

# Grouper and snapper movements and habitat use in Dry Tortugas, Florida

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**ABSTRACT:** Home ranges, activity patterns, and habitat preferences in and around no-take marine reserves (NTMRs) were evaluated for 5 exploited snapper-grouper species in diverse coral reef habitats in the Dry Tortugas, Florida. Movements of ultrasonic tagged reef fish were determined using a calibrated array of omnidirectional hydroacoustic receivers. Average home range sizes were  $2.09 \pm 0.39 \text{ km}^2$  ( $n = 28$ ; total length, TL = 45 to 66 cm) for red grouper *Epinephelus morio*,  $4.17 \pm 1.75 \text{ km}^2$  ( $n = 5$ , TL = 48 to 55 cm) for yellowtail snapper *Ocyurus chrysurus*,  $1.44 \pm 1.04 \text{ km}^2$  ( $n = 2$ , TL = 57 to 75 cm) for black grouper *Mycteroperca bonaci*, and  $7.64 \text{ km}^2$  ( $n = 1$ , TL = 70 cm) for mutton snapper *Lutjanus analis*. Red grouper and yellowtail snapper moved moderate distances (from 700 to 900 m) with moderate frequency. Observed movements for black groupers were relatively small and infrequent. Mutton snappers appeared to make short, frequent movements. A tracked gray snapper *L. griseus* made long-distance nocturnal migrations. Several exploited-phase groupers and snappers crossed into and out of reserve boundaries. They were most likely to do so in locations where boundaries were positioned over contiguous coral reef and close to home-range centers. We found that home ranges for red grouper, black grouper, and yellowtail snapper were relatively small in comparison to NTMR area. Our observations suggest that the Dry Tortugas NTMRs may reduce exposure to exploitation for these and other species with limited home ranges, especially where NTMR boundaries do not overlie contiguous reef.

**KEY WORDS:** Acoustic tracking · Snapper-grouper complex · Movement patterns · Home range · Marine reserves · Coral reef fishes

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## INTRODUCTION

The Florida coral reef ecosystem, stretching 220 km southwest from Miami to the Dry Tortugas, supports multibillion dollar tourism and fishing industries (Ault et al. 2005a). However, the region's lucrative multi-species snapper-grouper complex has been serially overfished since at least the late 1970s (Ault et al. 1998, 2005b, 2009).

The Dry Tortugas region, because of its relative isolation and upstream location where the Florida Current merges into the Gulf Stream, has long supported the Florida Keys reef fishery with recruits from regional spawning, and density-dependent emigration of adult biomass (Schmidt et al. 1999, Ault et al. 2006b). Because of growing stress on regional fisheries and

coral reefs, in January 2007, the National Park Service established a no-take marine reserve (NTMR), or Research Natural Area (RNA), covering  $158 \text{ km}^2$  of prime shallow-water reef habitat in the western half of Dry Tortugas National Park (DTNP). The eastern half of DTNP ( $101 \text{ km}^2$ ) has been closed to commercial fishing, recreational spearfishing, and lobstering since the 1960s. It is, however, open to recreational hook-and-line fishing. The RNA was designed as a shallow-water complement to 2 relatively large NTMRs (Tortugas North and South Ecological Reserves), established in 2001 by the National Oceanic and Atmospheric Administration (NOAA) in the Florida Keys National Marine Sanctuary (FKNMS). At the time of their implementation this was the largest regional network of NTMRs in the US, protecting unique and fragile coral

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reef habitats and helping to sustain the region's world-class fisheries resources. Evidence has already emerged that they are reaching their intended goals (Ault et al. 2006b).

Many marine fishes repeatedly use and move throughout particular areas, or home ranges (Burt 1943), for certain periods of the year or for particular life stages (Goeden 1978, Shapiro et al. 1994, Rooij et al. 1996, Zeller 1997, Kramer & Chapman 1999, Bell & Kramer 2000, Bolden 2001, Eristhee & Oxenford 2001, Baras et al. 2002, Lembo et al. 2002, Parsons et al. 2003). Occupation by marine fishes of a particular home range within a spatially heterogeneous landscape — given increased familiarity with key habitat features — may facilitate evasion of predators and increase foraging efficiency (review in Harris et al. 1990).

Quantifying short- and longer-term fish movement patterns, home ranges, and habitat use is critical for advancing understanding of the dynamics of reef-fish community ecology and for informing intelligent NTMR design (Russ & Alcala 1996, Palumbi 2001, Meester et al. 2004, O'Dor et al. 2004). Unfortunately, data of this type are extremely limited (Kramer & Chapman 1999, Meyer et al. 2007). As a result, most reserves have been implemented with little quantitative design analysis, and this 'faith-based' approach has generated over-confidence about resource productivity and protection (Eristhee & Oxenford 2001, Meester et al. 2001, 2004, Hilborn 2006).

There is a broad scientific and management interest in improving our understanding of how the Tortugas NTMRs may facilitate the rebuilding of regional reef fisheries and help to conserve and sustain marine biodiversity in the Florida coral reef ecosystem. However, improperly configured NTMRs that underestimate the magnitude of animal movements and resultant vulnerability to exploitation may deleteriously affect NTMR capacity to buffer against exploitation pressure and sustain regional productivity (Eklund et al. 2000, Eristhee & Oxenford 2001). Anti-reserve lobby groups, on the other hand — due to a misinterpretation of a tagging study by Tremain et al. (2004) — have claimed that NTMR implementation was management 'double-dipping'. In their proposed scenario, not only would the NTMR function as a sink for fisheries resources, but it would also attract animals from fished areas, who themselves would never again be vulnerable to the fisheries.

In this paper, we principally focus on describing movements of red grouper determined from novel application of acoustic telemetry in the rugose and complex coral reef habitats of the Dry Tortugas, Florida. To broaden the interpretation, auxiliary data for 4 other key exploited snapper-grouper species are also presented. We use these data to quantify expected movement patterns, diel activity, home range, and flux

into and out of NTMRs, as well as to evaluate preferred reef habitat. We view these efforts as necessary precursors to improved NTMR designs (i.e. locations, size and configurations) that might contribute to sustaining regional coral reef-fish fisheries.

## METHODS

**Acoustic tracking.** In March 2006, we deployed 25 VEMCO VR2 (VEMCO, [www.vemco.com](http://www.vemco.com)) hydrophone receivers in a grid array with 600 to 1000 m spacing in the RNA in Dry Tortugas National Park (Ault et al. 2007a; Fig. 1A,B,C). Receivers were strategically placed on either side of reserve boundaries to address cross-boundary movements. Receiver placement was guided by maps of bathymetry (10 m resolution), coral reef habitats (200 m resolution), and a comprehensive fishery-independent monitoring database to provide acoustic coverage over a representative range of depths and complex coral reef habitats (Ault et al. 2002, Franklin et al. 2003, Smith et al. 2011). Receivers were mounted 5 m above the seafloor to reduce benthic noise exposure, avoid signal blockage by habitat features (e.g. large blocks of coral reef), and maintain a superior listening angle for acoustically tagged reef fish (Voegeli & Pincock 1996). Vinyl-coated wire and 3-strand nylon lines reduced acoustic noise from the anchorages (e.g. Clements et al. 2005). Depths and benthic habitats were determined using shipboard multibeam and side-scan sonar, diver-based ground-truthing, airborne light detection and ranging (LIDAR), and photogrammetry methods (Franklin et al. 2003).

In January 2007, we expanded the footprint of the acoustic array with additional receivers and reconfigured the grid to better capture reserve cross-boundary movements over known reef habitats (Fig. 1C). Each omnidirectional VR2 hydrophone functioned as an underwater passive listening station, archiving unique acoustic transmission codes, dates, and times for all tagged fish passing within its detection range. Data were manually downloaded from receivers bimonthly between March 2006 and November 2007. The receiver array during 2006 provided partial coverage across approx 16 km<sup>2</sup>, while the 2007 array covered approx 30 km<sup>2</sup>. Average spacing between receivers was 832 m. Receiver detection ranges were calibrated both spatially and temporally using several statistical assessment techniques that included (1) long-term detections at fixed distances, (2) boat- and diver-based mobile range-testing, and (3) tag and receiver validations in controlled field tests.

Fish were captured by hook-and-line over a range of key habitats proximal to the acoustic grid array. Selected fish in excellent physical condition and large

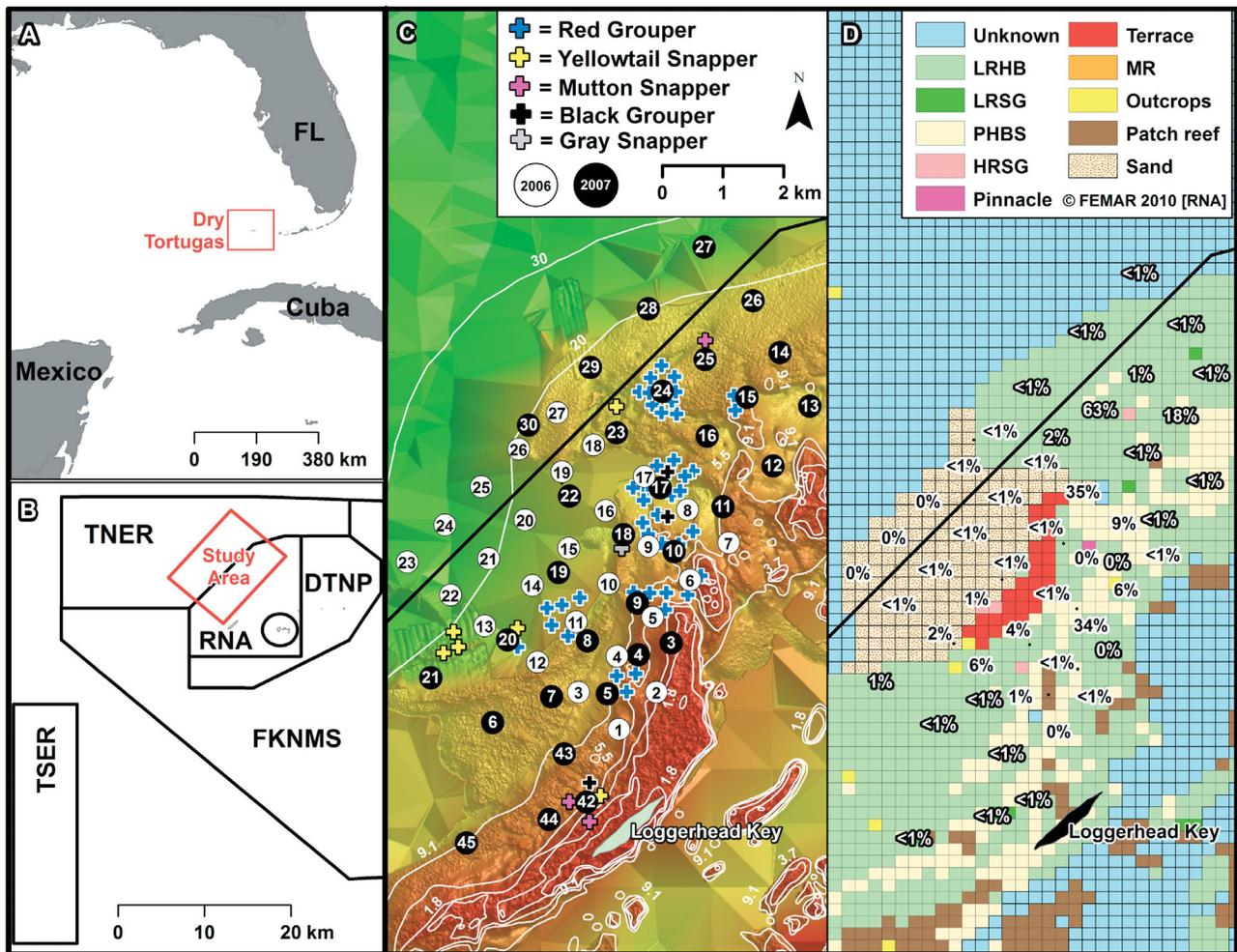


Fig. 1. Study area showing (A) Dry Tortugas, Florida; (B) study site relative to management zones, including fishable ('open') waters of Dry Tortugas National Park (DTNP) and Florida Keys National Marine Sanctuary (FKNMS), no-take Research Natural Area (RNA), no-take Tortugas North Ecological Reserve (TNER) and no-take Tortugas South Ecological Reserve (TSER); (C) hydroacoustic receiver placements in 2006 (white circles) and 2007 (black circles) overlain on bathymetry in RNA; and (D) percent detections by receiver for 2006 (white background) and 2007 (black background) relative to benthic habitats. LR: low relief; HB: hardbottom; SG: spur-and-groove; PHBS: patchy hardbottom in sand; HR: high relief; MR: medium relief

enough to accommodate an acoustic tag (e.g. >45 cm total length, TL) received surgically implanted acoustic transmitters (VEMCO V16). Transmitters were inserted into the abdominal cavity using a procedure modified from Bolden (2001). All implanted tags weighed 24 g and were 58 mm long and 16 mm in diameter. Tags were configured with randomized transmission times (Table 1), reducing the likelihood of tag signal collisions with other tagged individuals within the array (Pincock & Voegeli 2002). The relatively short delay times increased the probability of tag transmissions when in range of a specific receiver (Løkkeborg et al. 2002). Vicryl undyed

27 in chronic gut with 2/0 curved needles was used to close incisions with 3 to 5 individual stitches. In 2006, Floy FD-94 T-bar tags (www.floytag.com) were inserted between the dorsal pterygiophores using a Mark II pistol grip gun. In 2007, Floy FIM-96 double-

Table 1. Specifications for 69 kHz VEMCO V16 acoustic tags utilized in this study. Note 3H tags have higher transmission strength but shorter battery life

Fish ID	Year	N	Type	Power output (1 $\mu$ Pa @ 1 m)	Random delay (s)	Expected battery life (d)
862–872	2006	33	3H	158	20–69	56
170–194	2006	23	3H	158	30–79	62
32–59	2007	20	3H	158	60–180	130
873–884	2007	12	4H	153	20–69	570

barb anchor tags were inserted using a Floy 'jab stick'. Conventional tags were marked with a fish ID number; instructions to record the fish length, date, time, and location at time of capture; and a toll-free number and email address for reporting recaptures. Powder-form antibiotic Oxytetracyclin was applied to all punctures and incisions. Surgeries, which took from 2 to 5 min, were performed in a large sterilized cooler containing continuously cycled seawater. All fish receiving an acoustic transmitter tag were released at their capture location after a short (from 5 to 25 min) recovery period. Released fish were supervised during submergence to ensure that they escaped predators.

**Data analysis.** Prior to statistical analyses, VR2 receiver data were corrected for temporal drift using a linear correction formula that accounted for time of initialization, recorded time of download, and actual time of download (D. M. Webber, VEMCO, pers. comm.). Data were adjusted for daylight savings time. Any single, isolated detection occurring in a 24 h period was removed as potentially spurious (D. M. Webber, pers. comm.). Detections within 24 h of release were excluded to reduce the impacts of 'unnatural' post-surgical behaviors on analyses.

**Activity centers:** A position estimator employing weighted harmonic means was applied to the time-specific archived tag data from each fish, batched over 5 min and 120 min intervals. This modification of an approach by Simpfendorfer et al. (2002) allowed for creation of a time series of short term 'activity centers', calculated as the means of multiple receiver locations weighted by the estimated distance of the tag from each receiver during the specified batch interval. Weighting terms were derived from a logistic regression model fit to measurements of tag detection rate at 66 sites spaced at 150 m intervals, and from 0 to 850 m from any given receiver in the array. At each site, stationary acoustic tags were deployed 2 m above the seafloor for  $\geq 90$  min. Detection rate was defined as detections divided by expected transmissions per unit time. Expected transmissions were standardized by tag ping rate (Table 1). The estimated logistic regression model was used to express the probability of tag detection subject to distance from a receiver while controlling for receiver depth, surrounding habitat rugosity, tidal flow, and wind-generated noise within a heterogeneous coral reef environment (Farmer 2009).

Wind-speed data were obtained from the National Data Buoy Center's C-MAN Station at 'Pulaski Shoal Light, FL' (PLSF1; 24° 41' 36" N, 82° 46' 24" W), located 12 km east of the receiver array ([www.ndbc.noaa.gov](http://www.ndbc.noaa.gov)). Extensive tag and receiver range-testing indicated that 5 min intervals were most appropriate for evaluating movement patterns, while 120 min intervals were optimal for evaluating presence-absence detec-

tions. Overall mean activity centers for individual tagged fish were also computed using all post-screening tag detections. No formal statistical comparisons were made between species due to the substantial differences in samples sizes.

**Distances moved and relative frequency of movement:** Species mobility was evaluated using observed movement distance and the relative frequency of movement. Distances between consecutive 5 min position estimates were computed using custom software written in Java 6.10 (Sun Microsystems) and the Animal Movement Analysis Extension (AMAE) for ArcView (Hooge & Eichenlaub 2000). Relative frequency of movement was determined as percentage of consecutive 5 min intervals with a detected change in position.

The likelihood of a tagged fish's movements being undetected outside the array was tested by examining the ratio of 120 min intervals with detections to the total possible number of 120 min intervals between the first and last detections. Use of 120 min intervals reduced the potentially confounding influences of extreme ambient noise (e.g. high winds, rainfall) and other types of signal interference.

**Diel period and lunar brightness effects on movement patterns:** Under the assumption that a moving reef fish would have increased detection rates and be detected by multiple receivers, 2 generalized linear mixed models (Pinheiro & Bates 2000, Montgomery 2001, Zuur et al. 2009) were developed. The first examined daily detection rate dependent upon 'tag' as a random factor and the categorical variable 'diel period', consisting of Dawn (sunrise  $\pm 1$  h), Day, Dusk (sunset  $\pm 1$  h), and Night as a fixed factor. The second examined number of receivers recording detections dependent upon the same factors. To express overall differences in detection rates between diel periods, detection rates were standardized and averaged across individuals.

To examine the influence of lunar brightness on nocturnal movement, a generalized linear model was developed. This model examined nocturnal detection rate dependent upon 'tag' as a random factor and 'lunar period' as a fixed factor. Lunar period was expressed as a continuous wavelet function (Faraway 2006), ranging from 0 (new moon) to 1 (full moon). Model data were restricted to 'night' observations for individuals with detection periods longer than 1 mo. A quadratic regression was used to evaluate standardized detection rates dependent on lunar period.

**Reserve boundary crossings:** Fish were considered to have crossed an RNA boundary if subsequent 5 min activity centers were computed to be located on opposite sides of a boundary. Regression analysis was used to evaluate the relationship between distance of red grouper overall mean activity centers to RNA boundary and percent time spent outside the RNA.

**Home range utilization:** Daily minimum convex polygon (MCP; MacDonald et al. 1980) home ranges for each fish were computed using a procedure in AMAE applied to 5 min activity centers. The results were area-observation curves, and if they suggested an asymptote, home range estimates were considered reliable following Laundré & Keller (1984). Fish whose area-observation curves showed no asymptote were excluded from subsequent home range analyses. Home range size for fish with linear home ranges (i.e. detections at multiple receivers in a straight line) were estimated as the product of the detection area around the average midpoint between receivers [ $\pi(832/2)^2 \text{ m}^2$ ] and the number of receivers in the line. MCP home range estimates for 1 mutton snapper were computed, both including and excluding sites visited exclusively during presumed spawning runs. Exclusion of these sites appeared appropriate, given the sensitivity of the MCP method to peripheral observations; they did not appear to be part of the routine daily habitat for this individual (Burt 1943). Regression analysis was used to evaluate home range size, percent home range overlap, and distance between home range centers as a function of length and weight for red grouper.

**Habitat utilization:** Habitat types within  $200 \times 200$  m grid cells described by Franklin et al. (2003) were recategorized by coverage as contiguous (C), isolated (I) and spur-and-groove (SG), and by profile as low (L), medium (M) and high (H). Regression analysis was used to evaluate percent home range overlap and distance between home range centers as a function of habitat coverage and profile.

Following methods presented in Winter & Ross (1982) and Lowe et al. (2003), a habitat selection index was determined for each tagged fish as the ratio between the percentage of 5 min activity centers in a habitat grid cell and the percentage of  $200 \times 200$  m cells containing that identified habitat type within the fish's MCP home range. Habitat type was defined by a combination of coverage and profile as described above. Number of activity centers within each habitat type was computed for each fish using the Hawth's Tools 'Count Points within Polygons' extension for ArcGIS (Beyer 2004). Natural boundaries to movement were identified by examining dominant habitat types around receivers recording no detections.

## RESULTS

### Acoustic tracking

In 22 mo of study between March 2006 and November 2007, we acoustically tagged and tracked 58 ind. representing 5 snapper-grouper species (Table 2) and

obtained nearly 2.5 million tag detections. Red grouper comprised 79% of the acoustically tagged fish. Larger red grouper were, however, generally absent in our tagging study, despite the fact that they comprise a significant portion of the population as shown in estimates made by diver-based visual census methods (Ault et al. 2007a, Smith et al. 2011). Sample sizes for other species were limited. These other species are presented in Table 2 (and elsewhere herein) for reference.

Time at liberty for tagged fish ranged from 2 to 280 d, with an average of  $102 \pm 7.6$  d (mean  $\pm$  SE) for all species combined,  $135 \pm 31$  d for black grouper ( $n = 3$ ), 92 d for gray snapper ( $n = 1$ ),  $86 \pm 58$  d for mutton snapper ( $n = 3$ ),  $111 \pm 2$  d for red grouper ( $n = 45$ ), and  $83 \pm 9$  d for yellowtail snapper ( $n = 5$ ). With the exception of yellowtail snapper, most tagged fish were tracked beyond their expected transmitter battery life (Table 2).

In 2006, 5 tagged red grouper were recaptured using hook and line—2 by researchers and 3 by sport fishers. Of these, 2 occurred within 25 d of initial capture and were re-released in good condition (ID nos. 865 and 866; Table 2). The other recaptures occurred between 42 and 142 d after initial capture and were also reported in good condition. About 60% of recaptures were made within 100 m of the original capture-tagging site. Acoustically observed forays into nearby areas, conventional recaptures, and the apparent condition of recaptured fish alleviated our concerns of post-tagging mortality. No recaptures were reported following implementation of the RNA in January 2007, due presumably to reduced fishing effort in the RNA or to non-reporting.

### Movement patterns and distances moved

Movement patterns exhibited by individual fish were varied, and percent detections varied widely between receivers (Fig. 1D). Most red grouper and the few tagged black grouper were detected within a core habitat around 1 or 2 hydrophones over the life of their acoustic tags, although rare to occasional detections at other locations did occur, especially for fish with overall mean activity centers closer to the core of the array. Similar detection patterns were often observed for individuals tagged at the same location (e.g. Fig. 2).

Relative frequency (Fig. 3A) and distance (Fig. 3B) of detected movements varied between species. Red grouper and yellowtail snapper moved moderate distances (from 700 to 900 m) with moderate frequency. Observed movements by black grouper were relatively small and infrequent. Mutton snapper appeared to make short, frequent movements, although movements associated with spawning migrations were much broader in scale (Fig. 4). All observed move-

Table 2. Data for fish fitted with acoustic transmitters. Dates follow mo/d/yr format; TL: total length; W: weight; Rec: no. of receivers detecting fish; HR: home range; NA: not applicable (no detection of tagged individual)

Tag	Fish ID	Common name	TL (cm)	W (kg)	Date tagged	Last detect	Days	Tag life	Detects	Rec.	HR (km <sup>2</sup> )
<b>2006 configuration</b>											
3H	170	Red grouper	61	9	03/07/06	06/08/06	93	62	708	2	Linear
3H	172	Red grouper	49	4	03/07/06	03/10/06	3	62	471	8	NA
3H	171	Red grouper	60	6.5	03/07/06	06/13/06	98	62	2359	4	0.64
3H	173	Red grouper	49	4	03/07/06	06/07/06	92	62	613	5	1.28
3H	174	Black grouper	50	5.5	03/07/06	06/06/06	91	62	11466	4	0.39
3H	175	Red grouper	53	6	03/07/06	06/11/06	96	62	5190	2	Linear
3H	176	Red grouper	55	6.5	03/07/06	06/08/06	93	62	4512	4	0.64
3H	177	Red grouper	50	4.5	03/07/06	06/04/06	89	62	373	2	Linear
3H	178	Red grouper	65	10	03/07/06	06/05/06	90	62	2466	2	Linear
3H	179	Red grouper	57	6	03/27/06	04/19/06	23	62	229	14	NA
3H	180	Red grouper	55	6	03/27/06	05/06/06	40	62	382	5	3.19
3H	181	Red grouper	49	4	03/27/06	04/09/06	13	62	880	9	NA
3H	182	Yellowtail snapper	52	2.5	03/28/06	04/23/06	26	62	39374	9	2.57
3H	183	Red grouper	48	4.5	03/28/06	07/04/06	98	62	8491	3	3.22
3H	184 <sup>a</sup>	Red grouper	55	6.5	03/27/06	05/09/06	43	62	4915	7	1.91
3H	185 <sup>a</sup>	Red grouper	55	5	03/27/06	05/09/06	43	62	8895	7	1.90
3H	186	Red grouper	51	6	03/27/06	06/26/06	91	62	12077	8	3.49
3H	187	Red grouper	50	4.5	03/27/06	06/27/06	92	62	4806	8	1.89
3H	189	Red grouper	59	8	03/07/06	06/09/06	94	62	28035	1	Single
3H	190	Red grouper	62	9	03/06/06	06/15/06	101	62	55092	2	Linear
3H	191	Red grouper	51	4	03/06/06	06/07/06	93	62	36324	4	0.63
3H	194	Red grouper	54	6.5	03/06/06	06/08/06	94	62	12928	4	1.55
3H	862 <sup>a</sup>	Red grouper	54	4.5	03/06/06	05/31/06	86	56	73704	3	NA
3H	863	Red grouper	51	6.5	03/05/06	06/08/06	95	56	6728	3	0.31
3H	864	Red grouper	55	6	03/06/06	06/06/06	92	56	44890	2	Linear
3H	865 <sup>a</sup>	Red grouper	56	8	03/05/06	04/07/06	33	56	14616	6	1.28
3H	866 <sup>a</sup>	Red grouper	53	5	03/06/06	05/11/06	66	56	426	2	Linear
3H	867	Red grouper	55	5.5	03/05/06	06/02/06	89	56	42058	4	0.49
3H	868	Red grouper	49	4.5	03/05/06	06/01/06	88	56	24533	2	Linear
3H	869	Red grouper	60	–	03/06/06	06/01/06	87	56	21703	2	Linear
3H	870	Red grouper	45	2.5	03/05/06	03/30/06	25	56	2530	7	2.20
3H	871	Red grouper	57	8	03/05/06	05/20/06	76	56	402	2	Linear
3H	872	Red grouper	53	4.5	03/05/06	05/23/06	79	56	70316	4	0.49
<b>2007 configuration</b>											
3H	43	Black grouper	74.9	6.6	01/07/07	07/05/07	179	130	72644	6	2.48
3H	35	Black grouper	57	4.5	10/09/07	NA	0	130	0	0	–
3H	53	Mutton snapper	70	5.4	04/25/07	10/10/07	168	130	21805	18	7.64
3H	40	Mutton snapper	53	4.5	04/25/07	NA	0	130	0	0	–
3H	50	Mutton snapper	43	2.5	10/09/07	10/13/07	4	130	183	6	NA
3H	52	Mutton snapper	49	2	10/09/07	NA	0	130	0	0	–
3H	36	Red grouper	63.5	3.6	01/07/07	01/25/07	18	130	2051	15	NA
3H	37	Red grouper	47	1.4	01/07/07	07/05/07	179	130	64672	3	0.47
3H	41	Red grouper	47	1.1	01/07/07	07/05/07	179	130	75732	3	0.44
3H	42	Red grouper	48.3	1.8	01/07/07	07/05/07	179	130	21823	4	0.93
3H	47	Red grouper	48.3	1.8	01/07/07	01/18/07	11	130	1534	17	NA
3H	51	Red grouper	66	5.4	02/27/07	08/03/07	157	130	12329	6	1.95
3H	55	Yellowtail snapper	55	1.8	04/24/07	09/24/07	153	130	10566	6	10.72
3H	57	Yellowtail snapper	52	1.4	07/11/07	10/11/07	92	130	31804	7	4.65
3H	58	Yellowtail snapper	48	0.9	04/24/07	07/01/07	68	130	2238	3	0.75
3H	59	Yellowtail snapper	52	0.9	04/24/07	07/10/07	77	130	4791	5	2.17
4H	882	Gray snapper	54	2.7	07/10/07	10/10/07	92	570	25243	6	NA
4H	873	Red grouper	48.3	1.8	01/04/07	10/11/07	280	570	199933	2	6.44
4H	874	Red grouper	59.7	2.9	01/05/07	10/10/07	278	570	313237	5	1.40
4H	875	Red grouper	52.1	2	01/04/07	10/11/07	280	570	205442	5	1.68
4H	877	Red grouper	57.2	2.7	01/04/07	10/11/07	280	570	124104	4	0.83
4H	878	Red grouper	48.3	1.8	01/04/07	02/17/07	44	570	21144	9	5.76
4H	880	Red grouper	48.9	1.8	01/04/07	09/30/07	269	570	35439	3	2.59
4H	881	Red grouper	49.5	1.8	01/04/07	10/11/07	280	570	261025	7	9.17
4H	884	Red grouper	53.3	2	01/04/07	10/11/07	280	570	272798	5	1.68
<sup>a</sup> Recaptured											

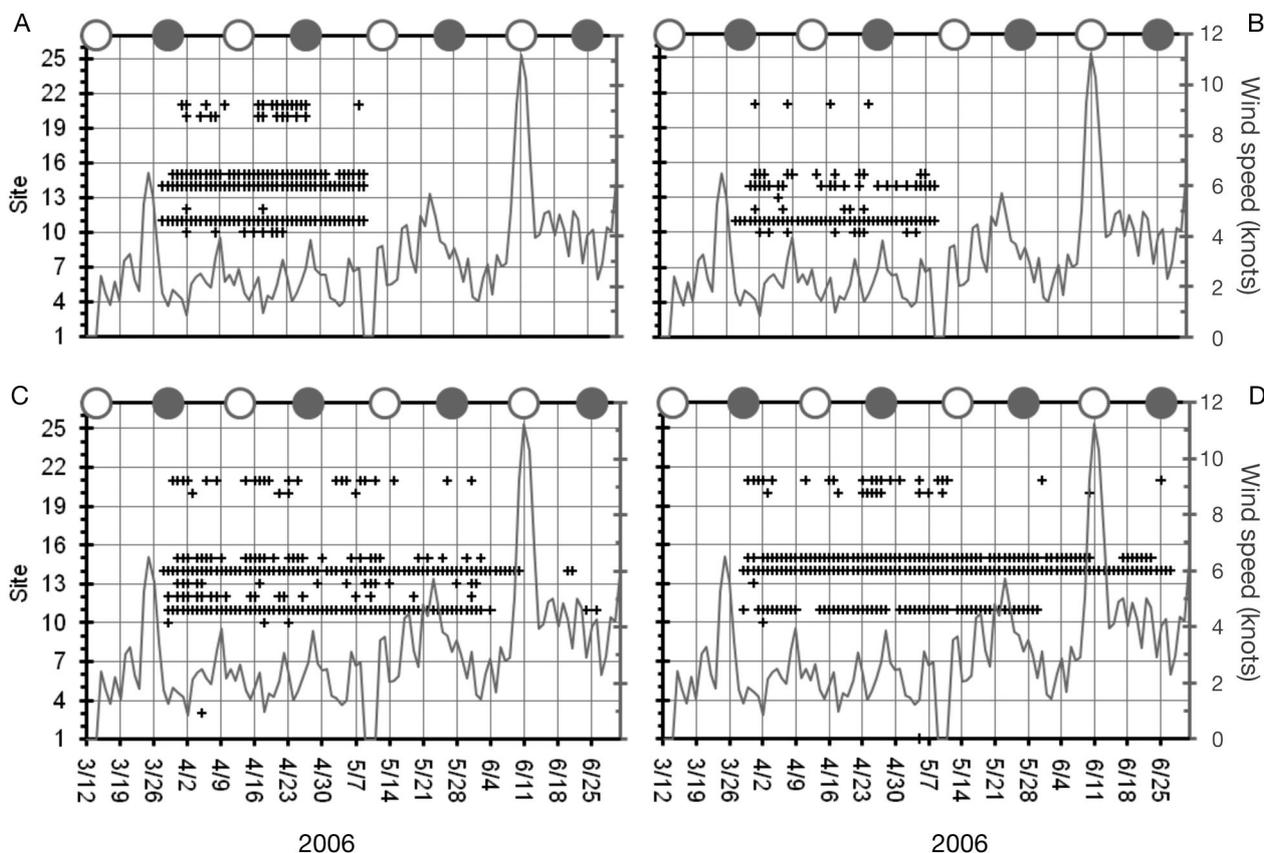


Fig. 2. *Epinephelus morio*. Detections in 2006 by site for individual (A) no. 184, (B) no. 185, (C) no. 186, and (D) no. 187, all tagged at the same location on the morning of March 27, 2006. Note the overlap in detections between individuals, suggesting similar space use and movement patterns. Wind speed and lunar cycle are co-plotted, with open circles denoting full moons. The passage of tropical storm Alberto is denoted, June 10–13, and appears to correspond with a brief lack of detections for fish no. 186. Fish nos. 184 and 185 were both captured and killed on May 9, 2006, by a charter boat captain

ments by the gray snapper exceeded 1000 m, and appeared to be associated with a nocturnal migration beyond the array.

Movements beyond the scope of the array would be undetected and could confound computations of movement frequency. Percent time fish were detected in the acoustic array ranged from 47 to 87% (Fig. 3C). These long-term detection rates suggested that most black grouper, red grouper, and yellowtail snapper did not move beyond the scope of the array. Fish captured near the center of the acoustic array (e.g. where edge effects would be minimal) were detected in >10% of 5 min batching intervals.

#### Diel period and lunar brightness effects on movement patterns

Red grouper detection rate varied by time of day (Fig. 3D, Table 3), with Day (29.4%) > Dawn (28.6%) > Dusk (27.7%) > Night (24.1%). For red grouper, re-

ceivers recording detections differed significantly (Table 3) by diel period: Day (1.32) > Night (1.27) > Dusk (0.87) > Dawn (0.80). Lunar period significantly influenced detection rates for red grouper (Table 3), quadratic regression indicating significantly higher detection rates ( $F_{2,38} = 7.9$ ,  $p < 0.005$ ) associated with moderately bright lunar periods (Fig. 5). For yellowtail snapper, number of detecting receivers differed significantly (Table 3) by diel period: Day (1.71) > Night (1.39) > Dusk (0.92)  $\approx$  Dawn (0.91). Low detection rates at night may be attributable to increased ambient noise rather than to sheltering activity or reduced movements (McCauley 1994).

#### Boundary crossings

Detected flux rates across reserve boundaries varied. In 2006, only 2 of 31 (6%) red grouper were detected moving across RNA boundaries. However, in 2007, after reconfiguring the acoustic array to cover more

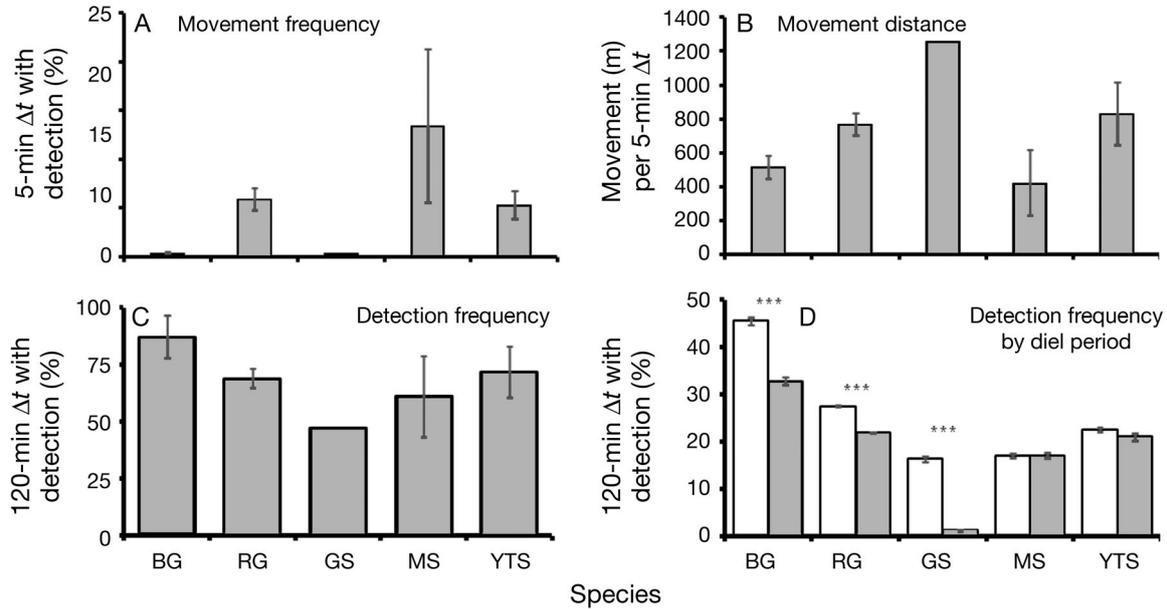


Fig. 3. Differences in (A) relative frequency of movement per 5 min interval ( $\Delta t$ ), (B) mean non-zero distances moved per 5 min  $\Delta t$ , (C) mean percentage of 120 min  $\Delta t$  with detections, and (D) mean percentage of 120 min  $\Delta t$  with detections at night (gray bars) and day (white bars), by species. BG: black grouper; RG: red grouper; GS: gray snapper; MS: mutton snapper; YTS: yellowtail snapper. Error bars: SE; asterisks: significant differences at  $p < 0.001$

Table 3. Summary statistics for tests of diel and lunar movement patterns. Time: time of day

Species	Variable	Factor	F	df	p
Red grouper	Detection rate	Time	10.9	3, 187	<0.001
		Tag	86.4	44, 132	<0.001
		Time $\times$ Tag	12.2	132, 18388	<0.001
	Detecting receivers	Time	63.2	3, 160	<0.001
		Tag	7.6	44, 132	<0.001
		Time $\times$ Tag	23.3	132, 18388	<0.001
	Detection rate	Lunar stage	4.4	40, 3685	<0.001
Tag		300.1	38, 3907	<0.001	
Lunar stage $\times$ Tag		0.5	1379, 3127	>0.05	
Yellowtail snapper	Detection rate	Time	2.7	3, 14	>0.05
		Tag	174.6	4, 12	<0.001
		Time $\times$ Tag	4.7	12, 1520	<0.001
	Detecting receivers	Time	36.2	3, 15	<0.001
		Tag	65.9	4, 12	<0.001
		Time $\times$ Tag	2.9	12, 1520	<0.001
	Detection rate	Lunar stage	1.5	39, 136	>0.05
Tag		29.6	3, 151	<0.001	
Lunar stage $\times$ Tag		1.3	106, 211	<0.05	

reef habitats (see Fig. 1C), 4 of 14 (29%) red grouper were detected moving across RNA boundaries into Tortugas North Ecological Reserve (TNER). No black grouper were detected moving across reserve boundaries in either year. Only 1 of 5 yellowtail snapper moved across the reserve boundary; this fish crossed the boundary 62 times, but spent less than 2% of its total time in TNER. The one gray snapper was detected

crossing the boundary 10 times, spending 3.4% of its time in TNER. Only 1 of 2 mutton snapper was detected moving across reserve boundaries, but it did so 702 times, spending 9% of its time in TNER. For red grouper, log-transformed distance of overall mean activity center from RNA boundary explained 40% of the variability in percent time spent outside the RNA ( $\beta = -0.64$ ,  $F_{1,43} = 29.5$ ,  $p < 0.001$ ).

### Home range utilization

Most acoustically tagged grouper and snapper utilized home ranges contained within the bounds of the acoustic array (Table 4, Fig. 6). Ten red grouper were detected at only 1 or 2 receivers. Inclusion of linear home ranges reduced the red grouper home range estimate from

$2.09 \pm 0.39 \text{ km}^2$  ( $n = 28$ ) to  $1.30 \pm 0.16 \text{ km}^2$  ( $n = 38$ ). No significant relationships were found between red grouper length ( $F_{1,31} = 0.05$ ,  $p > 0.05$ ) or weight ( $F_{1,31} = 0.14$ ,  $p > 0.05$ ) and home range size.

High levels of MCP home range overlap ( $43.01 \pm 7.12\%$ ) were observed among red grouper captured at the same location (mean =  $0.54 \pm 0.13 \text{ km}^2$ ;  $n = 25$ ). Percent overlap between red grouper MCP home ranges

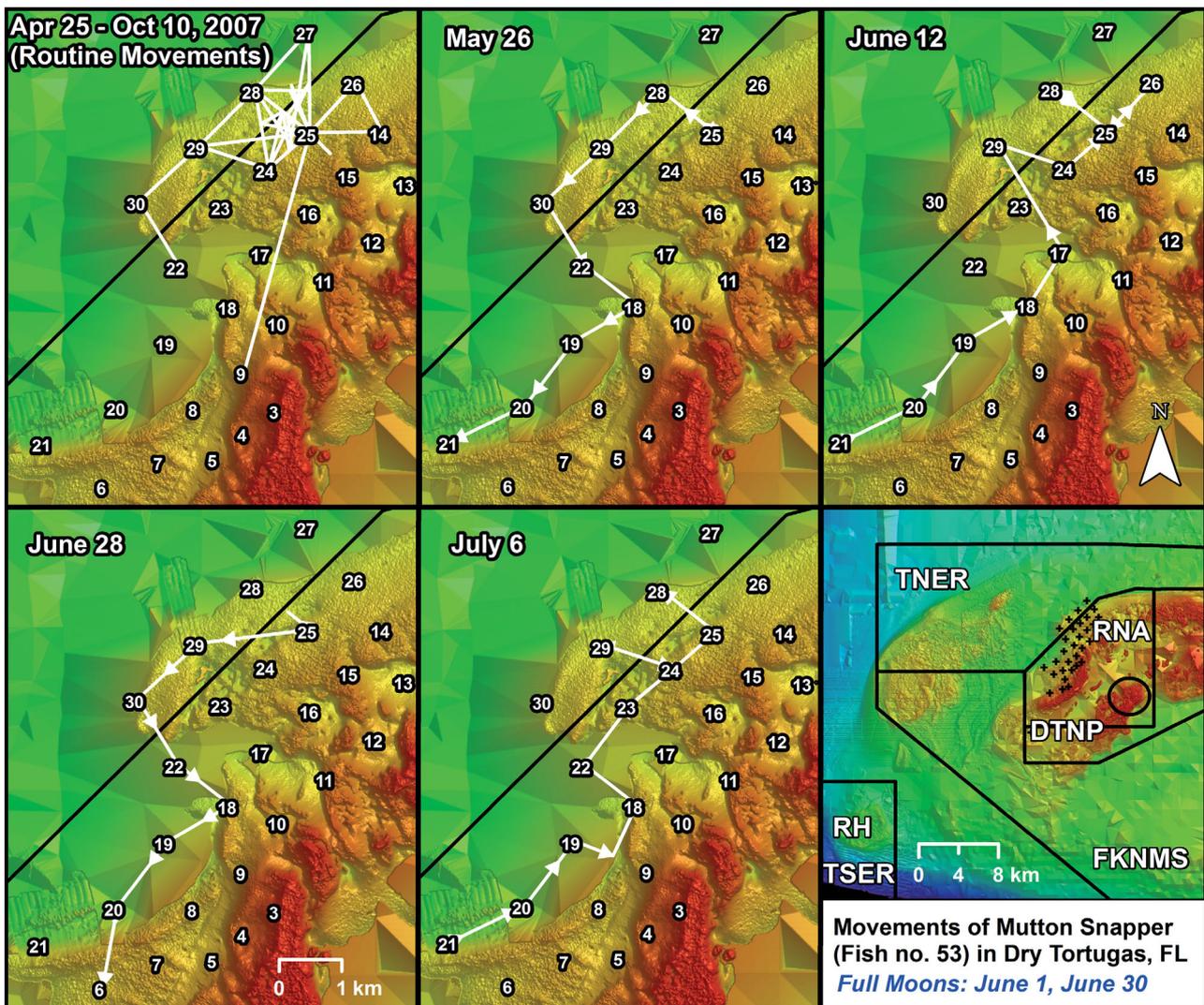


Fig. 4. *Lutjanus analis*. Routine daily movements (upper left) and possible spawning migration movements (May 26, June 12, June 28, and July 6) by fish no. 53 (70 cm TL, 5.4 kg). Fish no. 53 was tagged April 25, 2007 and tracked for 168 d. Lower right panel illustrates inferred broad scale movements across multiple management areas during periods with no detections (May 27 to June 13, June 13 to July 6). These absences followed unique directional movements to the southwest, corresponding with full moons, coinciding with timing of a known spawning aggregation at Riley's Hump (RH) in Tortugas South Ecological Reserve (TSER), and were followed by unique directional movements back into the array from the southwest. FKNMS: Florida Keys National Marine Sanctuary; DTNP: Dry Tortugas National Park; RNA: Research Natural Area; TNER: Tortugas North Ecological Reserve. See Fig. 1 for details of receiver placements

increased significantly with increasing fish TL ( $\beta = 2.88$ ,  $F_{1,48} = 5.4$ , adj.  $r^2 = 0.08$ ,  $p < 0.05$ ) and weight ( $\beta = 23.41$ ,  $F_{1,48} = 10.2$ , adj.  $r^2 = 0.16$ ,  $p < 0.05$ ).

Habitat was a significant controlling factor for percent overlap (Table 5). Red grouper in contiguous habitat had significantly lower MCP home range overlap than red grouper in isolated habitat and spur-and-groove habitat. Red grouper in high-relief habitats had significantly higher MCP home range overlap than red grouper in low-relief habitats. Mean distance between home range centers for red grouper caught at the same

time and location ( $n = 25$ ) was  $611.36 \pm 179.53$  m. No significant relationships were detected between distance between home range centers and TL, weight, dominant habitat type, or dominant level of relief.

#### Habitat utilization

Red grouper underutilized low-relief, isolated reef structures relative to their availability, showing preference for high-relief, contiguous structures (Fig. 7). Yel-

Table 4. Minimum convex polygon (MCP) home range estimates for acoustically tagged fish, and time required to obtain asymptotic MCP home range estimate (mean  $\pm$  SE). –: no asymptote was reached, and no home range estimate could be generated following the procedures described in 'Methods'

Common name	Species	n <sup>a</sup>	Time to asymptote (d)	MCP home range (km <sup>2</sup> )
Black grouper	<i>Mycteroperca bonaci</i>	2 of 3 (66%)	46.5 $\pm$ 0.5	1.44 $\pm$ 1.04
Red grouper	<i>Epinephelus morio</i>	28 of 45 (62%)	38.5 $\pm$ 6.4	2.09 $\pm$ 0.39
Gray snapper	<i>Lutjanus griseus</i>	0 of 1 (0%)	–	–
Mutton snapper	<i>Lutjanus analis</i>	1 of 3 <sup>b</sup> (33%)	72 <sup>c</sup>	7.64 <sup>b</sup>
Yellowtail snapper	<i>Ocyurus chrysurus</i>	4 of 5 (80%)	47.6 $\pm$ 28.8	4.17 $\pm$ 1.75

<sup>a</sup>Number of acoustically tagged fish meeting assumptions of home range contained within acoustic array  
<sup>b</sup>Transmissions were detected for only 2 mutton snapper  
<sup>c</sup>Home range estimate excludes presumed spawning migration

Table 5. *Epinephelus morio*. Percent minimum convex polygon (MCP) home range overlap for acoustically tagged red grouper

Habitat	MCP home range overlap			t	df	p
	n	Mean (%)	SE (%)			
Contiguous	31	38.0	5.4	–	–	–
Isolated	7	90.1	5.7	-4.42	36	<0.001
Spur-and-groove	2	97.4	2.6	-2.74	31	<0.05
High-relief	6	87.3	6.5	–	–	–
Low-relief	34	43.5	5.8	3.09	38	<0.01

lowtail snapper appeared to avoid high-relief, isolated habitats in favor of low-relief, contiguous reef (Fig. 7).

Broad, deep, continuous expanses of sand appeared to be a natural boundary to movement for reef fish. In 2006, receivers at sites A23, A24, and A25 were located in sand habitats off the reef shelf (see Fig. 1A). These 3 receivers were the only receivers in either phase of the study never to register reef fish detections (see Fig. 1B).

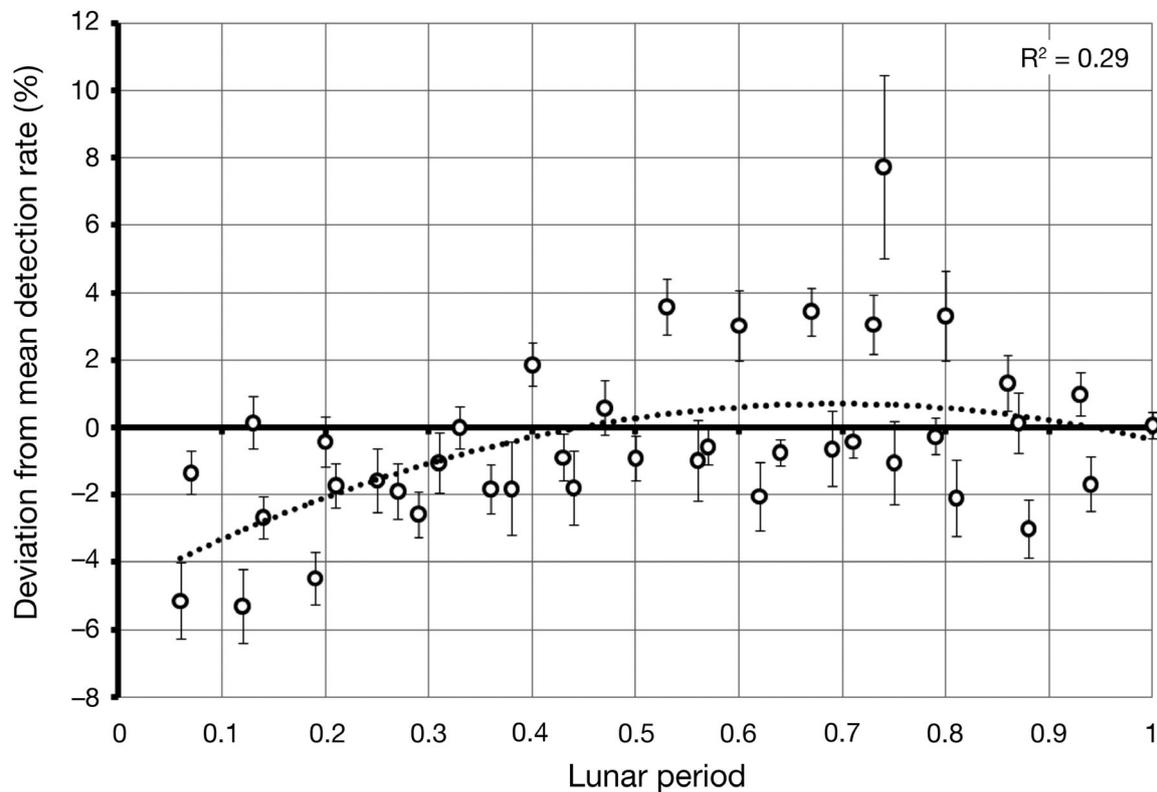


Fig. 5. *Epinephelus morio*. Quadratic regression fit to mean deviations (across individuals) of detection rates of tagged individuals (n = 39) per lunar interval (a nighttime observation of percent detections within a time interval, i.e. batching interval), relative to individual mean detection rates across lunar periods (stage of the moon from 0 [new moon] to 1 [full moon]). Error bars: SE

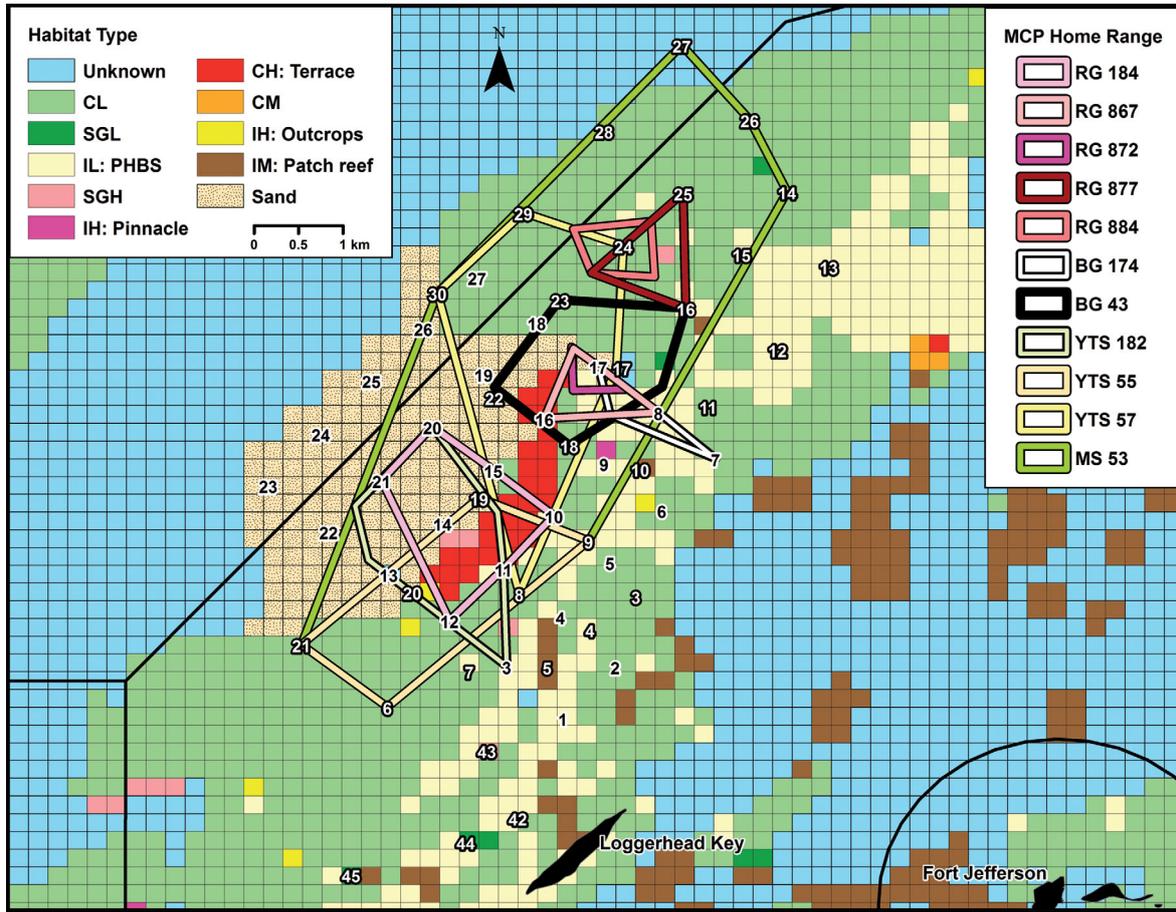


Fig. 6. Examples of minimum convex polygon (MCP) home range areas computed from 5 min harmonic mean positioning estimates for tracked black grouper (BG), mutton snapper (MS), red grouper (RG), and yellowtail snapper (YTS). MCPs are depicted relative to habitat type and 2006 (black numbers) and 2007 (white numbers) receiver positions. C: contiguous; I: isolated; SG: spur-and-groove; H: high; M: medium; L: low relief; HB: hard bottom; PHBS: patchy HB in sand

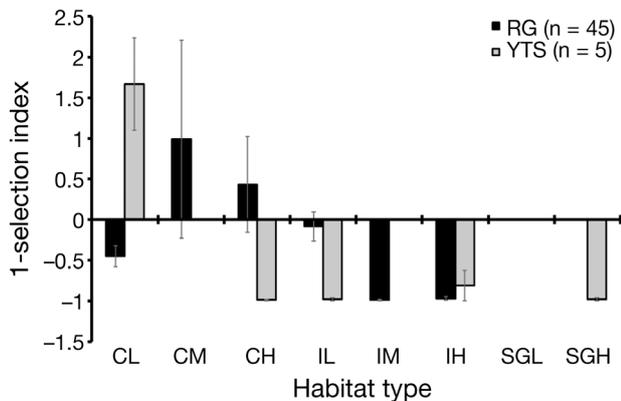


Fig. 7. Mean habitat selection index values ( $\pm$ SE) for red grouper (RG) and yellowtail snapper (YTS), depicted as deviation from 1. Positive values indicate habitats utilized above their percent availability within the MCP home range; negative values indicate habitats utilized below percent availability. Habitat types categorized by coverage (C: contiguous; I: isolated; SG: spur-and-groove) and profile (L: low; M: medium; H: high)

## DISCUSSION

For NTMRs to provide sufficient buffering against exploitation, Barrett (1995) recommended their diameter be, at minimum, an order of magnitude larger than the daily movements of the targeted organisms. Mean home range sizes for the 5 snapper-grouper species studied were from 1 to 2 orders of magnitude smaller than the Tortugas NTMRs. Assuming our tagged organisms were representative of these stocks, the NTMRs of the Tortugas may afford significant protection from exploitation for the species and life stages we evaluated. Future tagging studies should increase the sample sizes and size ranges of fish tracked, which would help verify our findings and the range of their interpretation.

Although most fish remained within range of a few receivers throughout their tracking period, occasional NTMR boundary crossings were detected. All observed boundary crossings by reef fish occurred where NTMR boundaries overlie contiguous coral reef habitats.

Boundary crossings for tagged snappers appeared to be associated with daily or spawning migrations. Fish no. 53 was a sexually mature (Claro 1981) mutton snapper. This fish had 2 extended absences (16 d and 8 d) from the array during its 168 d tracking period. These departures roughly corresponded to the full moon and were characterized by a sequence of detections at receivers that were never revisited at any other time (see Fig. 4). The direction of travel and the presence of a documented spawning aggregation of mutton snapper over Riley's Hump in the TSER during full moons during the period May to July suggest that these movements were 2 spawning migrations (Burton et al. 2005). Two sexually mature yellowtail snapper (fish nos. 58 and 59) appeared to depart the array during July. Lindeman et al. (2000) suggested that this species spawns between May and June in the lower Florida Keys and possibly at Riley's Hump in the TSER. Interestingly, a larger, concurrently tagged yellowtail snapper (fish no. 55) showed similar patterns of daily space use, but was detected every day for 153 d. It is unclear whether the disappearances of fish nos. 58 and 59 corresponded to spawning movements; further research into the importance of the Tortugas NTMRs for spawning yellowtail snapper is recommended. Consistent with observations by Moe (1972) and Luo et al. (2009), a tagged gray snapper made routine nocturnal migrations between site B19 (see Fig. 1C) and presumed foraging habitats west of the array, possibly outside the RNA.

In addition to these detected departures from the RNA, there may have been undetected movements out of the array. For example, some red grouper (11%) were detected for fewer than 25 d, as compared to the mean tracking period for the species of 102 d. A greater amberjack *Seriola dumerili* tagged during this study was detected briefly in the array and then subsequently recaptured about 2.5 yr later off the Yucatán coast near Cancún. The limited scope of our acoustic array relative to the scale of the RNA makes it difficult to empirically quantify the rate of spillover. Mixed technologies, such as combination of acoustic and satellite tagging, may be required to fully resolve the rate and impacts of spillover. Low rates of spillover would reduce the rate of stock recovery but may increase fisheries yields, especially when fishing effort redistributes along reserve boundaries (Kellner et al. 2007, Farmer 2009). High rates of spillover might critically compromise NTMR protection (Kellner et al. 2007, Farmer 2009).

Although NTMR protection appears substantial for our tagged fish, the movements we observed may not be representative of all size classes for the grouper and snapper observed. Several studies have suggested that smaller, less competitive individuals are more likely to make large daily movements (Young 1963, Kramer &

Chapman 1999, Bell & Kramer 2000). For many reef fish species, migration toward deeper (>36 m) habitats begins near the onset of sexual maturity (Lindeman et al. 2000). All fish in this study were captured in shallow habitats (<36 m). All tagged red grouper (from 45 to 66 cm TL) were likely females (Collins et al. 2002) near sexual maturity (Fitzhugh et al. 2006). It is unclear if red grouper within the RNA would emigrate to spawn, since red grouper spawn in depths >25 m and do not form aggregations (Coleman et al. 1996). No spawning migrations were observed among the tagged black grouper, although winter (January to April) spawning aggregations in Florida (Eklund et al. 2000) and Belize (February to March; Paz & Sedberry 2007) have been reported. It is unlikely any of our 3 tagged black grouper were sexually mature (Crabtree & Bullock 1998, Ault et al. 2005b, 2007b). Sexually mature fish might leave the RNA in search of deeper habitats or spawning aggregations.

The spatial arrangement of resources within fragmented landscapes has significant structuring effects upon space use and behavior (MacDonald 1983, Atwood & Weeks 2003). Although we failed to detect differences in overall home range size by habitat, we did find greater overlap in red grouper home ranges in isolated (90%) as compared to contiguous (38%) habitats. As isolated reefs represent compressed habitats, it is not surprising that home range overlap would be higher due to space limitations. Home range overlap may be viewed as a proxy for territoriality (Nemtzov 1997). High levels of overlap in MCP home ranges were observed for red grouper tagged in the same location. These observations suggest that if red grouper are territorial fish, their defended home ranges (Schenkel 1966) must be smaller than the area covered by a single receiver in this study. However, the threshold biomass to induce density-dependent emigration in this species is still unclear.

Low-profile contiguous reefs are the most common habitats in the Dry Tortugas (Ault et al. 2006a) and contain the highest densities of red grouper (Smith et al. 2011). Tagged red grouper underutilized isolated habitats relative to their availability. Food-value theory (Stenger 1958, Wilson 1975) and cost-benefit analyses (Brown 1964) have suggested that resource availability plays a major role in determining animal home range size and overlap. High-profile coral reef habitats provide higher prey densities for red grouper (Ault et al. 2007a), and likely contain more locations for shelter. High-quality habitats may allow animals to maximize energy intake in a small undefended space, whereas larger defended ranges may be advantageous in moderate-quality habitats (Carpenter & MacMillen 1976). Red grouper home range overlap was higher in high-profile habitats than in low-profile habitats.

Table 6. Published home range estimates for fish in ascending order of home range area, with method, duration, and periodicity of tracking. MCP: minimum convex polygon

Common name	Species name	Life stage	N <sup>a</sup>	Method of tracking	Study duration (d)	Tracking periodicity	Study habitat	Study location	Study area (m <sup>2</sup> )	MCP home range (m <sup>2</sup> )	Source
Blue tang	<i>Acanthurus coeruleus</i>	Juvenile	35	Markers (diver)	14	Non-continuous	Reef	Barbados, West Indies	n/a	0.07–15.65 (mean = 2.18)	Bell & Kramer (2000)
Red hind	<i>Epinephelus guttatus</i>	Adult	22	Visual (diver)	152	Non-continuous	Reef	Puerto Rico	10000	112–5636 (mean = 867)	Shapiro et al. (1994)
Stoptight parrotfish	<i>Sparisoma viride</i>	Juveniles and adults	88	Visual (diver)	<1 to >365	Non-continuous	Fringing reef	Bonaire	10940	240–820	Roosj et al. (1996)
Bluespine unicornfish	<i>Naso unicornis</i>	Adult?	5	Active	14–21	Non-continuous	Reef	Hawaii, USA	n/a	325–7650 (mean = 3717)	Meyer & Holland (2005)
Graysby	<i>Cephalopholis cruentata</i>	Adult	10	Active	<7	Non-continuous	Reef	St. Lucia, West Indies	n/a	1200–4000 (mean = 2120)	Popple & Hunte (2005)
Kelp bass	<i>Paralabrax clathratus</i>	Adult	12	Active	30	Non-continuous	Kelp, rock reef, sand	Santa Catalina Island, USA	n/a	3349–3328 <sup>b</sup>	Lowe et al. (2003)
Coral trout	<i>Plectropomus leopardus</i>	Juveniles and adults	39	Active	30–90	Non-continuous	Fringing & patch reef	Lizard Island, Australia	n/a	10458 ± 962	Zeller (1997)
Nassau grouper	<i>Epinephelus striatus</i>	Adult	22	3 radio-linked buoys	21 per reef	Continuous	2 isolated patch reefs	Bahamas	~100000	18305 ± 5806	Bolden (2001)
Bermuda chub	<i>Kyphosus sectatrix</i>	Adult	11	Active	5–51 (mean 21.5)	Non-continuous	Reef	St. Lucia, West Indies	n/a	30514–39114	Eristhee & Oxenford (2001)
Blacktip shark	<i>Carcharhinus limbatus</i>	Juvenile	74	Acoustic array	1–167	Continuous	Coastal bay	Florida, USA	~70000000	700000–1200000 <sup>c</sup>	Heupel et al. (2004)
Black grouper	<i>Mycteroperca bonaci</i>	Adult	2	Acoustic array	>587	Continuous	Reef	Dry Tortugas, Florida	30000000	390000–2480000	Present study
Red grouper	<i>Epinephelus morio</i>	Adult	28	Acoustic array	>587	Continuous	Reef	Dry Tortugas, Florida	30000000	310000–9170000	Present study
Yellowtail snapper	<i>Ocyurus chrysurus</i>	Adult	5	Acoustic array	>587	Continuous	Reef	Dry Tortugas, Florida	30000000	750000–10727000	Present study
Mutton snapper	<i>Lutjanus analis</i>	Adult	1	Acoustic array	>587	Continuous	Reef	Dry Tortugas, Florida	30000000	7640000	Present study

<sup>a</sup>Number of fish observed or tagged<sup>b</sup>95% kernel utilization distribution home range (MCP not provided)<sup>c</sup>Daily MCP

Home range size may also be a function of predation risk, body size and bioenergetic requirements, intra-specific interactions and territoriality, or reproductive dynamics (reviews in Harris et al. 1990, McLoughlin & Ferguson 2000). Relative to most marine habitats in the Florida Keys, the coral reefs of the Tortugas have high concentrations of resources, high conspecific competition, and high predation risk. As such, theory would suggest that snapper and grouper home ranges in other regions might be larger than those observed in this study. Our home range estimates for all tracked species higher than those previously estimated for other reef species (see Table 6). However, it is important to note that the perception of mobility is dependent upon the scale of time and space over which movement is monitored (Steingrímsson & Grant 2003). Most active tracking and diver-based studies of fish movement are constrained in the duration and periodicity of observations, often representing less than 1 mo of sporadic observations of animal movements and missing important diel and ontogenetic transitions in space use (Table 6). In our study, most fish required longer than 1 mo to reach asymptotic home range size. Many previous studies have been constrained in the diel period of observations. In our study, red grouper moved greater distances and with greater frequency during daylight hours, and nocturnal movement frequency was highest when fish could take advantage of moderate light levels to more efficiently capture prey (Helfman 1993). Finally, many previous studies have been constrained in their spatial scale. Undetected movements out of a study area would result in underestimation of home range size. The broad spatial and temporal scale of our study may partially explain our relatively large observed home ranges.

NTMRs such as the RNA may provide numerous benefits, including increased biomass of exploited species through reduced harvest, and unexploited species through reduced bycatch, restoration of natural community dynamics, and protection of coral reef habitats (see review in Bohnsack et al. 2004). Thus, the value of the Tortugas NTMR network as a habitat and foraging ground for sedentary and highly mobile species may increase through time (Bartholomew et al. 2008). Our observations suggest that these NTMRs may promote surrounding fisheries, in the near-term through spillover into fishable areas, and in the long-term through increased spawning stock biomass. Recent assessments have suggested improvements in the status of mutton snapper (SEDAR-15 2008), red grouper (SEDAR-12 Update 2009, SEDAR-19b 2010) and black grouper (Ault et al. 2006b; SEDAR-19a 2010) stocks, which may be partially attributable to the Tortugas NTMR network. NTMR effectiveness probably depends upon the reserve being sited over large expanses of contiguous

reef. Alignment of NTMR boundaries with natural deterrents to movement may minimize spillover, especially if the NTMR encompasses preferred habitats. Key habitat features, such as nocturnal foraging habitats and spawning aggregation sites, may also require protection. Future studies should focus on expanding the temporal and spatial scales of acoustic monitoring and the numbers and size ranges of individuals tagged and tracked to fully quantify the rate of flux between protected and unprotected areas.

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