000–2400 h. All hours adjusted to Eastern Standard Time (EST).

$P = 0.901[\text{night}]$.

3.4. Spawning activity

A large aggregation of Mutton Snapper (~ 4000 individuals) was documented on June 12, 2009, between 1415 and 1715 h, 5 d after the full moon, along the south slope of Riley's Hump at water depths between 35 and 50 m (Supplemental Fig. S1). At 1615 h, approximately 60 fish separated into a tightening spiraling subgroup above the

aggregation and released a cloud of gametes that were dispersed by tail thrusts as the fish separated and descended (Supplemental Video S1). This sequence was observed 20 m below the surface three times in 7 min, along with one similar event without a release of gametes.

Similar spawning behavior was also confirmed July 8–10th, 2009, 1–3 d after the full moon, between 1610 and 1645 h. Direct spawning events were recorded on five separate occasions over this three day period. Observation of distended abdomens and intensified darkened (red) caudal fins were also documented at this time (Supplemental Fig.

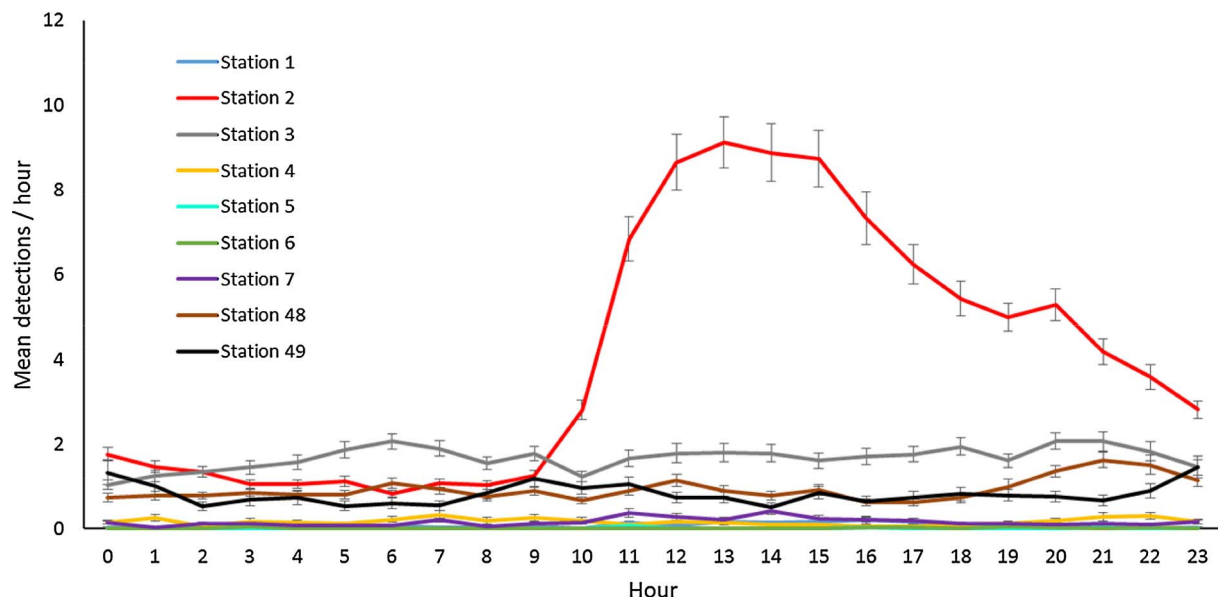


Fig. 6. Number of detections per day by receiver for pooled Mutton Snapper over all reproductive cycles on spawning grounds at Riley's Hump binned in one hour increments (EST). Vertical bars indicate the standard deviation. See Fig. 5 for location of stations.

S2). A few fish (presumably female) were observed being chased into the bottom habitat (27 m) several times before being pursued upward into the water column by fish from the main school. The subgroup swam upwards in close proximity to one another, approximately 10 m vertically, followed by a release of gametes and a subsequent return to the bottom (Fig. 7). Indirect spawning evidence of other fish species were also documented on Riley's Hump during June and July of this study. Groups of Cubera Snapper *Lutjanus cyanopterus*, Dog Snapper *Lutjanus jocu* and Permit *Trachinotus falcatus* were present, and spawning coloration displays by Blue Runner *Caranx crysos*, Horse Eye Jack *Caranx latus* and Crevalle Jack *Caranx hippos* and nesting behavior of Ocean Triggerfish *Canthidermis sufflamen* were also observed.

3.5. Home sites

Kernel density estimates and detection records indicated that 13 tagged *L. analis* were resident fish within Dry Tortugas NP. Twelve of these home sites were located within the RNA, while one fish appeared to be resident along the fore reef within the HAU/NCZ (ID: 52502) (Table 1). The area of habitat use for resident fish near their home site was $2.50 \pm 1.31 \text{ km}^2$ (mean \pm SD). Spatial estimates of home sites were not significantly dependent on fish size (TL ; $n = 13$; $P = 0.81$). Fig. 2A and B demonstrates the detection records for two Mutton Snapper (ID: 61851, 52507) indicative of a home site (the square markers have overlapped to create a solid line). Both fish exhibited a tendency to return to the same home site in the RNA over a period of several years, with numerous migrations to the spawning grounds.

3.6. Functional migration area

Functional migration areas were determined by MCP for the subset of 13 resident Mutton Snapper (Table 2). These fish were all at-liberty for a minimum of 2 months, had an array index greater than 20% and reached an MCP asymptote. These fish were monitored for approximately two years ($787 \pm 319 \text{ d}$ [mean \pm SD]) and were detected a mean $46 \pm 29\%$ of total days at-liberty. Time to reach an asymptotic value of area ranged between 240–982 days; two fish (52508, 56744) did not reach a clear asymptote (Table 2, Fig. 8). The average functional migration area was $109.59 \pm 61.01 \text{ km}^2$ (mean \pm SD). Spatial estimates of functional migration area were not significantly dependent on fish size (TL ; $n = 13$; $P = 0.89$).

3.7. Catchment area

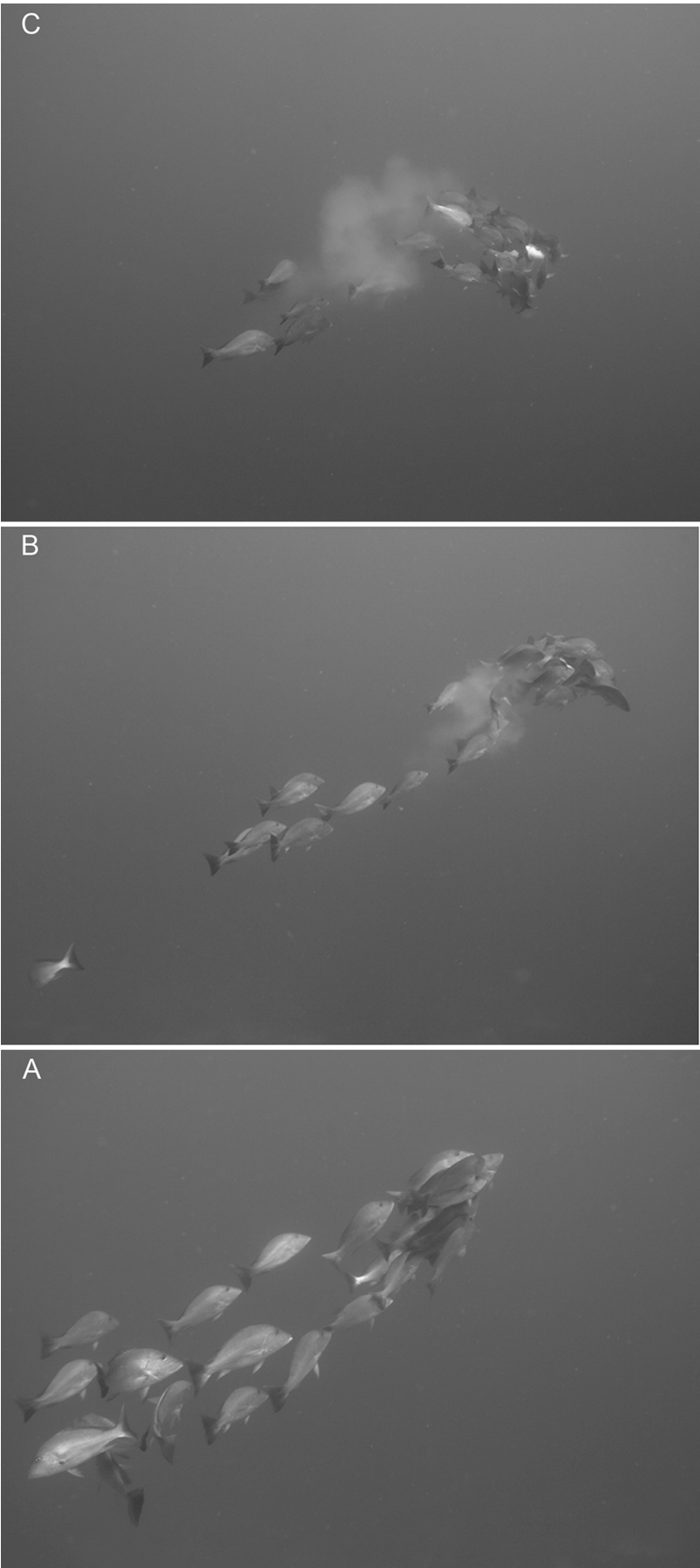
The minimum catchment area based on 13 resident fish functional migration areas was 291.3 km^2 . The maximum linear distance migrated from an established home site was 35.2 km. Examples of functional migration area and estimates of home range and habitat use on the spawning grounds of resident RNA fish are plotted in Fig. 9. These four fish (ID: 2177, 2198, 52514, 56744) were residents in the RNA and had similar home site spatial patterns as fish 61851 and fish 52507 (Fig. 2A and B). These fish showed a tendency to return to the same home site in the Dry Tortugas with repeated movements to the spawning site. The functional migration areas for all these fish connected the managed zones within Dry Tortugas NP to Riley's Hump within the TSER.

4. Discussion

4.1. Function of migrations and habitat linkages

In the Tortugas adult Mutton Snapper showed a clear connection between home sites and offshore spawning grounds on Riley's Hump. Resident Mutton Snapper were documented migrating multiple times throughout the spawning season over several years with minimum linear distances traveled ranging from 23.4–35.2 km. These fish demonstrated strong philopatry: habitually returning to shallow water home sites around the islands of the Dry Tortugas and to the spawning grounds on Riley's Hump. Repeated directional use along the contiguous reef edge near and south of Long Key coinciding with the full moon suggests that this area is an important migration corridor. Farmer and Ault (2011) reported similar directional movements of one Mutton Snapper along the contiguous reef edge northwest of Loggerhead Key, but were unable to document the full extent of movement due to spatial limitations of their array.

Fish in our study likely migrated greater distances than indicated by the minimum linear movements documented (23.4–35.2 km). For example, fish swam at 2.25 km h^{-1} (62.5 cm s^{-1}) along the Long Key Reef, but took approximately 25 h to swim the remaining 17 km linear distance to Riley's Hump. Pittman et al. (2014) modeled nonlinear movement of 40.2 km for a 27 km minimum linear distance migration for one Mutton Snapper to a shelf-edge spawning aggregation in the U.S Virgin Islands. Evidence along the Long Key corridor suggested fish movements were directed towards the spawning grounds or back to a



(caption on next page)

Fig. 7. A) A small subgroup ($n = \sim 25$) of Mutton Snapper on the south edge of Riley's Hump (~ 27 m depth) rapidly swim upward in close proximity to one another; B) in a spiraling motion release a cloud of gametes approximately 10 m above the bottom, which is C) dispersed further by tail thrusts as the fish separate and descend during the fish spawning aggregation of July 2009. (Photos© Christopher Parsons).

home site, i.e. fish did not mill around as they migrated.

Migration swimming speed for Mutton Snapper is the first reported for adult lutjanids. Mean swimming speed is higher than reported for migrating Coral Trout *Plectropomus leopardus* (0.66 km h^{-1} , Zeller, 1998), Nassau Grouper *Epinephelus striatus* ($1.69\text{--}1.96 \text{ km h}^{-1}$, Starr et al., 2007; Rowell et al., 2015; Stump et al., 2017) and Yellowfin Grouper *Mycteroperca venenosa* (2.03 km h^{-1} , Rowell et al., 2015). If swimming speeds are standardized to body length, Mutton Snapper mean swimming speed (1.0 BL s^{-1}) is higher than reported by (Starr et al., 2007) for Nassau Grouper females (0.6 BL s^{-1}) and males (0.8 BL s^{-1}). Mutton Snapper migration swimming speeds are approximately four times greater than the mean migration swimming speed of Atlantic Cod *Gadus morhua* (0.23 BL s^{-1} , Rose et al., 1995).

The seasonal migrations of Mutton Snapper establish an ecological link between the Dry Tortugas and spawning grounds at Riley's Hump. Spawning movements and release of gametes confirm the transfer of energy between shallow and deep water habitats and nearshore and offshore reefs proposed by Nemeth (2009). Functional migration areas can be estimated when enough information is available on home sites, spawning sites and migration distance pathways (Nemeth, 2009). These conditions were met, but documenting precise migration pathways was not always possible due to a lack of receiver overlap. Hence, functional migration areas may be overestimated whenever a migration pathway forms a relatively narrow link between a home site and the spawning grounds.

Claro (1981) first described similar cross-shelf movements of Mutton Snapper to spawning grounds near the shelf drop-offs along the

northwestern coast of Cuba. Garcia-Cagide et al. (2001) estimated a functional migration area for Mutton Snapper of 90 km^2 from inner reef areas along the north Cuban shelf to spawning sites located on reef promontories. The functional migration areas for Mutton Snapper in our study all extended northeast from Riley's Hump with a mean area of 109.59 km^2 . Based on these movements we estimated a minimum total catchment area of 291.3 km^2 for resident fish using Riley's Hump. However, Dry Tortugas NP is certainly not the only location from which Mutton Snapper migratory movements originate. Of the 28 fish tagged at Riley's Hump, forty-six percent were not detected elsewhere through the study period. The balance of fish tagged on the spawning grounds moved through different locations within our array or were confirmed residents of Dry Tortugas NP (Table 2; Fig. 9). The last receiver detections for migrating fish were all on the south and east side of Riley's Hump (#2, #4, #7, #48, #49; see Fig. 5) indicating that no fish seem to depart towards the west. Several other tagged fish (2168, 2201, 52509, 56742) were detected on a few receivers (1–2) during the study period but did not migrate to Riley's Hump. Inclusion of the Mutton Snapper recapture 50 km to the east expanded the possible catchment area for the population to 732.0 km^2 . An even a greater distance of reproductive migration was documented when one Mutton Snapper tagged at Gladden Spit, Belize during a spawning aggregation was caught 410 km north at Akumal, Mexico, 21 days after tagging (W. Heyman, unpublished data). Rhodes et al. (2012) also reported a total catchment area range of 100 km^2 but expanded the range to 175 km^2 when they included tagged recaptures of Brown-Marbled Grouper *Epinephelus fuscoguttatus*.

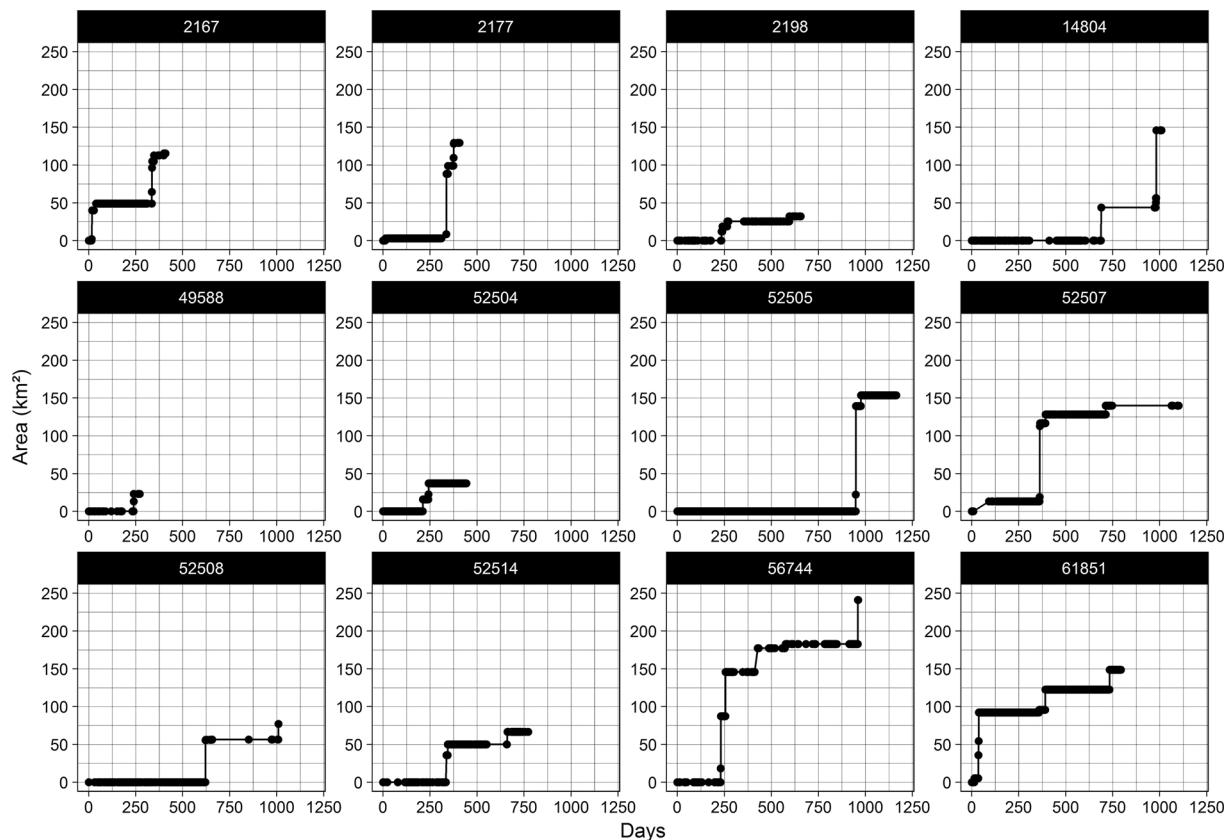


Fig. 8. Cumulative functional migration Minimum Convex Polygon (MCP) area estimates (km^2) for twelve resident fish in Dry Tortugas National Park recalculated each day with a new detection location (•) since the day of first detection (days). Each fish reached an asymptote (d) during the study period except fish 52508 and fish 56744. Fish 52502 is not shown to conserve space.

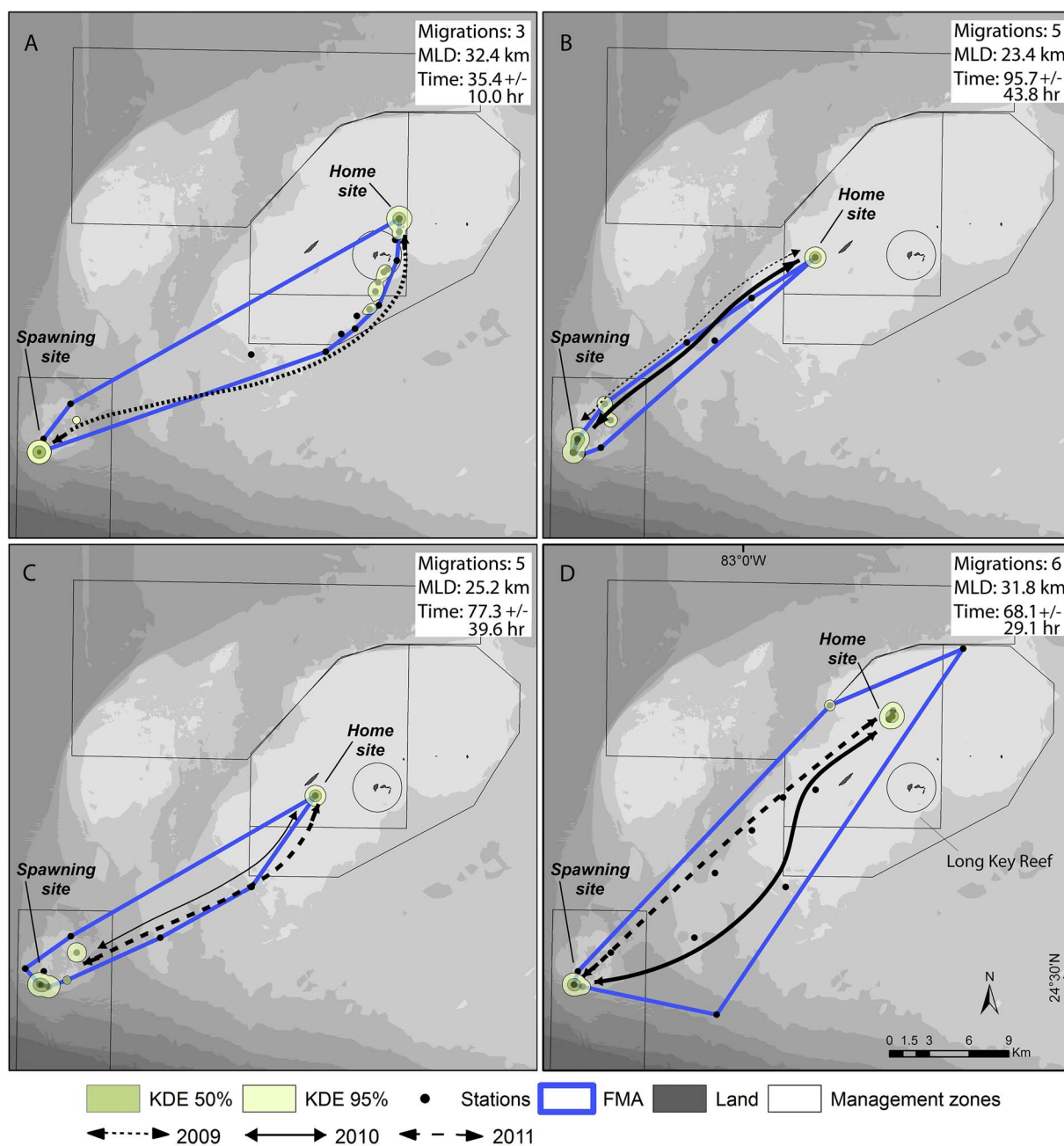


Fig. 9. Polygon plots of the functional migration area (FMA), home site and spawning grounds habitat use (KDEs), stations with detections recorded, and spawning migration pathways by year for four selected Mutton Snapper: A) 2177 (64.5 cm TL), B) 2198 (60.3 cm TL), C) 52514 (73.7 cm TL), and D) 56744 (76.2 cm TL). Total roundtrip migrations and migrations per year (2 = thin line; 3 = heavy line), the minimum linear distance (MLD) traveled to the spawning site and average migration time (mean \pm SD) between arrival and departure from the spawning grounds and home site is presented.

Due to the non-overlapping coverage of the array, the percentage of time that individuals were tracked varied and total areas of home sites are likely underestimated. However resident fish records indicate the relative location of a home site and likely minimum linear distance moved across the functional migration area. Our mean 95% home site kernel of 2.50 km² was smaller than Farmer and Ault's (2011) estimate of home range (7.64 km²), although greater than home ranges reported for Red Snapper *Lutjanus campechanus* on artificial reef structures (0.0029–0.0095 km²) (Topping and Szedlmayer, 2011). Home site areas in our study were not dependent on total fish length, although size may influence home range area in reef fishes (Kramer and Chapman, 1999).

4.2. Spawning grounds

This study provides direct evidence of the spawning of this species for the first time in Florida. Direct confirmation of spawning is relatively rare and accounts for only 25% of the aggregation records kept by SCRFA (Sadovy de Mitcheson et al., 2008). Observations of Mutton Snapper spawning between 1610 and 1645 h coincide with the peak frequency of detections on the upper south slope of Riley's Hump between 1300 and 1600 h. Total area of activity utilized on the spawning grounds was 4.51 km². However, this area may represent a more general staging area/courtship arena used by fish throughout their residency on Riley's Hump. The core use kernels became centralized and compressed on the upper slope between 1200 and 2000 h. These kernels (50%: 0.97–1.11 km²) may be indicative of the scale and location of the

actual spawning site. Biggs and Nemeth (2016) identified 1.4–1.5 km² of habitat used for spawning in Dog Snapper and Cubera Snapper between 1645 and 2000 h.

The main cues for spawning are believed to be ocean temperature, the lunar cycle, and tides (Sale et al., 2010). Direct observations of Mutton Snapper spawning one to five days after the full moon at Riley's Hump correlates well with D'Alessandro et al.'s (2010) peak in back-calculated estimates of spawning based on density of Mutton Snapper larvae collected in the Straits of Florida (4–6 days after the full moon). Peak spawning activity or densities relative to the full moon period have also been reported for Mutton Snapper, Cubera Snapper, and other Caribbean reef fishes (Colin, 1992; Shapiro et al., 1993; Heyman et al., 2005; Nemeth, 2005; Kadison et al., 2006; Nemeth et al., 2007; Starr et al., 2007; Heyman and Kjerfve, 2008). With the exception of two Mutton Snapper that were occasionally present in the TSER (13677 and 52516), time on the spawning grounds was restricted to the days immediately surrounding the full moon.

The influence of temperature on spawning activity in the wild has been documented for several species of snappers and groupers (Heyman et al., 2005; Kadison et al., 2006; Nemeth et al., 2007; Heyman and Kjerfve, 2008). Spawning migrations of Mutton Snapper in the Tortugas occurred seasonally from April to August and were synchronized with an increase in water temperature at Long Key Reef from 25 to 30 °C. However day of arrival and departure at the spawning site relative to full moon seemed to be shifted later by a day or two each month possibly due to seasonal increase in water temperature (Fig. 4). The spawning season for Mutton Snapper in Belize is more protracted (February–September) than demonstrated at Riley's Hump (Heyman and Kjerfve, 2008). This may be due in part to the water temperature reaching 26.5 °C sooner and staying elevated for a longer period of time than at Riley's. Similar temperature ranges (26.2–30 °C) were also documented for the annual spawning period of Cubera Snapper in Belize (Heyman et al., 2005) and St. Thomas, USVI (26.9 °C, Kadison et al., 2006; 26.7–28.7 °C, Biggs and Nemeth, 2016).

The majority (88%) of tagged Mutton Snapper migrating to Riley's Hump did so at least two times per year, but only once per lunar cycle. Fish arrived and departed from Riley's Hump within a few days of one another and stayed for approximately a week. This pattern differs from the multiple monthly spawning trips made by individual Serranidae fishes documented by Zeller (1998) and Starr et al. (2007). The majority of multiple movements of Coral Trout were limited to day or overnight trips to the aggregation site and were restricted primarily to males (Zeller, 1998). Unfortunately we were unable to interpret gender-specific spawning migration patterns. While sex catch ratios for Mutton Snapper have been reported in St. Croix (2:1; Kojis and Quinn, 2011) and Belize (1:1.2; Graham et al., 2008), the importance of gender-related spawning migration patterns in lutjanids remains unknown and should be investigated.

Our research focused primarily on Mutton Snapper utilizing one known spawning site, but other ecologically and economically important species may also use Riley's Hump as a spawning site (e.g., Black Grouper *Mycteroperca bonaci*; Red Grouper *Epinephelus morio*; Red Hind *Epinephelus guttatus*; Lindeman et al., 2000; Locascio and Burton, 2016). The groups of numerous other species we observed exhibiting spawning behavior and spawning coloration provides additional indirect evidence that the TSER shelters multispecies fish spawning aggregations (FSAs). Multispecies spawning behaviors at Riley's Hump are similar to the FSAs described at Gladden Spit, Belize by Heyman and Kjerfve (2008), and the east end of Little Cayman, Cayman Islands (Whaylen et al., 2004). Sargassum Triggerfish *Xanthichthys ringens* was also abundant on the south slope of Riley's Hump, the first documented resident habitat for this species in Florida. Further, we observed White Shark *Carcharodon carcharias*, Bull Shark *Carcharhinus leucas*, Sandbar Shark *Carcharhinus plumbeus*, Silky Shark *Carcharhinus falciformis* and Lemon Shark *Negaprion brevirostris* at the aggregation site, which supports the hypothesis that predation on FSAs may be vital for sustaining

apex predator populations (Graham and Castellanos, 2012; Mourier et al., 2016; Pickard et al., 2016; Erisman et al., 2017).

4.3. Implications for management

Repetitive seasonal migrations by multiple Mutton Snapper over multiple years provide empirical based evidence of an ecological connection between the Tortugas no-take reserves. No-take marine reserves can be effective in sustaining fish populations when spawning occurs within their boundaries or when connectivity exists within no-take marine reserve boundaries and FSAs located elsewhere (Sale et al., 2010). In south Florida, Lutjanidae and Serranidae FSAs are associated with deep offshore reefs (i.e., outer-reef tracks or outlier reefs, Lidz et al., 1991; Eklund et al., 2000; Gleason et al., 2011). Thus, spawning movements in these commercially important families may cover relatively long distances (30–50 km). Therefore it may not always be practical to establish a single large reserve that protects multispecies movements across all critical habitats. Additional protection of movement corridors does not seem practical until habitat maps and multispecies corridors are further defined.

Seasonal fishing closures that span the entire spawning season are another possible management option. Based on our results a fishing closure from April through August is recommended to protect Mutton Snapper spawning aggregations in Florida. However, equally important to either area or seasonal protection strategies, is that an adequate law enforcement plan exists for management. Compliance of no-take regulations in a remote area such as the Tortugas becomes optional without real-time support for enforcement patrols and application of available resources and surveillance technologies. Results from this study justifies investment in management strategies that prioritize locations and time periods that will benefit most from enforcement presence.

Protection of critical habitat for transient reef fish aggregating to spawn is critical to the sustainable management of these species (Sadovy de Mitcheson, 2016; Erisman et al., 2017). Our results indicate that the Tortugas no-take reserves provide refuge on home habitats and seasonal spawning grounds for Mutton Snapper. High site fidelity was shown by individual fish reusing both habitats and pathways during migrations. A small re-formation of several hundred Mutton Snapper was documented on Riley's Hump 3–4 years after the reserve was created (Burton et al., 2005). Burton et al.'s (2005) and our observations suggest that aggregating numbers of spawning Mutton Snapper at Riley's Hump has increased after the TSER closure and support the hypothesis that this FSA has rebounded after the spatial closure of the Riley's Hump area. Fisheries independent surveys also show the Tortugas network has increased the densities and occupancy of Mutton Snapper within the other Tortugas managed areas (Ault et al., 2013).

An understanding of movement dynamics and catchment area help define the geographic boundaries necessary to conserve this multispecies spawning aggregation site and the species utilizing this site. Although the total protected area of the Tortugas is smaller than originally recommended to achieve targeted levels of recovery, it has, as predicted by Dahlgren and Sobel (2000), made a significant contribution to rebuilding overfished stocks (Ault et al., 2013). The downstream Florida Current combined with seasonal cycles of the Tortugas gyre and coastal counter currents facilitate larval retention to the Florida Keys (Lee and Williams, 1999). Domeier's (2004) drifter study supports the idea that there is consequently greater larval dispersal and recruitment of fish from Riley's Hump to southeast Florida. Hence, recruitment and densities for this species should improve across hundreds of kilometers of the Florida Keys and southeast Florida from this single source.

Acknowledgements

This research was supported by the USGS State Partnership Program (Project Number: 007-0083-023 and Grant # 08ERAG0007), NOAA's

Coral Reef Conservation Program (MOA-2001-683 Amendment No. 004/7477 (1007-2009), (Amendment No.006)/7910; NOS Agreement No. MOA-2010-026/8081), and Discover Florida's Ocean Tag Grant (DFO 0809-03) through the Wildlife Foundation of Florida and conducted under scientific research permits issued by the National Park Service (DRTO-2008-SCI-0003, DRTO-2010-SCI-0006) and the Florida Keys National Marine Sanctuary (FKNMS-2008-015, FKNMS-2013-040). Special thanks to Bob McMichael, James Colvocoresses, Harold Pratt, Kristen Hart, Todd Kellison, Chris Parsons, Don DeMaria, Jack Javech, James Kidney, James Locascio, Rod Bertelsen, Judd Patterson, Jeb Redwine, Jeff Renchen, Rick Nemeth, FWRI staff, FKNMS, Dry Tortugas National Park staff and crews of the *MV Fort Jefferson*, *MV Spree* and the *Peter Gladding*. In memoriam: FWRI biologist Jeff Simonds (April 24, 1978–February 18, 2010) and NOAA National Marine Sanctuaries Regional Science Coordinator Brian D. Keller (April 26, 1948–March 10, 2010) contributed to this study.

Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at <https://doi.org/10.1016/j.fishres.2018.02.020>.

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